Intake and conversion of food in the fish *Limanda limanda* exposed to different temperatures

T. J. PANDIAN

Biologische Anstalt Helgoland (Meeresstation); Helgoland, Germany (FRG)

and

Zoology Department, Bangalore University; Bangalore, India

Abstract

In the flat fish *Limanda limanda* L., feeding rate and conversion efficiency were studied as functions of body weight, sex, temperature and food quality. When offered herring meat at 13 °C (series I), females (live weights 1 to 150 g) consume more food than males; the magnitude of this difference is body weight-dependent. With increasing weight, both females and males consume less food per unit body weight per day. Variations in daily ration are considerable; the range of deviation from mean feeding rate is about 60% for males and 40% for females. The range of deviation does not vary significantly among females and males of different body weights. At the same temperature level (13 °C; series II), females consume almost the same, or even less, cod meat than males. Among individuals of series I and II, there is a little difference in the feeding rate; however, herring-fed individuals obtain about 2 times more energy than cod-fed individuals. Each gram wet weight of herring meat yields 2001, each gram cod meat 1137, calories. Small individuals completely cease to feed at 3 °C; they feed little at 8 °C. Larger females consume maximum amounts at 8 °C. Small individuals consume maximum amounts at higher temperatures. Thus, with increasing body weight (age), the temperature for maximum feeding shifts downwards. Feeding with cod or herring meat results in considerable changes in composition and calorific content of *L. limanda*. The magnitude of these changes depends both on temperature and food quality. Food conversion efficiency values of herring-fed individuals are about 1½ times higher than of cod-fed individuals. In series I and II, females are more efficient converters than males. In individuals weighing more than 50 g, conversion efficiency decreases in the order: 8°, 13°, 18 °C; in smaller individuals this order is 13°, 18°, 8 °C. Conversion rate is about 2 to 5 times faster in individuals fed herring meat than those receiving cod meat. Conversion rate decreases in the order 13°, 8°, 18 °C in males, and in the order 18°, 13°, 8 °C in females; females of more than 80 g are exceptional in that they reach the maximum at 8 °C. From the data on food intake and food conversion, the biologically useful energy available for metabolism has been calculated for each test individual kept at 13° and 18 °C. At these temperature levels, the weight exponents are about 0.6; the 'a' value or metabolic level for the 18 °C series is about 2 times higher than that at 13 °C. Thus, temperature affects metabolic rate but not the exponential value. The exponential value for the body weight-metabolism relation at 13 °C is for dab fed herring meat 0.9; the 'a' value amounts to about half that for dab fed cod meat. Food quality, unlike temperature, alters not only the exponential value but also metabolic rate.

Introduction

Supply of energy is imperative for the normal course of life processes; energy enters the animal in the form of food. The food is subjected to a series of physical and chemical changes. Changes through which energy becomes dissipated are collectively called catabolism; changes which lead to deposition in the organism are known as anabolism. These 2 processes occur simultaneously, and are together spoken as metabolism in a broad sense. Energy is released or dissipated through oxidation; biological oxidation implies transfer of a pair of electrons to an atom of oxygen and, hence, oxygen consumption has been regarded as a measure of metabolism. There exists an enormous literature on metabolism of fishes as studied by oxygen consumption (FRY, 1947, 1957; WINBERG, 1956; BEAMISH and DICKIE, 1966).

KINNE (1960) regarded "conversion of food into body substance and into biologically useful energy" as an additional, in many cases more suitable and more sensitive, parameter for assessing rates and efficiencies of metabolic processes. This view of KINNE has recently received support from PALOHEIMO and DICKIE (1966a, b) who summarized the available information on food conversion in fishes. Feeding-rate and conversion efficiency estimates are considered better parameters of metabolic rates for the following reasons:

(1) The less restricted maintenance conditions during feeding experiments represent better analogies to natural conditions than do the restricted test conditions during determinations of oxygen consumption. (2) Repeated observations on one and the same individual over long periods of time provide data for detailed studies on the contribution of individual versus environmental variations to average metabolic rates. Due to technical difficulties, appropriate data (such as those by SMITH, 1935) have rarely been obtained from direct respiration studies. (3) Conversion

studies allow the direct measurement of the effects of quantitative and qualitative aspects of feeding on metabolism; this is essential for an understanding of the production process (see also PALOHEIMO and DICKIE, 1966a).

Previous workers like IVLEV (1939, 1945) and GERKING (1952, 1954) have shown an indirect relation of body weight (age) to conversion efficiency in the fishes studied by them. This relationship is altered to a greater or lesser extent through environmental factors; of these temperature is the most important one, particularly in thermo-conformers of temperate waters. The pioneering work of KINNE (1960, 1962) presents extensive information on temperature relations with regard to food intake, food conversion and growth in the euryplastic fish *Cyprinodon macularius*. There exist only a few papers (DAWES, 1930—31; HATANAKA et al., 1956a, b, 1957; MENZEL, 1960) which are concerned with temperature effects on food intake and food conversion in marine fishes. The paucity of information on food requirements of marine fishes is primarily due to the difficulties encountered in maintaining marine fishes under laboratory conditions. DAWES and HATANAKA and co-workers estimated the food conversion efficiency of flat fishes kept at ambient temperatures, while MENZEL carried out 3 sets of experiments on food conversion efficiency of the Bermuda reef fish *Epinephelus guttatus* maintained at 3 different constant temperature levels. The present paper reports on feeding rate and conversion efficiency of the dab *Limanda limanda* assessed as functions of body weight, sex, temperature, and food quality.

Material and methods

Material: The dab *Limanda limanda* LINAEUS (Family: Pleuronectidae) is a marine fish, occurring in the North Sea. Its distribution extends from the Biskaya to the Barents Sea; it is also found on the continental shelf of Iceland and in the western Baltic Sea. In this vast area, *L. limanda* is most abundant in the southern North Sea at depths of 20 to 40 m. With increasing water depth, the number of individuals per unit space decreases; at 100 m *L. limanda* is already scarce; it is completely absent at depths of more than 200 m. *L. limanda* also occurs in brackish waters, but in less numbers (RÜHMER, 1954; LUNDBECK, 1955).

The *Limanda limanda* used in the present study were procured near Helgoland in the southern North Sea. During the years 1966—1967 the temperature of surface water at 'Kabeltonne-Helgoland' ranged from 1.9° to 17.3 °C; the lowest winter and highest summer means were 2.9° and 16.5 °C, respectively, and daily fluctuations ranged from 1° to 2 °C, being higher along the shore (courtesy: Dr. E. HAGMEIER and Herr E. HARMS; Biologische Anstalt Helgoland). During the winter months, the larger dabs leave the swiftly cooling coastal waters for the open sea. Over the winter months

they stay at some distance from the coast and, after spawning, return to the spring-warmed shallow coastal waters (BOHL, 1957). As temperature of the open waters does not sink below 3 °C, it is reasonable to conclude that the annual temperature variations to which the dab population is subjected range from 3° to 16.5 °C.

During the same period, the range of salinity variations was rather narrow; the monthly means varied around 30‰, with maximum and minimum salinities of 28 and 34‰, respectively.

Methods: *Limanda limanda* were collected by the research cutter "Uthorn"; several collections were made during the years 1966—1967. The duration of trawling was restricted to about 15 to 20 min in order to reduce injuries. The dabs caught were immediately transferred into wooden troughs with running sea water and brought to the laboratory on Helgoland, where they were stocked in a large concrete tank. In general, highest mortality rates occurred during the first two or three days. Individuals which survived this period usually remained healthy afterwards.

Diseases: A day or two after the arrival of a new dab collection, a number of individuals suffered from the "red disease" said to be caused by the bacterium *Vibrio anguillarum* (SINDERMANN, 1966); the symptoms were typical: reddening of the dorsal or ventral fin close to the caudal fin, or the caudal fin, and subsequent loss of the infected fin area; these individuals died within a week. Another frequent disease was "intramuscular lesions", causing deep wounds and eventual death. This disease appeared to be similar to the one described by DANNEVIG and HANSEN (1952) in the plaice *Pleuronectes platessa* infected by the bacterium *Pseudomonas dermis*. All individuals showing symptoms of infections or injury were immediately removed from the tank. A few experimental individuals showed the symptoms of both diseases; when an individual ceased to feed, it was eliminated from the experiment. Though a bordering wooden frame was placed on each aquarium to prevent the experimental individuals from jumping out, there were instances in which dabs jumped the frame and were found dead on the floor next morning. These also had to be eliminated from the experiment; as in BÜCKMANN's (1952) experiments, no compensatory individual was introduced to replace losses due to disease or jumping.

Acclimation: Acclimation (used synonymously with acclimatization, e.g. BULLOCK, 1955; KINNE, 1964) to test temperatures was gradual, i.e. at the rate of 1 °C per day until the required temperature level was reached; the fishes were then left at that temperature level for a minimum period of 15 days and, in the case of 3 °C (from 8 °C), 20 days (BRETT, 1956). During the period of acclimation, the dabs were "trained" to feed *ad libitum*.

Temperature: Experiments were performed in cement aquaria of about 200 l capacity (125 × 80 × 20

cm); 8 such aquaria were available, so that 8 experiments could be carried out simultaneously. Sea water was pumped into the laboratory reserve tank, from where it was allowed to percolate through fine sand kept in a large filter tank; the filtered sea water was then run into a cooling-aggregate (Linde, Solekühler) with a capacity of 6,000 Cal/h. From this aggregate, cooled or warmed sea water was run into branch pipes, which continuously fed the aquaria with running sea water. The outflowing water was received in the stock tank, vigorously aerated, and again run into the cooling-aggregate. Once a week, fresh sea water was added from the reserve tank, while emptying the used water from the stock tank. Only at 18 °C, in addition to warming in the aggregate, the water had to be heated by attaching separate thermo-regulating heaters to the walls of the aquaria. The temperature was maintained constant within ± 0.4 °C, except for rare cases when the temperature varied about ± 1.6 °C.

Light and location: The experimental aquaria were set up in a laboratory where, except during observation and feeding, there was no other disturbance. Glass windows on three sides of the laboratory let in natural sunlight. Experiments at higher temperature levels were carried out during summer, those at low temperature levels during winter, with a view to provide, simultaneously, long and short day light conditions, respectively.

Experimental food: *Limanda limanda* has been reported to feed on a number of invertebrates, chiefly crustaceans, molluscs and polychaetes (KÜHL, 1961). In preliminary experiments (June—July, 1966) the fish were fed *Crangon crangon* (previously frozen) and subsequently found to evacuate faecal pellets which were hardly digested. DAWES (1930) observed the same phenomenon in plaice, *Pleuronectes platessa*, frequently fed on the mussel *Mytilus edulis*. The dab tends to feed on whatever food is offered, irrespective of incomplete digestion and absorption. Incompletely digested faecal pellets accumulated in such quantities in the aquaria that, even with regular siphoning once a day, the aquaria remained dirty. Finally, herring and cod meat were chosen and found to be digested fully. Herring *Clupea harengus* was obtained from the aquarium of the Biologische Anstalt Helgoland (Herr A. HOLT-MANN); cod *Gadus morhua* was purchased from a private firm. The food was preserved at -20 °C in a deep freezer; it was quite uniform in chemical composition and calorific properties (Table 1).

Feeding: The dabs were fed until satiation once a day; those kept at 3°, 8° and 13 °C (herring-fed) at about 11 a.m., the others at about 3 p.m. The frozen food was allowed to thaw (without heating) 2 to 3 h before feeding; the flesh was then blotted and cut into small weighed pieces. Feeding lasted for about 10 min. The fishes were killed 29 days after initiation of the experiment in order to estimate the amount of food converted.

The "sacrifice method" described by MAYNARD and LOOSLI (1962) was employed. It is generally used to test the growth of laboratory mammals fed different foods. This procedure was first employed in experiments with fishes by GERKING (1952, 1954, 1955), later also by MENZEL (1959, 1960) and PANDIAN (1967 a, b, c, d). A group of 7 to 10 individuals of dab of the same sex and similar ($\pm 10\%$) body weight were taken from the stock tank; all individuals had been starved for 2 days in order to empty their alimentary canals. Five individuals (the experimental ones) were, after weighing, transferred into the experimental aquarium, while the others were weighed and killed for calorific estimations. Conversion of food into body substance was estimated by subtracting the calorific content of the experimental fish at the beginning of the experiment from the content at the end of the experiment.

Table 1. Calorific content and composition of food (meat of herring *Clupea harengus* and cod *Gadus morhua*)

Food	Mean values	Coefficient of variation
Herring meat		
Water	68.8% $\pm$ 1.2	1.7%
Ash	4.2% $\pm$ 0.6	14.2%
Energy	6411 cal/g $\pm$ 103	1.6%
Cod meat		
Water	78.7% $\pm$ 0.4	0.5%
Ash	4.4% $\pm$ 0.4	9.1%
Energy	5339 cal/g $\pm$ 96	1.8%

Weighing: After removing adhering water particles, live weights of the fishes were made in a Mettler single pan balance to an accuracy of ± 0.1 g; in this balance, weighing could be performed within a few seconds so that the fish were little disturbed. The dried fishes were also weighed in this balance. The food was weighed in a balance with an accuracy of ± 10 mg. All samples used for estimation of ash and calorific contents were weighed in a Sartorius balance (Type 2604; sensitivity 0.01 mg).

Drying and homogenization: Calorific analyses were made on material dried in an oven at 80 °C for 24 h; the temperature was then raised to 105 °C until weight constancy. The entire dry fishes were minced and ground (Braun Coffee Miller, Type KM 32) into fine homogenized powder. Of this, an aliquot was preserved in a glass vial kept in a desiccator. A sample of about 150 to 200 mg of the homogenized powder was pressed into a pellet in a copper pelletor; the pellet was kept in an oven, maintained at 80 °C for a minimum period of 20 min, until it was weighed previous to calorific analysis.

Calorific contents were determined using a PARR 1412 semi-micro bomb calorimeter, following the

standard procedure described in the instructions for Parr bomb calorimetry Nos. 128 and 130. For every 10 to 12 estimates the bomb was standardized using a pellet of standard Benzoic acid. In a few cases the sample was not completely oxidized; the results obtained in these instances were discarded. The values for ash contents of the samples used for calorimetry varied from 12 to 17%; only in a few cases ash contents of about 20% were recorded. Since ash contents never exceeded 25% in any of the samples, no special correction was made to account for endothermy (PAINE, 1966).

Ash contents were estimated by maintaining a sample of about 200 mg in a crucible of known weight in a muffle furnace for a period of 5 h at 600 °C.

Results

Food intake

Effects of body weight and sex

A total of 18 experiments (9 females, 8 males and 1 juvenile) were carried out to study the effects of body weight and sex on food intake of the dab *Limanda limanda*. Three to 5 individuals of similar body weight

Table 2. Feeding rate as function of body weight and sex in the dab *Limanda limanda*. Each value represents the average of 5 individuals, which were fed once a day ad libitum with herring flesh for a period of 28 days at 13 °C

Body weight (g)	Feeding rate (% body weight/day)	Body weight (g)	Feeding rate (% body weight/day)
Female		Male	
1.1	4.0	7.1	4.0
5.4	4.7	16.2	1.7
16.9	2.5	35.5	3.1
33.1	4.4	41.2	3.5
47.1	3.8	49.1	3.2
61.3	3.5	77.2	2.0
79.5	3.4	101.2	2.4
104.4	3.2	121.5	2.0
115.5	2.1		
150.7	1.9		

and sex were kept in an aquarium in running sea water maintained at $13.0^{\circ} \pm 0.4^{\circ}\text{C}$. They were fed herring meat once a day, until satiation, for a period of about 10 min. The quantity of food consumed fluctuated considerably from day to day; the range and frequency of these fluctuations are described in the ensuing section. Upon averaging the data obtained, a general trend became apparent. Feeding rate has been expressed as percent body weight/day in order to be able to compare the data with those reported in previous papers. The smallest fish used weighed 1.1 g and its

sex could not be distinguished externally. On an average, it consumed an amount of food equivalent to 4.0% of its own body weight/day (Table 2). Feeding rate of a female weighing 5.4 g was 4.7% body weight/day and thereafter decreased progressively with increasing body weight; the largest female used (150.7 g) consumed 1.9% body weight/day. Among the males a similar trend was apparent. Feeding rate of a male weighing 7.1 g was only 4.0% body weight/day; it decreased to 2.0% body weight/day in a 121.5 g individual.

The amount of food taken in was greater in females (irrespective of body weight) than in corresponding males; the magnitude of the difference was dependent upon body weight. In individuals of about 6, 34, 103 and 122 g weight, feeding rates of females were 16, 42, 28 and 8% higher than in the respective males. It is of interest to note that, while males lose about 1 to 2% body weight, females lose as much as 5 to 7% body weight during spawning (see also HATANAKA et al., 1956b, for the Japanese plaice *Kareius bicoloratus*). This observation suggests that females must store about three times more energy in their gonads than males. Since the feeding experiments were performed during August and September (when the dab begins to accumulate energy for increase of body weight as well as for gonad growth), the extra amount of food consumed by the females may, at least in part, have been utilized for the growth of the developing gonads. However, food intake of larger females was only a little higher than in equal-sized males. As will be shown, these females feed voraciously in subsequent months, even when the temperature is low.

A notable feature in the relationship between feeding rate and body weight of the dab is the absence of a very high feeding rate among individuals of less than 10 g body weight. A curvilinear trend has been reported for the feeding rate-body weight relation in fishes, e.g. *Micropterus salmoides* (WILLIAMS, 1959), *Epinephelus guttatus* (MENZEL, 1960), *Megalops cyprinoides* and *Ophiocephalus striatus* (PANDIAN, 1967b). In all these fishes growth rate is fastest during the earliest life stages, and later falls with advancing age (increasing body weight). On the other hand, in the dab as well as in many other flat fishes, growth rate is remarkably slow during the first one or two years, which are followed by a rapid growth phase and eventual decrease in growth rate with increasing age and body weight (WIMPENNY, 1953; BOHL, 1957). The low feeding rates of young dabs may be related to their slow growth rates.

A striking feature noted from daily feeding and observation records is the considerable individual and temporal variations in the feeding rate of *Limanda limanda*. PALOHEIMO and DICKIE (1966a, b), who re-examined the feeding records available in literature, reported that the temporal and individual variations were remarkably great among the flat fishes *Pluero-*

nectes platessa (DAWES, 1930—31), *Limanda yokahamae* and *Karierus bicoloratus* (HATANAKA et al., 1956a, b).

In the following paragraphs, an attempt is made to provide a quantitative estimate of the temporal variations in food intake of the dab *Limanda limanda*. Some 9 experiments from the 13°C series fed on herring meat were chosen at random; from the respective daily feeding records, the average feeding rate of a single individual for each day was calculated and the values obtained plotted (Fig. 1). None of the test fish

Fig. 1. Day-to-day fluctuations in the rate of food uptake of the dab *Limanda limanda*. Each value represents the average feeding rate of a single fish; average data are based on 5 individuals fed a restricted supply of herring (*Clupea harengus*) meat at 13°C

ever attained a constant feeding level during the 28 day experimental period. A period of heavy feeding (1 to 3 days) is generally followed by a day in which little or no food is ingested, and hence the total intake does not vary greatly from one fortnight to the next.

The first impression that one gains while comparing the heights and frequencies of oscillations in the feeding curves (Fig. 1) is that, with increasing body weight, temporal variations are reduced to a narrow range. However, this is not true. In relation to the lower feeding rate among the larger individuals, the heights of the oscillations are reduced, but not the frequencies. In order to make a more convincing case, I have

calculated the standard deviations for the feeding rates of each individual (Table 3).

Considering males of 7.1, 41.2, 77.2 and 121.5 g body weight, the first one has a mean feeding rate of 4.0% body weight/day with a standard deviation of ± 2.68 , which amounts to 67.0% (coefficient of variation) deviation from the mean feeding rate. Similarly, for the remaining randomly chosen 3 test individuals, mean feeding rates are 3.5, 2.0 and 2.0% body weight/day, with standard deviations of ± 2.53 , 1.38 and 1.38;

Table 3. Estimates of daily fluctuations in the feeding rate of the dab *Limanda limanda*. Five individuals of similar body weight, fed at 13°C once a day till satiation with herring meat for a period of 28 days

Body weight (g)	Sex	Mean feeding rate (% body weight/day)	Coefficient of variation (%)
1.1	Juvenile	4.0 $\pm$ 1.78	44.5
5.4	♂	4.7 $\pm$ 2.04	43.4
33.1	♂	4.4 $\pm$ 1.77	40.2
61.3	♂	3.5 $\pm$ 1.39	39.7
115.5	♂	2.1 $\pm$ 1.24	59.0
7.1	♂	4.0 $\pm$ 2.68	67.0
41.2	♂	3.5 $\pm$ 2.53	72.3
77.2	♂	2.0 $\pm$ 1.38	69.0
121.5	♂	2.0 $\pm$ 1.38	69.0

their deviation ranges amount to 72.3, 69.0 and 69.0% of the respective mean feeding rates.

Females of different body weights show about 40% deviation from the mean feeding rate (only the largest female displayed a higher value of 59.0%). Thus, the range of daily variation in feeding rates differs markedly among the sexes, but not among the individuals of different body weights; the range of variation in the male is about 1½ times greater than that in the female.

Effects of food quality

In order to find out to what extent food quality modifies the feeding rate-body weight relation, dabs were fed cod (*Gadus morhua*) meat (series II); the results were then compared with those obtained on dabs fed herring (*Clupea harengus*) meat (series I). The individuals of series II were kept in groups of five and fed cod meat until satiation once a day for a period of about 10 min, at 13°C. All other conditions were the same as those in series I, except that the experiments of series I were performed during late August—September 1966, while those of series II were carried out in early June—July 1967. The main differences were the food quality used: herring meat contains 68.8% water and 6411 cal/g dry weight, while cod flesh has 78.7% water and 5339 cal/g dry weight (Table 1). In other words, 1 g herring meat (wet weight) yields as

much as 2001 calories, while the same amount of cod meat yields only 1137 calories; thus, for the same volume or weight of food, herring meat supplies nearly 2 times more energy.

As in series I, feeding rate decreases with increasing body weight of the test individuals used in series II. A female dab weighing 6.2 g consumed 4.8% body weight/day, and feeding rate decreased to 1.2% body weight/day in a 156.3 g individual; it was 5.4% body weight/day in a male of 14.1 g and progressively decreased to 1.6% body weight/day (Fig. 2).

Fig. 2. Feeding rate as function of body weight of *Limanda limanda* fed a restricted supply of herring (*Clupea harengus*) meat (series I) or cod (*Gadus morhua*) meat (series II) at 13°C

However, there were remarkable and unexpected differences: (1) within series II, the feeding rate of males was higher than that of females, just the reverse of what had been observed in series I. The difference in feeding rate between the sexes within series II was about 0.3% body weight/day or 0.4 cal/g/day, and this magnitude of difference was the same throughout the weight-range tested. (2) Irrespective of body weight, feeding rate in both sexes was slightly less in series II than in series I. However, this slight difference, when expressed in cal/g/day becomes considerable (Fig. 2). The magnitude of the difference was again dependent on both sex and body weight. Average daily food intake

of a dab female of about 6 g body weight was 4.7% of its body weight in the case of herring meat (9.4 cal/g/day), and 4.8% in the case of cod meat (5.4 cal/g/day). Although there was a little difference in the weight of food consumed, the herring-fed dabs received about 70% more energy than the cod-fed individuals. Among the fast-growing females of the size range 33 to 115 g (BOHL, 1957; p. 19), however, even greater differences became apparent. In females of about 50 and 100 g, feeding rates were 2.4 and 1.6% body weight/day (2.7 and 1.7 cal/g/day) when on a cod meat diet, but 3.9 and 3.2% body weight/day (7.7 and 6.3 cal/g/day) when on a herring diet. From the point of energy input, individuals fed on herring meat obtained about 3 times more energy than cod-fed dabs. The difference in food intake among the males of series I and II was rather less, and uniform throughout the weight-range tested. Thus, irrespective of changes in food quality, individuals of about 41 and 78 g body weight consumed 3.5 and 2.1% body weight/day, respectively.

Effects of temperature

The annual temperature variation to which the dab population is subjected in its natural habitat ranges from about 3° to 16.5°C. In the present investigation, modifying effects of temperature on the feeding rate-body weight relationship have been studied, choosing the following temperature levels: 3°, 8°, 13° and 18°C. As many as 60 experiments were carried out during the period from October 1966 to November 1967. In general, experiments at higher temperature levels were performed during summer, those at lower temperature levels during fall and early winter. No experiment was made during March and April 1967, when the dabs spawn. Eight experiments were set up at a given temperature level and each experiment lasted for a period of about 28 days (except for one series at 3°C, which had to be terminated after 10 days feeding, as the test individuals began to spawn).

Average feeding rates of the tested fishes at different temperature levels are presented in Table 4. Except for the females at 8°C, feeding rate decreased with increasing body weight. In males of less than 35 g, feeding rate decreased in this order: 18°, 13°, 8° and 3°C, while in the larger individuals tested, the decrease was in the order 13°, 18°, 8°, 3°C. The following are the orders in which feeding rate decreased in the females: group 1 (less than 30 g): 13° > 18° > 8° > 3°C; group 2 (between 31 and 80 g): 18° > 13° > 8° > 3°C; group 3 (heavier than 80 g): 8° > 18° > 13° > 3°C.

Sixteen experiments were performed at 3°C; at this low temperature dabs of less than 60 g did not feed at all; 2 to 3 individuals died during each of these experiments. It may be presumed that the lower lethal temperature of these small dabs lies near 3°C. SIMPSON (1953), who investigated the mortality of fish and the distribution of plankton in the southern North

Sea during the severe cold winter 1946–1947, reported 0.0° to 0.9 °C as lower lethal temperatures for the dab. It is interesting that females weighing less than 61.7 g, and males of less than 44.0 g body weight, did not feed throughout the 26 day experimental period at 3 °C.

Table 4. Feeding rate as a function of temperature in the dab *Limanda limanda*. Each value represents the average of 2 individuals, which were fed once a day ad libitum with cod flesh for a period of 28 days. 0.0 indicates that the test individuals did not feed throughout the experiment

Body weight (g)	Feeding rate (% body weight/day)	Body weight (g)	Feeding rate (% body weight/day)
Female		Male	
3 °C			
10.3	0.0	10.0	0.0
21.3	0.0	20.1	0.0
39.9	0.0	32.2	0.0
61.7	0.0	44.0	0.0
63.8	1.2	59.7	1.0
84.9	0.9	81.7	0.5
121.2	0.7	114.4	0.6
163.1	0.8		
274.1	0.2		
8 °C			
2.7	0.0	13.2	0.6
16.4	0.5	28.0	1.4
17.4	0.5	38.7	1.7
36.7	1.4	61.3	1.9
54.2	1.6	80.0	0.9
78.7	1.6	101.2	0.8
107.1	2.0	124.7	1.2
130.9	2.1		
168.5	1.5		
13 °C			
6.2	4.8	14.1	5.4
16.4	3.6	25.6	4.0
31.5	4.2	41.2	3.6
32.7	3.1	65.8	2.8
52.8	2.4	77.6	2.6
59.7	2.5	104.3	1.8
87.6	1.7	129.8	1.6
113.6	1.4		
156.3	1.2		
18 °C			
8.2	4.2	10.1	6.9
16.4	2.3	34.3	4.4
35.5	3.2	58.1	1.9
45.5	3.4	96.7	1.6
66.8	2.6		
84.2	2.2		
110.3	1.9		
160.7	1.3		

They refused to feed even when the food was left for a longer period (even throughout the entire day). Among the larger individuals which were feeding, food uptake was very irregular and their responses were not normal; they were lying around inactively in the corners of the aquaria, close to each other, or sometimes even

partially over each other. At 8 °C, similar behaviour was observed among individuals of 2.7 g; on the other hand, at temperatures of 13° and 18 °C, the dabs were either actively swimming or lying apart from each other on the ground. The small amount of food con-

Fig. 3. Feeding rates of *Limanda limanda* fed a restricted supply of cod meat at 4 different temperature levels

sumed by the 13.2 g male and 16.4 g female at 8 °C was ingested by them in the early half of the experiment; in the latter half, they completely ceased to feed. Feeding rate of these test individuals was about 0.6% body weight/day as against 5.4 and 3.6% body weight/day at 13 °C, respectively. While dabs weighing less than 13 g did not feed at 8 °C throughout the experiment, females of more than 80 g fed at maximum rates.

In February 1968, 40 specimens of *Limanda limanda* were collected near Helgoland and their stomach contents analysed. Most individuals weighing less than 50 g had virtually no food in their stomachs, while the others contained traces of food. Of the 3 larger individuals caught (about 80 g), two contained a fair amount of food, while the other had a stomach full of food. It is well known that temperate fishes cease to feed during winter (NIKOLSKY, 1963; p. 258). Interestingly, DAWES (1930–31) observed that the plaice *Pleuronectes platessa* ceased to feed in the latter half of November, when the habitat temperature was less than 10 °C; however, DAWES (p. 908) reported that, during the same period, 3 individuals (2 ♀♀ and 1 ♂), weighing more than 100 g, continued to feed.

In view of the complicated trends observed, I have attempted to present a generalized picture of the effects of different temperature levels on food intake of the dab. The feeding rates of 4 females and 4 males of different body weights are given in Fig. 3. Three interesting conclusions may be drawn. (1) The "normal temperature" for the test individuals varies with the body weight. Under "normal temperature" or "temperature norm" is understood: the range of environmental temperature "which allows the undisturbed functioning of metabolic processes, i.e. the processes which convert and use material for maintenance, growth, reproduction and repair and which make energy available to the organism" (KINNE, 1960; p. 313). The lowest temperature at which normal feeding is possible lies between 8° and 13 °C for dabs of less than 13 g (about 2 years old), between 3° and 8 °C for dabs between 13 to 60 g, and just above 3 °C for dabs over 60 g. (2) The feeding behaviour of smaller dab changes considerably as a function of temperature; they either feed and gorge themselves as at 13° and 18 °C, or cease to feed completely as at 8° and 3 °C. With increasing body weight (age), the magnitude of the temperature effect is progressively reduced. (3) Females of less than 10 g feed at maximum rates between 13° and 18 °C; larger females of less than 80 g reach their maximum food intake at 18 °C; females weighing more than 80 g attain their maximum already at 8 °C. Males of less than 40 g feed at maximum rates at 18 °C, while larger ones reach their maximum food intake at 13 °C. There is a decrease in optimum temperature for maximum feeding rates with increasing body weight (age).

Food conversion

Changes in composition and calorific content of test fishes fed cod or herring meat

Effects of body weight and sex

Water content values obtained for females of *Limanda limanda* before feeding at 13 °C (series I) revealed a progressive decrease from 85.1% in a female

of 1.1 g to 75.3% in a female of 150.7 g (the heaviest female used). A similar decrease of body water content with increasing body weight was also noted among males. Average water contents of all females and males were 77.2% and 76.3%, respectively. Body water content values of dab reported in literature range from 83.1 to 78.1% (VINOGRADOV, 1953; p. 481). As found in the present study, JAKOVLEV (1957) reported an indirect correlation between water content and body size (length) of the dab *L. limanda*. Calorific contents of individuals of *L. limanda* used in the present study varied from 4569 to 5564 cal/g dry weight¹, ash contents from 19.0 to 11.3%. No definite correlation between body weight and calorific content was apparent. Although ash content averaged 14.8% for males as well as females, females, on the whole, contained more energy (5219 cal/g) per unit weight than males (5132 cal/g). On an average, both sexes contained, at the beginning of the experiment, 76.8% water, 14.8% ash and 5181 cal/g (Table 5).

Compared to these high water and ash contents of the dabs, herring meat has lower water (68.8%) and ash (4.2%) contents per unit weight than that of the dabs at the commencement of the feeding experiments. Therefore, considerable changes in the composition of dab fed herring meat for 28 days may be expected. The average values obtained for herring-fed females were 74.1% for water, 12.1% for ash, and 5659 cal/g for energy; the respective values for males were more or less the same except for calorific content (5472 cal/g; Table 5). On the whole, there was a considerable increase in calorific content (5575 cal/g; 7.6% more energy than initially), while water (2.5%) and ash (2.7%) contents decreased.

Limanda limanda which were to be fed cod meat contained an average of 78.0% water, 15.7% ash, and 4983 cal/g energy (Table 5). The feeding experiments were made during May and June 1967, when the dabs were recovering from spawning. Throughout spawning

¹ Unless otherwise qualified, hereafter values for calorific and ash contents are given per dry weight, water content per wet weight.

Table 5. Average changes in the composition of the dab *Limanda limanda*, which received a restricted food supply of herring or cod meat at 3 different temperatures

Dabs fed at the temperature level of		Initial composition			Final composition		
		Water (%)	Ash (%)	Energy (cal/g)	Water (%)	Ash (%)	Energy (cal/g)
8 °C, cod-fed series	♂♀	75.3	12.3	5324	75.1	12.3	5514
18 °C, cod-fed series	♂♀	76.4	17.0	4776	76.2	16.2	4896
13 °C, series I (herring meat)	♀	77.2	14.8	5219	74.1	12.1	5659
13 °C, series I (herring meat)	♂	76.3	14.8	5132	74.6	12.1	5472
13 °C, series I (herring meat)	♂♀	76.8	14.8	5181	74.3	12.1	5575
13 °C, series II (cod meat)	♂♀	78.0	15.7	4983	77.9	14.8	5206

dabs lose a considerable amount of gonadal substance (2 to 7% of their body weight) containing about 5800 cal/g (FLÜCHTER and PANDIAN, 1968). This may be the reason for the low calorific content of the individuals used in the present experiments.

The cod meat used as food contained 5339 cal/g, i.e. 7.2% more energy per unit weight than the dabs at the commencement of feeding (herring meat contains 23.8% more energy than that of the dab). A 30-day feeding period with cod meat enriched the calorific content of the dabs to 5206 cal/g, i.e. the dabs contained, per unit weight, 4.5% more energy than before the feeding experiment. There was a wide difference in the ash contents (cod meat 4.4% ash; dab meat before feeding 15.9% ash), while the difference in water content was very small (78.7% water in cod meat; 78.0% water in dab meat; Table 5). Thirty-day feeding decreased the ash content of the dabs to 14.8%.

Both herring (series I) and cod (series II) feeding decreased the water content (about 1 to 2%) of the dabs. The calorific increases per unit dab weight was 7.6% if herring-fed, but only 4.5% if cod-fed. In series I, there was a greater decrease in ash content (from 14.8 to 12.1%) than in series II (from 15.7 to 14.8%).

During the course of experimental feeding at 3 °C, some dabs spawned; unfortunately, these were the only individuals which were feeding amounts equivalent to at least 1% of their own body weight/day. The other dabs ceased to feed at this low temperature. Since it was not possible to say which of the test individuals spawned, the data obtained on the composition of the 3 °C dabs have been excluded. At 8 °C, individuals of less than 17 g body weight (used in 4 experiments) did not feed or fed only very little. They starved, and lost considerable body weight. The data obtained on these dabs were also excluded while averaging the values obtained for the other 8 °C individuals.

Calorific contents of the dabs before feeding averaged 5324 cal/g at 8 °C, 4983 cal/g at 13 °C, and 4776 cal/g at 18 °C. After feeding 28 days at 8 °C, 30 days at 13 °C and 20 days at 18 °C, the resulting calorific contents of the test fishes showed considerable changes; the average energy content values were 5514, 5206 and 4896 cal/g, respectively. At all 3 temperature levels the calorific contents increased per unit dab weight; the increases amounted to 3.6, 4.5 and 2.5% per unit weight before feeding. Water and ash contents showed no appreciable changes (Table 5).

Efficiency and rate of food conversion

The total amount of food converted has been estimated by subtracting the energy content of the dabs at the beginning of the experiment from that at the end of the feeding period. In order to compare the data, the average amount of energy converted by a

single individual per day has been calculated for each experiment. Gross efficiency of food conversion was calculated by relating the amount of energy converted to the energy contained in the food consumed.

Effects of body weight and sex

Among the test individuals of series I fed on herring meat at 13 °C, conversion efficiency of the smallest individual (1.1 g) was 43.2%. It increased to 47.9% in a female of 33.1 g body weight and, thereafter, decreased to 34.2% in the heaviest individual used (150.7 g). Among males a similar trend was apparent;

Fig. 4. Food conversion efficiency as function of body weight of *Limanda limanda* fed a restricted supply of herring meat at 13 °C

an individual of 16.2 g converted 46.6% of the energy contained in the food consumed. Conversion efficiency then decreased to 26.8% in an individual of 101.1 g, although the heaviest male (121.5 g) showed, unexpectedly, a higher value (35.4%). With increasing body weight, conversion efficiency decreased in both sexes. The females were more efficient food converters than the males (Fig. 4).

HATANAKA et al. (1956a) fed the Japanese dab *Limanda yokohamae* with annelid worms or clam at an ambient temperature of 13.1 °C. They also found an indirect relation between body weight and conversion efficiency; the efficiency was 21.8% for an individual of 68 g, and decreased to 15.8% in a larger individual

of 148 g. The values reported by HATANAKA et al. for clam-fed dabs are also low, and not very different from those obtained for the annelid-fed dabs. On the whole, *L. limanda* appeared to be about 2 times more efficient than *L. yokohamae*. With a view to checking my data, I have calculated the efficiency relating the wet weight gained to the wet weight of food consumed (as did HATANAKA et al.). Most of these values are far lower than the corresponding values based on "energy index" (Fig. 4). Even the values based on "wet weight index" are $1\frac{1}{2}$ times higher than those reported for the Japanese dab. This is because 1 g wet weight of the dab *L. limanda* contains 1201 calories (based on average values of 76.8% water, 5181 cal/g), while 1 g herring meat has 2001 calories. In other words 1 g herring (fresh weight) corresponds to about 1.7 g dab (fresh weight). It is likely that 1 g annelid or clam used as food corresponded to 1 g Japanese dab, from the point of wet weight, as well as energy.

Effect of food quality

Fig. 5 shows the efficiency values obtained for dabs of series II fed with cod meat at 13 °C. The efficiency decreased from 34.1% in a female of 6.2 g to 28.1% in a female of 156.3 g body weight. A similar trend was obtained for the males. The efficiency decreased from 33.1% in the smallest male (6.2 g) to 19.9% in a male of 129.8 g body weight. As in series I, cod-fed males

Fig. 5. Food conversion efficiency as function of body weight of *Limanda limanda* fed a restricted supply of herring meat (series I) or cod meat (series II) at 13 °C

were less efficient than the corresponding females. Herring-fed dabs, on the whole, were more efficient converters than cod-fed dabs. As 1 g wet weight of cod meat contains 1137 calories, and 1 g wet weight of dab 1096 calories, there was no appreciable difference between the efficiency values based on "wet weight index" and "energy index".

Effects of temperature

As already reported, test individuals fed at 3 °C ceased to feed, or fed only a little (less than 1% body weight/day), and some spawned during the experiment. Therefore, only results obtained for individuals fed at 8°, 13° and 18 °C are reported here.

Individuals weighing more than 30 g reached, in both sexes, their maximum efficiency at 8 °C (Fig. 6). Females of 50 to 150 g converted as much as 40% of the consumed food at 8 °C, and only about 22% at 18 °C; the males displayed a similar trend. To yield 1 g body substance, a dab of 90 g body weight must eat 5 g food at 18 °C, but only 2.5 g food at 8 °C.

Among males and females of more than 30 g, the efficiency decreased in the order 8°, 13°, 18 °C. For smaller fishes, the decreasing order was 13°, 18°, 8 °C. Female dabs attain sexual maturity at a body weight

Fig. 6. Food conversion efficiency of the dab *Limanda limanda* fed a restricted supply of cod meat at 3 different temperature levels

of about 40 g, the males at about 30 g (BOHL, 1957). Conversion efficiency of sexually mature and actively reproducing dabs (> 40 g) attains a maximum at 8°C; the maximum is 13°C in young, immature dabs (< 40 g). Thus, optimum temperature for efficient conversion decreases with increasing body weight.

Conversion rate

Fig. 7 shows that conversion rates of herring-fed dabs were about 2 to 4 times higher than those of cod-fed dabs. The magnitude of this difference depends

Fig. 7. Food conversion rate of *Limanda limanda* as function of body weight. The test individuals were offered a restricted supply of herring meat (series I) or cod meat (series II) at 13°C

upon body weight and sex. A 15 g individual (series I and II) converts about 150 cal/day; a 100 g individual of series II, whether male or female, converts about 450 cal/day; a female of 100 g of series I converts 2000 cal/day, a corresponding male only 1300 cal/day. Among individuals of any body weight, from either series I or II, the conversion rate of the female is greater than that of the corresponding male.

Irrespective of body weight, males reveal fastest conversion at 13°C (Fig. 8). The slowest conversion in dabs under 50 g occurs at 8°C; in the larger males (over 50 g) at 18°C. Conversion rate decreases in females of more than 50 g body weight in the order 8°, 18°, 13°C; for smaller females in the order 13°, 18°, 8°C. At all 3 temperature levels, conversion rates are higher

among females than among males, e.g. at 8°C, a 100 g male converts 350 cal/day, a female 950 cal/day (Fig. 8).

Quantitative relationships between food intake, metabolism and body weight

The quantitative relationship between food intake and body weight was calculated on the basis of the allometric formula $y = bx^a$, where y is metabolism, x body weight, and a and b are constants. As the smaller fishes did not feed at 3° and 8°C, data obtained at 13° and 18°C were used. When plotting the average

Fig. 8. Food conversion rate of the dab *Limanda limanda* fed a restricted supply of cod meat at 3 different temperature levels

daily food intake against body weight in a double logarithmic graph, the difference in food intake between males and females appears to be less significant (Fig. 9). The weight exponents are 0.54 for 13°C and 0.57 for 18°C (cod meat) and 0.88 for 13°C (herring meat). Thus, food quality strongly alters the weight exponent, while temperature changes seem to have little influence. The "a" value is lowest for herring-fed dabs (92.1 cal/day); it is 178.2 cal/day at 13°C and 142.2 cal/day at 18°C in cod-fed dabs².

Effects of temperature and food quality on the relation between metabolic rate and body weight have also been calculated using the allometric formula.

² I am grateful to Prof. Dr. F. KRÜGER (Biologische Anstalt Helgoland, Hamburg) for his kind evaluation of my calculations.

I have no direct information on the amount of energy used for metabolism by dabs, but appropriate values can be calculated from data on food intake and food conversion. Following the procedure used by PALOHEIMO and DICKIE (1966a), I have employed WINBERG's (1956) "utilization coefficient" for calculating the amount of energy contained in the food absorbed. From these values, the amount of energy contained in the food converted was subtracted to obtain the amount of energy which may have been used for metabolism. The values so obtained were related to body weight in order to calculate 'a' and 'b' values. The slopes of the curves (or weight exponents) are 0.61 for 13 °C and 0.58 for 18 °C (cod meat); these curves are

Fig. 9. Quantitative relations of body weight of *Limanda limanda* to rates of food uptake (left) and metabolism (right). Open circles: females; closed circles: males. Test individuals of series I received herring meat, those of series II cod meat

almost parallel to each other, but differ due to a higher 'a' value (78.2 cal/day) of the 18 °C series ('a' value for 13 °C: 64.5 cal/day). In herring-fed series, at 13 °C, the exponent is 0.93 (in cod-fed: 0.61); however the 'a' value (33.5 cal/day) is only about 50% of the 'a' value (64.5 cal/day) obtained for cod-fed dabs.

The analyses of the effects of different food quality and temperature permit two conclusions. (1) Temperatures between 13° and 18 °C influence the metabolic level but not the weight exponent. (2) Food quality influences the metabolic level as well as the weight exponent.

Discussion

The results presented have shown that temperature and food quality modify the feeding rates and the relations between food conversion and body weight in

the flat fish *Limanda limanda*. There exist considerable individual and temporal variations in food intake and food conversion, even when the test individuals are kept under almost identical conditions. In regard to food intake, the range of deviations from mean feeding rates was about 60% for males and about 40% for females fed herring meat at 13 °C. In other words, temporal variation in food intake is about 1½ times greater in males than in females. Among males and females of different body weights, however, the values for the range (coefficient) of deviations did not vary significantly. These values (Table 3) represent the average performance of 4 to 5 individuals; the deviation range might have been even wider, if the test individuals had been fed individually. For want of similar data in previous studies, I have not been able to compare these results. However, several workers have at least suggested pronounced day-to-day fluctuations in feeding rates of fishes (MOORE, 1941; HUNT, 1960; PANDIAN, 1967b, c). MOORE has probably been the first author who presented daily feeding records in a comprehensive figure. He reported that his test fishes never attained any constant level of food consumption. However, the few data reported by him do not permit detailed quantitative assessments of the daily variations observed.

For technical reasons, I have not been able to study daily variations in rates and efficiencies of food conversion. But such variations must be assumed in view of the daily variations in food intake; food intake is the most potent factor affecting food conversion (BROWN, 1957). PALOHEIMO and DICKIE (1966a, b), who re-examined literature data on food intake and conversion, showed that flat fishes (DAWES, 1930–31; HATANAKA et al., 1956a, b) display considerably greater individual and temporal variations than other fishes. This behaviour is supported by the present study.

Why should dab kept under almost identical environmental conditions show such wide variations in rates of food intake and food conversion? A possible reason may be that, at the population level, dabs spawn over several months; at the individual level, they spawn repeatedly (a few thousand eggs each time). The spawning period of *Limanda limanda* spreads over a period of 9 months; it begins early in January and lasts until July, or even to the end of September in the middle of the North Sea (EHRENBAUM, 1910). Peak spawning extends from March to May, when the surface water temperature rapidly increases from about 3 °C to about 10 °C, a most rapid change for such a short period. Unlike other flat fishes, spawning in the dab is largely independent of hydrographic conditions (BOHL, 1957); for this reason the dab has been considered "propagative eurytherm" (AURICH, 1940). AURICH, who investigated the distribution and density of pelagic fish eggs in the North Sea over 12 years, reported that *L. limanda* spawns at water temperatures

varying from 2°–3 °C to over 16 °C (optimum 3° to 7 °C) and in salinities ranging from 28–29‰ to 35‰. Thus, the freshly spawned eggs of the dab are subjected to a wide variety of salinity-temperature conditions, which further vary from year to year, and from place to place.

KINNE (1962) reported that rates of feeding and food conversion in the euryhaline fish *Cyprinodon macularius* were consistently higher in individuals hatched from eggs that remained in the spawning salinity, than in offspring from eggs which had been transferred to another salinity level. He suggested that the spawning medium affects the physical properties of the immediate environment of the embryo, thus "imprinting" different functional and structural properties that tend to persist — at least in part — throughout the individual's life span. Such "conditioning" by the spawning medium may not only affect metabolic processes (KINNE, 1962), but also morphological aspects (SWEET and KINNE, 1964). Comparable: irreversible, non-genetic changes due to temperature history have been demonstrated in *Lebistes reticulatus* (GIBSON, 1954; GIBSON and HIRST, 1955; TSUKUDA and KATAYAMA, 1957; TSUKUDA, 1960). TSUKUDA's valuable contribution demonstrates that the process of temperature acclimation is affected by the thermal history. Though similar investigations are wanting for *Limanda limanda*, some evidence is available on temperature effects during early development of other flat fishes. The vertebra number is determined at an early developmental stage (gastrula) in *Pleuronectes platessa* (DANNEVIG, 1950). FLÜCHTER and PANDIAN (1968) showed that temperature not only controls the rate of development, but also affects the hatching size, by altering the yolk utilization efficiency, of the sole *Solea solea*. In the light of such information it may be suggested that the individual variations observed in rates of food intake and conversion in dabs are possibly due to "irreversible nongenetic adaptation" (KINNE, 1962) induced in freshly spawned eggs, subjected to a wide variety of temperature-salinity combinations.

The results obtained on the average rates of food intake and conversion in dabs provide evidence that body weight affects rate and efficiency of metabolism. Intake of food per unit fish weight per unit time decreases with increasing body weight (except for females at 8 °C); this trend is also seen in body weight-conversion efficiency relationships. An indirect negative correlation between body weight and feeding rate has been shown by previous workers such as KINNE (1960), MENZEL (1960) and PANDIAN (1967b). Feeding rate apparently decreases at a faster rate than respiratory metabolism, i.e. the increase in energy input (food intake) is not proportionate to the increase in energy output through metabolism. Per gram dab weight increase, food intake increases by a factor of 0.54 at 13 °C, 0.57 at 18 °C (0.88 for dabs fed herring meat at 13 °C); the respective values for metabolic increase are

0.61, 0.58 (and 0.93). Data published by PANDIAN (1967b) for 2 tropical fishes fed with prawn *ad libitum* at 28 °C demonstrated that food intake increases by a factor of 0.71 in *Megalops cyprinoides* and 0.76 in *Ophiocephalus striatus*, while the energy expended on metabolism increases 0.77 and 0.88, respectively. Decrease in conversion efficiency with increasing body weight is, therefore, not directly due to body weight, but to the reduced feeding rate. PALOHEIMO and DICKIE (1966b) also concluded that body weight affects feeding, but is not a determining factor for conversion efficiencies.

With regard to the differences in feeding rates observed among female and male dab, the following is to be said: My observation that males feed less than the females, differs from the findings of DAWES (1930–31) in plaice *Pleuronectes platessa*. DAWES fed plaice in their natural habitat, and reported that the maintenance feeding level of male plaice was greater than that of the female in Cowsand (England), and in individuals of less than 80 g body weight in Lympstone (England). PALOHEIMO and DICKIE (1966a), who re-examined DAWES data, found that the differences reported by DAWES were not statistically significant. In general, growth rates among males and females differ considerably in flat fishes; such differing growth rates become particularly apparent only at a definite size, which varies from species to species (BOHL, 1957). Differences in growth rate become apparent in *P. platessa*, when it reaches about 20 cm standard length (about 150 g body weight) at the beginning of the 4th year of its life, while in *Limanda limanda* it becomes apparent at 12 cm standard length (less than 10 g body weight) at the beginning of the 2nd year. DAWES used 2 year old plaice of less than 120 g body weight, in which growth differences due to sex are not yet pronounced, while the dab used (> 10 g) in the present study were already showing marked differences in growth rates of females and males. Therefore, the results obtained for dab, though of the same body weight, are not strictly comparable to those reported for plaice by DAWES.

For a similar reason, my data are not strictly comparable to those reported for the Japanese dab *Limanda yokohamae* (HATANAKA et al., 1956a). Japanese dab, varying from 68 to 259 g body weight, were fed at 13.1 °C. Since male and female individuals were kept together in groups, no differences in feeding rates of males and females could be observed. Sexual differences in growth rate become apparent only when *L. yokohamae* attain body weights of about 167 g at the commencement of their second year of life. Also for similar reasons, my data are not directly comparable to the results reported by HATANAKA et al. (1956b) for the Japanese plaice *Kareius bicoloratus*.

The feeding responses of dab to temperature permits three interesting conclusions (Fig. 3).

(1) The temperature optimum for maximum food uptake shifts downward with increasing body weight in both sexes. That the temperature optimum for growth or metabolism is body weight-dependent has only recently been recognized and hence there is scant evidence. Studies on the growth of the desert fish *Cyprinodon macularius* by KINNE (1960) offer such evidence. In *C. macularius* the temperature level 30 °C is optimal for smaller individuals; in larger individuals (older than 22–28 weeks) the temperature optimum shifts gradually downwards to 22°–26 °C. From his oxygen consumption studies on *Salvelinus fontinalis*, JOB (1955) concluded that the smaller individuals were “better off” at higher temperatures (15° and 20 °C) than at the lower temperature levels (5° and 10 °C), whereas, for the larger ones, the opposite was true.

(2) Differences in the feeding response of dab due to temperature changes are more pronounced in smaller individuals than in larger ones. The smaller dab either fed and gorged themselves at the higher test temperatures, or completely ceased to feed at the lower temperatures. Data by HATANAKA et al. (1956a) for the Japanese dab *Limanda yokohamae* show that individuals of about 100 g body weight consumed about 1½ times more food at an average ambient temperature of 19.0 °C, than at 8.4 °C, although larger individuals (200 g) showed almost no difference. The results of MENZEL (1960) on *Epinephelus guttatus* revealed that the increase in food intake is about 224% and 190% higher at 28 °C, than at 19 °C, for individuals of 100 and 600 g body weight, respectively. Such body weight-dependent temperature effects can even be evident in fishes fed during the acclimation period. Feeding rate of *Lepomis gibbosus* is about 5 times higher in smaller individuals (of about 14 g) at 20 °C than at 10 °C (this difference is only 3 times in larger individuals of 44 to 81 g; HATHAWAY, 1927). WOOD (1952) and PANDIAN (1967c) reported that, in regard to variations in food quality, there are wide differences in the feeding rates of smaller individuals; the magnitude of the differences decreases progressively with increasing body weight. Such weight-related differences have not only been observed in regard to food intake, but also to oxygen uptake. Due to a change in temperature from 5° to 20 °C, metabolism (non-dependent active) of a 5 g *Salvelinus fontinalis* rises 2.8 times (an individual weighing 1,000 g exhibited an increase of 1.3 times). Thus, smaller individuals are more sensitive and their responses are more pronounced to changes in environmental factors, such as temperature and food quality, than larger individuals.

(3) The “normal temperature” is narrower in dabs of less than 40 g (13° to 18 °C) than in larger individuals (3°–8° to 18 °C). Although records of such body-weight-related differences in “normal temperature” ranges are lacking, there exists a considerable amount of literature concerning temperature requirements for maturation of sexual products, spawning and early

development, which differ from the ones at which the animal feeds and actively grows (KINNE, 1963). The dab's gonads ripen during fall, when temperatures rapidly decrease; the optimum temperature for spawning ranges from 3° to 7 °C (AURICH, 1940). Dabs weighing more than 40 g belong to the actively-reproducing group, while those of less than 40 g are either immature, or their contribution to the egg production of the total population is almost negligible (BOHL, 1957). The wide “normal temperature” range of larger adult individuals may be considered to be a non-genetic adaptation, acquired possibly due to seasonal temperature variations over a period of about 3 to 4 consecutive years.

The optimum temperature for food conversion efficiency lies between 13° and 18 °C for immature *Limanda limanda*, and at 8 °C for mature individuals of both sexes; the optimum temperature for food conversion efficiency decreases with increasing body weight. Furthermore, taking any one of the 4 different body weight groups into consideration (Fig. 3), optimum temperature for maximum conversion is lower than the temperature at which the dab consumes maximum amounts of food. Exceptions are females over 80 g body weight, which display maximum rates of feeding and conversion efficiency at the same temperature (8 °C). The results of HATANAKA et al. (1956a) showed that Japanese dab *Limanda yokohamae*, of less than 100 g, reveal maximum consumption at an ambient temperature of 23.1 °C, but convert most efficiently at a lower temperature of 19.0 °C. KINNE (1960) also reported that *Cyprinodon macularius* feed maximally at 30 °C, while the optimum temperature for efficient conversion is 20 °C. The fact that food conversion efficiency and food intake have different temperature optima indicates the complex nature of metabolic interactions taking place (PALOHEIMO and DICKIE, 1966a). Two aspects may be discussed here. (1) Relative to larger dab, smaller dab appear to have to expend considerably more energy on activity (e.g. swimming, hunting for prey) at a higher temperature (18 °C) than at 13 °C, and hence can convert only a lesser percentage of the food consumed for growth. There is supporting evidence in literature. For example, JOB (1955) found that, at higher temperature levels (20 °C), the non-dependent active metabolic rate of a 5 g individual of *Salvelinus fontinalis* was about 352% higher than its standard rate; this difference amounts to only 276% for the larger individual (1,000 g). (2) Although larger dabs (over 40 g) of both sexes consume relatively less food at 8 °C (except females > 80 g), they display maximum conversion efficiencies at this temperature. The feeding experiments at 8 °C were begun in late November, and lasted until early January 1967. The maintenance requirements of these test fishes appear to have been only fractions of the summer maintenance requirements; thereby they have been able to use the food consumed most efficiently.

Maintenance requirements of the plaice *Pleuronectes platessa* is significantly reduced during October to December; the magnitude of reduction varied from 50 to 66% of the summer maintenance requirement (DAWES, 1930—31).

The response of the dabs to changes in food quality were surprising; dabs which received herring meat (series I), consumed and converted considerably more food than the individuals fed cod meat (series II). Consequently, conversion (growth) rates in individuals belonging to series I were 2 to 4 times greater than in those of series II. A similar situation has been observed in natural habitats. For instance, the plaice *Pleuronectes platessa* were transplanted from the spawning ground (Horn Reef Ground) to other places (e.g. Dogger Bank, North Sea). Due to the availability of a better food quality at Dogger Bank, the transplanted plaice grew 2 to 4 times faster than those left at Horn Reef Ground (NIKOLSKY, 1963; p. 207).

The weight exponents for the relationship between food intake and body weight are 0.54 at 13 °C, and 0.57 at 18 °C, for dabs fed with cod meat. The corresponding values for the relationship between metabolic rate and body weight are 0.61 and 0.58. PALOHEIMO and DICKIE (1966a) recalculated the data obtained by DAWES (1930—31) for the plaice *Pleuronectes platessa*, and HATANAKA et al. (1956a) for the Japanese dab *Limanda yokohamae*. They reported a weight exponent for the metabolism-body weight relation of 0.62 for plaice and 0.65 for Japanese dab. A remarkable feature is that the weight exponents of all the three flat fishes are significantly lower than the values reported for other fishes investigated. However, it is not possible to arrive at any definite conclusion, as the weight exponent obtained for dab fed with herring meat is 0.93, and that obtained by DAWES (1930—31) for plaice (which received an intermediate food supply between *ad libitum* and minimum maintenance feeding) is also 0.93 (PALOHEIMO and DICKIE, 1966a).

The weight exponents displayed only small variations at temperatures ranging from 13° to 18 °C; however, there was a change in the 'a' value. The 'a' value, for instance, for the metabolism-body weight relation at 18 °C (78.2 cal/day) is 18% higher than at 13 °C (64.5 cal/day). The fact that temperature influences not the weight exponent but only the metabolic level, has been demonstrated by PALOHEIMO and DICKIE (1966a), using KINNE's (1960) data on *Cyprinodon macularius*. Within the range 20° to 30 °C, *C. macularius* displays weight exponents of 0.63 ± 0.10 . The 'a' value of the slope for 30 °C was about 3 times higher than the one for 20 °C.

Food quality exerts significant influences not only on the weight exponent, but also on the metabolic level. *Limanda limanda* fed with herring meat at 13 °C display a weight exponent of 0.93, which is significantly greater than that (0.61) obtained in cod-fed individuals at 13 °C. The 'a' value of the former is 33.5 cal/day,

i.e. only half that of the latter (64.5 cal/day). As there is no previous work available for comparison, further discussion is not possible. However, the fact that food quality affects not only the weight exponent, but also the metabolic level, calls for further investigation.

Summary

1. Intake and conversion of food were studied as functions of body weight, sex, temperature and food quality in the flat fish *Limanda limanda* from the southern North Sea.

2. With increasing body weight, both female and male *L. limanda* consume less food per unit body weight; irrespective of body weight (1 to 150 g), females consume more food than corresponding males when offered herring meat at 13 °C (series I); the degree of this difference is body weight-dependent.

3. Temporal and individual variations in daily feeding rates are considerable; deviation from mean feeding rate amounts to about 60% for males and 40% for females. The degree of deviation does not vary significantly among females and males of different body weights.

4. Females consume almost the same amount, or less, cod meat than males, at 13 °C (series II). Among individuals of series I and II, feeding rates differed somewhat. Herring-fed individuals receive about 1.7 times more energy than those fed cod meat. One gram wet weight of herring and cod meat yields 2001 and 1137 calories, respectively.

5. Smaller *Limanda limanda* (less than 60 g) do not feed at 3 °C, while larger individuals consume about 1% of their body weight/day. Although large individuals feed normally at 8 °C, small ones (less than 17 g) refuse to feed. Females weighing over 80 g feed at maximum rates at 8 °C. Smaller individuals of both sexes consume maximum amounts of food at 13° and 18 °C. The optimum temperature for maximum food intake decreases with increasing body weight.

6. Feeding with cod or herring meat for about 30 days results in considerable changes in regard to composition and calorific content in the dab *L. limanda*. The degree of these changes depends on both temperature and food quality. At 13 °C, herring-fed dabs contain as much as 7.6% more energy per unit weight than at the beginning of the feeding experiment, the corresponding increases are only 3.6% at 8 °C, 4.5% at 13 °C and 2.5% at 18 °C for dabs which receive cod meat.

7. Food conversion efficiency values in herring-fed dabs are about 1½ times higher than those in individuals fed cod meat. In both series I and II, females are more efficient converters than males. In dabs weighing more than 50 g, conversion efficiency decreases in the order 8°, 13°, 18 °C; for smaller individuals the order of decrease is 13°, 18°, 8 °C. Thus, optimum

temperature for maximum conversion efficiency decreases with increasing body weight. In each tested individual, the optimum temperature for maximum conversion efficiency was lower than the temperature at which maximum food intake occurred.

8. Conversion rates are about 2 to 5 times faster in herring-fed dab than in cod-fed ones. Conversion rates decrease in males in the order 13°, 8°, 18 °C; in females in the order 18°, 13°, 8 °C; females of more than 80 g respond exceptionally, they reach maximum conversion rates at 8 °C.

9. The weight exponents obtained for the relationship between body weight and rates of food intake and metabolism of cod-fed dabs at 13° and 18 °C amount to about 0.6; 'a' values, or metabolic levels, are about 2 times higher at 18 °C than at 13 °C. Thus, the temperature affects the metabolic level but not the exponential value.

10. The weight exponents obtained for the body weight relation to rates of food intake and metabolism of herring-fed dabs at 13 °C are about 0.9; 'a' values amount to only about one half of those obtained for dab fed on cod meat. Food quality, unlike temperature, alters not only the weight exponents, but also the metabolic level.

Acknowledgements. The work presented was conducted under the guidance of Prof. O. KINNE (Hamburg) and submitted to the University of Kiel in candidature for the degree of Dr. rer. nat. I am deeply indebted to Prof. KINNE for help and support. It is a pleasure to thank Prof. K. PAMPAPATHI RAO (Bangalore University, India) for critically going through the manuscript and for valuable suggestions. I am grateful to Herrn J. K. HOLTSMANN and Frl. A. REYMERS (Biologische Anstalt Helgoland) for technical assistance. Thanks are extended to Mrs. KATRE SHAKUNTALA and to my wife SHANTHA PANDIAN, who have kindly assisted in preparing figures and manuscript. A fellowship awarded by the DAAD, Bad Godesberg (Germany), is gratefully acknowledged.

Literature cited

- AUBICH, H.: Die Verbreitung der pelagischen Fischbrut in der südlichen Nordsee während der Frühjahrsfahrten 1926—1937. Helgoländer wiss. Meeresunters. **2**, 183—225 (1940).
- BEAMISH, F. W. H. and L. M. DICKIE: Metabolism and biological production in fish. Int. biol. Symposium, Reading, 215—242 (1966).
- BOHL, H.: Die Biologie der Kliesche (*Limanda limanda* L.) in der Nordsee. Ber. dt. wiss. Kommn. Meeresforsch. **15**, 1—57 (1957).
- BRETT, J. R.: Some principles in the thermal requirements of fishes. Q. Rev. Biol. **31**, 75—87 (1956).
- BROWN, M. E.: Experimental studies on growth. In: The physiology of fishes, Vol. 1, pp 361—400. Ed. by M. E. BROWN. New York: Academic Press 1957.
- BULLOCK, T. H.: Compensation for temperature in the metabolism and activity of poikilotherms. Biol. Rev. **30**, 311—342 (1955).
- BÜCKMANN, A.: Vorläufige Mitteilung über Fütterungs- und Wachstumsversuche mit Schollen im Aquarium. Kurze Mitt. fischbiol. Abt. Max-Planck-Inst. Meeresbiol. Wilhelmsh. **1**, 8—21 (1952).
- DANNIEVIG, A.: The influence of environment on number of vertebrae in plaice. FiskDir. Skr. (Havundersøk.) **9**, 9 (1950).
- and S. HANSEN: Faktorer av betydning for fiskeeggenes og Fiskeyngelens oppvekst. FiskDir. Skr. (Havundersøk.) **10**, 5—36 (1952).
- DAWES, B.: The absorption of fats and lipoids in the plaice (*P. platessa* L.). J. mar. biol. Ass. U.K. **17**, 75—102 (1930).
- Growth and maintenance in the plaice (*P. platessa* L.). Pts 1 & 2. J. mar. biol. Ass. U.K. **17**, 103—174; 877—947 (1930—31).
- EHRENBAUM, E.: Eier und Larven von Pleuronectiden der Nordsee und benachbarter Gewässer. Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer **12** (C 3), 1—32 (1910).
- FLÜCHTER, J. and T. J. PANDIAN: Rate and efficiency of yolk utilization in developing eggs of the sole *Solea solea*. Helgoländer wiss. Meeresunters. **18**, 53—60 (1968).
- FRY, F. E. J.: Effects of environment on animal activity. Univ. Toronto Stud. biol. Ser. (= Publ. Ont. Fish. Res. Lab. **68**) **55**, 1—63 (1947).
- The aquatic respiration in fish. In: The physiology of fishes, Vol. 1, pp 1—63. Ed. by M. E. BROWN. New York: Academic Press 1957.
- GERKING, S. D.: The protein metabolism of the sunfishes of different ages. Physiol. Zool. **25**, 358—372 (1952).
- The food turnover of a bluegill population. Ecology **35**, 490—498 (1954).
- Influence of rate of feeding on body composition and protein metabolism of bluegill sunfish. Physiol. Zool. **28**, 267—282 (1955).
- GIBSON, M. B.: Upper lethal temperature relation of the guppy *Lebistes reticulatus*. Can. J. Zool. **32**, 393—407 (1954).
- and B. HIRST: The effect of salinity and temperature on the pre-adult growth of guppies. Copeia **241**—243 (1955).
- HATANAKA, M., M. KOSAKA and Y. SATO: Growth and food consumption in plaice. 1. *Limanda yokohamae* (GÜNTHER). Tohoku J. agric. Res. **7**, 151—162 (1956a).
- — — Growth and food consumption in plaice. 2. *Kareius bicoloratus* (BASILEVSKY). Tohoku J. agric. Res. **7**, 163—174 (1956b).
- , K. SAKINO, T. TAKAHASHI and T. ICHIMURA: Growth and food consumption in young mackerel *Pneumatophorus japonicus* (HOUTTUYN). Tohoku J. agric. Res. **7**, 351—368 (1957).
- HATHAWAY, E. S.: The relation of temperature to the quantity of food consumed by fishes. Ecology **13**, 423—434 (1927).
- HUNT, B. P.: Digestion rate and food consumption of Florida gar, warmouth, and largemouth bass. Trans. Am. Fish. Soc. **99**, 206—210 (1960).
- IVLEV, V. S.: Balance of energy in carps. Zool. Zh. **18**, 303—318 (1939).
- The biological productivity of waters. [Transl. from Russ.]. Adv. contemp. Biol. (= Russ. Rev. Biol. = Usp. sovrem. Biol.) **19**, 98—120 (1945).
- JAKOVLEV, V.: Vorläufige Mitteilung über die Untersuchung des Wassergehalts bei Schollen und Klieschen. Mitt. Inst. Fischbiol. Univ. Hamburg **7**, 23—26 (1957).
- JOB, S. V.: The oxygen consumption of *Salvelinus fontinalis*. Univ. Toronto Stud. biol. Ser. (= Publ. Ont. Fish. Res. Lab. **73**) **61**, 1—39 (1955).
- KINNE, O.: Growth, food intake and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiol. Zool. **33**, 288—317 (1960).
- Irreversible nongenetic adaptation. Comp. Biochem. Physiol. **5**, 265—282 (1962).
- The effect of temperature and salinity on marine and brackish water animals. 1. Temperature. Oceanogr. mar. Biol. A. Rev. **1**, 301—340 (1963).
- Non-genetic adaptation to temperature and salinity. Helgoländer wiss. Meeresunters. **9**, 433—458 (1964).
- KÜHL, H.: Nahrungsuntersuchungen an einigen Fischen im Elbe-Mündungsgebiet. Ber. dt. wiss. Kommn. Meeresforsch. **16**, 90—104 (1961).
- LUNDBECK, J.: Fischkunde für Jedermann, Vol. 1, 231 pp. Neumünster: Plambeck 1955 (Praxis der Fischwirtschaft).

- MAYNARD, A. L. and K. J. LOOSLI: Animal nutrition, 5th ed., 533 pp. New York: Mc-Graw Hill 1962.
- MENZEL, D. W.: Utilization of algae for growth by the angel fish. *J. Cons. perm. int. Explor. Mer* **24**, 308—313 (1959).
- Utilization of food by a Bermuda reef fish *Epinephelus guttatus*. *J. Cons. perm. int. Explor. Mer* **25**, 216—222 (1960).
- MOORE, W. G.: Studies on the feeding habits of fishes. *Ecology* **22**, 91—96 (1941).
- NIKOLSKY, G. V.: The ecology of fishes, [Transl. from Russ.], 352 pp. New York: Academic Press 1963.
- PAINE, R. T.: Endothermy in bomb calorimetry. *Limnol. Oceanogr.* **11**, 126—129 (1966).
- PALOHEIMO, J. E. and L. M. DICKIE: Food and growth of fishes. 2. Effects of food and temperature on the relation between metabolism and body weight. *J. Fish. Res. Bd Can.* **23**, 869—908 (1966a).
- Food and growth of fishes. 3. Relations among food, body weight and growth efficiency. *J. Fish. Res. Bd Can.* **23**, 1209—1248 (1966b).
- PANDIAN, T. J.: Food intake, absorption and conversion in the fish *Ophiocephalus striatus*. *Helgoländer wiss. Meeresunters.* **15**, 637—647 (1967a).
- Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. *Mar. Biol.* **1**, 16—32 (1967b).
- Transformation of food in the fish *Megalops cyprinoides*. 1. Influence of quality of food. *Mar. Biol.* **1**, 60—64 (1967c).
- Transformation of food in the fish *Megalops cyprinoides*. 2. Influence of quantity of food. *Mar. Biol.* **1**, 107—109 (1967d).
- RÜHMER, S.: Fische und Nutztiere des Meeres, 256 pp. Ebenhausen/München: Rühmer 1954.
- SIMPSON, A. C.: Some observations on the mortality of fish and the distribution of plankton in the southern North Sea during the cold winter 1946—1947. *J. Cons. perm. int. Explor. Mer* **19**, 150—177 (1953).
- SINDERMANN, C. J.: Diseases in marine fishes. *Adv. mar. Biol.* **4**, 1—89 (1966).
- SMITH, H. W.: The metabolism of the lung fish. 2. Effects of feeding on meat in the metabolic rate. *J. cell. comp. Physiol.* **6**, 335—349 (1935).
- SWEET, J. G. and O. KINNE: The effects of various temperature-salinity combinations on the body form of newly hatched *Cyprinodon macularius* (Teleostei). *Helgoländer wiss. Meeresunters.* **11**, 49—69 (1964).
- TSUKUDA, H.: Temperature adaptation in fishes. 3. Temperature tolerance of the guppy *Lebistes reticulatus* in relation to the rearing temperature before and after birth. *Biol. J. Nara Women's Univ.* **10**, 11—14 (1960).
- and T. KATAYAMA: Temperature adaptation in fishes. 1. The influence of rearing temperature on the temperature tolerance, growth rate and body form. *Seiro-Seitai* **7**, 113—122 (1957).
- VINOGRADOV, A. P.: The elementary composition of marine organism. [Transl. from Russ.], 647 pp. New Haven: Yale University Press 1953. (Mem. Sears Fdn mar. Res. 2).
- WILLIAMS, W. E.: Food consumption and growth rates for large and small mouth bass in the laboratory aquaria. *Trans. Am. Fish. Soc.* **88**, 125—127 (1959).
- WIMPENNY, R. S.: The plaice, 145 pp. London: Arnold & Co. 1953.
- WINBERG, G. G.: Rate of metabolism and food requirements of fishes, 253 pp. Minsk: Belorusskogo Nauchnye Trudy Belorusskogo Gosudarstvennogo Universiteta imeni V.I. Lenina 1956. (Transl. Fish. Res. Bd Can. No 362).
- WOOD, E. M.: Method of protein studies with trout with applications of four selected diets. Ph. D. thesis, Ithaca, N.Y., Cornell Univ. (1952).
- Author's address: Dr. T. J. PANDIAN
Zoology Department
Bangalore University
Bangalore 1, India

Date of final manuscript acceptance: October 28, 1969. Communicated by N. K. PANIKKAR, New Delhi, and O. KINNE, Hamburg