

FEEDING, METABOLISM, AND GROWTH OF TROPICAL FLATFISH

R. R. C. EDWARDS

Marine Laboratory, Aberdeen, Scotland

J. H. S. BLAXTER¹

Natural History Department, The University of Aberdeen, Scotland

U. K. GOPALAN and C. V. MATHEW

Biological Oceanography Division, National Institute of Oceanography, Ernakulam, Cochin, India
and

D. M. FINLAYSON

Marine Laboratory, Aberdeen, Scotland

Abstract: Observations have been made during a 3-month period on the growth, feeding and metabolism of five species of *Cynoglossus* from the Arabian Sea on the southwest coast of India; two other types of sole, *Brachirus* and *Synaptura* were also studied.

Growth increments of samples of *Cynoglossus* taken at regular intervals from the sea varied between 0.9 and 2.0 mm per week.

From samples taken throughout a 24-h period in the sea, there is evidence of a diel feeding rhythm with the greatest activity at night.

Measurements of standard oxygen consumption at 28 °C indicated a relationship between oxygen consumption (Q ; mg O₂/h) and live weight (W ; g) of, $Q = 0.372 W^{0.734}$ for *Cynoglossus* and of $Q = 0.362 W^{0.682}$ for *Brachirus* and *Synaptura*.

The standard oxygen consumption of *Cynoglossus* was temperature-dependent between 15 and 30 °C, but temperature-independent between 30 and 37.5 °C, where a plateau of oxygen consumption was observed.

Cynoglossus were fed at 28 °C with the polychaete *Diopatra neopolitana* Delle Chiaje: a maintenance food intake of 25 % of the body weight per week was indicated. The metabolic level, as indicated by the oxygen uptake, of the fish was related to food intake, being highest at the highest feeding levels. Efficiencies of conversion of assimilated food into growth of 11 to 12 % were observed.

INTRODUCTION

The International Biological Programme has been sponsoring visits by United Kingdom biologists to the Biological Oceanography Division, National Institute of Oceanography in Cochin, S. India, for collaboration with Indian biologists in the field of tropical marine ecology. It is especially intended that the energetics of sandy shore communities in the tropics should be compared with similar communities on a temperate shore, and so related to the studies developed by the Marine Laboratory, Aberdeen in Loch Ewe on the west coast of Scotland (see McIntyre & Eleftheriou, 1968; Steele & Baird, 1968; Trevallion, Steele & Edwards, 1969).

Following work in 1968 on the invertebrates, particularly bivalve species (see *e.g.*

¹ Present address: The Dunstaffnage Marine Research Laboratory, Oban, Argyll, Scotland.

Ansell & Trevallion, 1969), a visit to India was made by the first two authors from January to March 1969 and a research programme carried through on the local species of flatfish. Some results on the effects of temperature on oxygen uptake have already been published (Edwards *et al.*, 1970), showing that the response of temperate and tropical flatfish to temperature change is similar, except that the tropical species show a plateau of temperature-independence in the upper part of the range of temperature tolerance, *i.e.*, 30–37.5 °C. In the zone of overlap of temperature tolerance from 15–25 °C, both types showed Q_{10} values of about 2.6.

The main part of the investigation is described below and comprises of field work in which the environment, growth rate, feeding behaviour, including the organisms eaten and diel rhythms were investigated and experimental work including the effect of size and temperature on oxygen uptake, the feeding rate, food conversion rate, metabolic level, digestion efficiency, analyses of protein, lipid, carbohydrate and ash, as well as some starvation experiments.

TABLE I
Principal species encountered.

Family	Species	Length range used (cm)
Cynoglossidae	<i>Cynoglossus bilineatus</i> (Lacépède)	8.8–37.2
	<i>C. brevis</i> (Gunther)	7.7–15.1
	<i>C. cynoglossus</i> (Hamilton)	5.6–10.5
	<i>C. lida</i> (Day)	8.2–17.0
	<i>C. puncticeps</i> (Richardson)	7.5–16.8
Soleidae	<i>Brachirus orientalis</i> (Bloch)	14.5–20.5
	<i>Synaptura commersoni</i> (Swainson)	9.2–20.6
	and <i>albomaculata</i> (Day)	

The principal species investigated and length range available are shown in Table I (*q.v.*, for taxonomic authorities).

FIELD WORK

METHODS

Two sampling areas were chosen. The more important was about one mile west of the entrance to Cochin harbour to the north side of the navigation channel. Hauls of 20–30 min duration were made there, usually twice per week, from the motor boat *Neendakara* with a 4-m beam trawl. At Sherthallai, a sandy beach 20 miles south of Cochin had been used by the investigators in 1968. Here, small flatfish, mainly *Cynoglossus cynoglossus*, were taken in commercial beach seines. The nets were usually hauled from at least half a mile offshore over a period of 1½–2 h. Samples were taken weekly or fortnightly.

Fish were measured in the laboratory to the nearest mm from the snout to the end of the longest caudal fin ray (total length). The wet weight was determined after blotting to remove excess moisture, and the dry weight after drying to constant weight in an oven at about 50 °C (requiring two days in small specimens, three days in larger ones). Where stomach contents were to be examined the fish were preserved in 4 % formalin and formalin injected into the body cavity.

In the 24-h sequence of hauls made in order to investigate the possibility of a diel rhythm of feeding, samples were taken every 3 to 4 h by both day and night. The fish were measured on board and then fixed in formalin after killing in strong MS222. Light intensity readings in metre-candles (mc) were taken at the surface and on the sea bed by means of a battery operated photometer (Craig & Lawrie, 1962) with a broad spectral response between 475 and 525 nm and a rapid fall-off in the red.

RESULTS

The environment

Because there was no research boat at Sherthallai it was difficult to compare the conditions with those at Cochin. The beach at Sherthallai appeared to be sandy and gently shelving in the sublittoral but about 200 m from the shore the bottom became muddy. The sea was calm in the pre-monsoon period and the temperature remained ~29 °C. The main species caught at Sherthallai was *Cynoglossus cynoglossus*. Off Cochin, the water was much more turbid due to the outflow from the backwater system and the operations of a dredger further offshore. The hauls were made mainly in depths of 4–8 m. The usual number of fish taken was ~30 in a 20-min haul. In the shallower sandy areas near the sand banks to the side of the navigation channel, *C. cynoglossus* was more abundant. In somewhat deeper water all the other species were taken in sandy mud or in thick muddy areas. The larger individuals were taken in the deepest water adjacent to the channel; there was also a tendency for larger individuals to be caught at night. The main invertebrate species taken were a large crab, *Neptunus pelagicus* L., shrimps and, in the mud, heavy concentrations of a tubicolous polychaete *Diopatra neopolitana* Delle Chiaje. Light readings with the photometer showed that the depth at which the light intensity was 1 % of the surface value ranged from 3–5.8 m; Qasim, Battathiri & Abidi (1968) have reported similar values for the backwaters around Cochin. At times the surface tidal current reached 2 kt while the surface water temperature ranged from 28.5–29.5 °C.

Growth

The total length–wet weight–dry weight relationships are given in Fig. 1. The regressions of weight (W ; g) on length (L ; cm) were calculated after logarithmic transformation and are shown in Table II which gives the values of K and b in the equation $W = KL^b$.

In an attempt to measure the natural growth rate, length distributions were plotted for consecutive samples of the four species taken in greatest abundance. The resulting

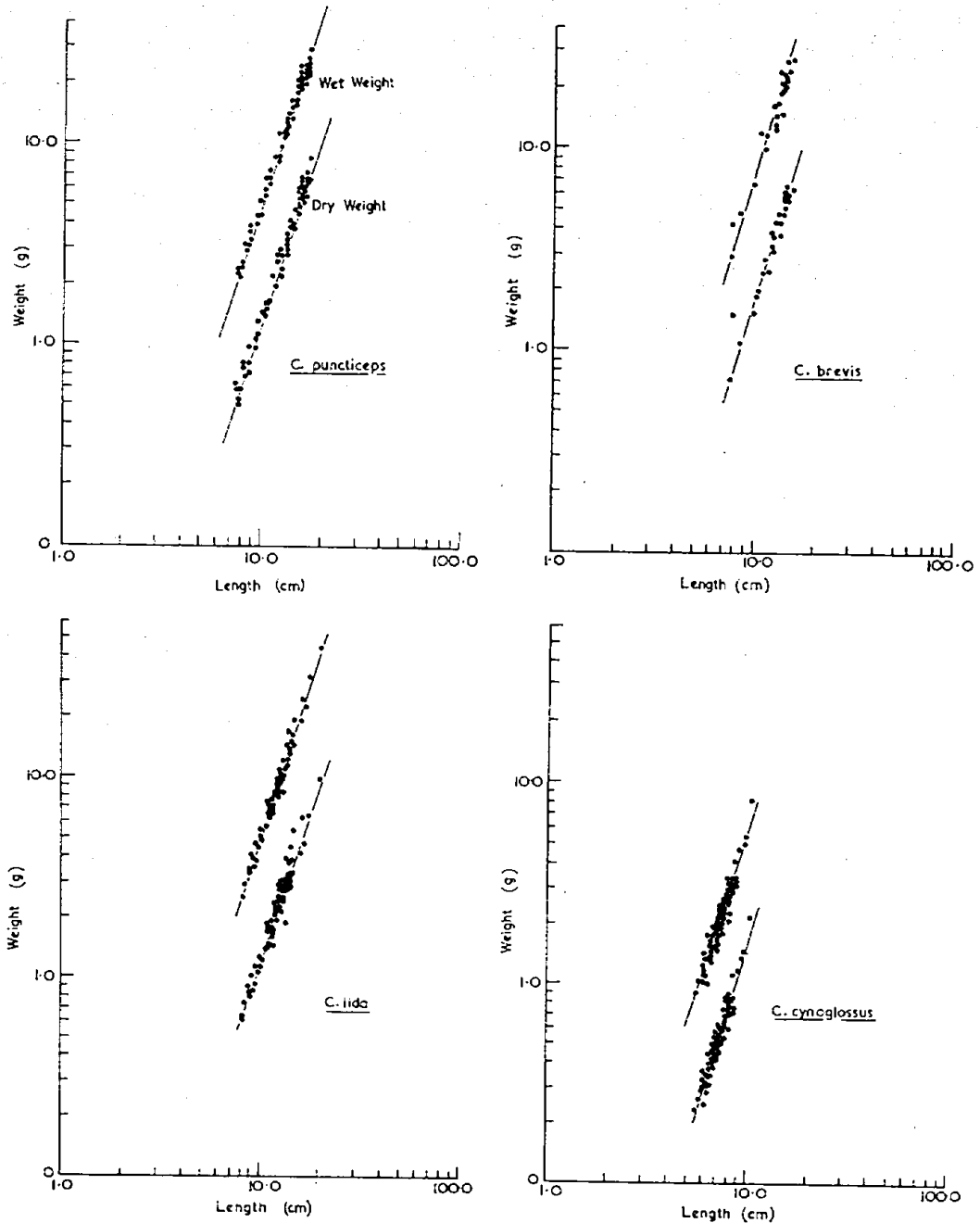


Fig. 1. Length/wet weight and dry weight relationship of four species of *Cynoglossus*.

histograms with the size of the sample are shown in Fig. 2. It may be seen that the sample sizes were small (other samples below ten individuals are not shown), except for *C. cynoglossus* (from the commercial seine), due to the poor catches from the beam trawl. The mean lengths of fish above and below 11 cm are given in an appendix (examination of the data having indicated that this size gave the best separation

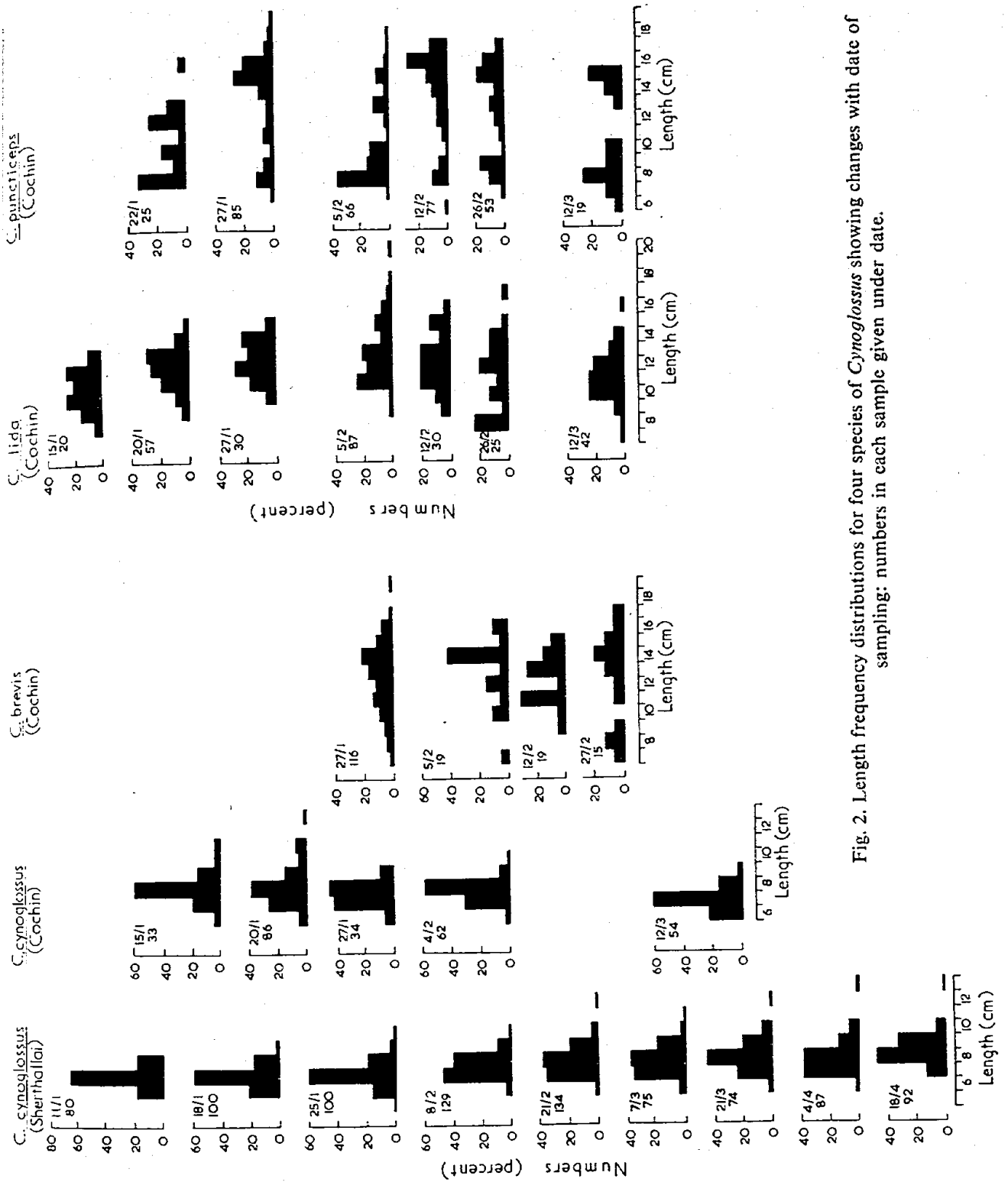


Fig. 2. Length frequency distributions for four species of *Cynoglossus* showing changes with date of sampling: numbers in each sample given under date.

TABLE II

Total length (L)—wet weight (W_w)—dry weight (W_d) relationships with standard error of the exponent b in parentheses.

Species	Wet weight (g)	Dry weight (g)	Number of observations	
			Wet weight	Dry weight
<i>Cynoglossus brevis</i>	$W_w = 0.005 L^{3.156} (\pm 0.091)$	$W_d = 0.001 L^{3.175} (\pm 0.093)$	27	27
<i>C. cynoglossus</i>	$W_w = 0.004 L^{3.155} (\pm 0.074)$	$W_d = 0.001 L^{3.245} (\pm 0.071)$	139	139
<i>C. lida</i>	$W_w = 0.004 L^{3.096} (\pm 0.057)$	$W_d = 0.001 L^{3.070} (\pm 0.079)$	74	74
<i>C. puncticeps</i>	$W_w = 0.004 L^{3.161} (\pm 0.028)$	$W_d = 0.001 L^{3.264} (\pm 0.049)$	102	82

between 0- and 1-group fish). There are no signs of a steady increase in size; presumably this was due to either an irregular recruitment of small fish or an emigration of older fish from the area. Growth may prevent escape through the meshes and influence the results. It is highly unlikely that a fishing mortality, at least off Cochin, affected the apparent population growth. In some cases the data seem adequate for a rough estimate of the growth rate of a particular year-class from samples taken close together in time; the results are given in Table III.

TABLE III

Estimates of growth rate in the sea.

Species	Approx. initial length (mm)	Length increase (mm/week)	Equivalent wet weight increase (g/week)
<i>Cynoglossus cynoglossus</i>	70	1.9	0.17
<i>C. lida</i>	130	2.0	0.43
<i>C. puncticeps</i>	150	0.9	0.43

Assuming a uniform growth rate, a value of about 2 mm/week would indicate that *C. cynoglossus* had been spawned in the early summer of 1968 and the *C. lida* well over a year previously. The low growth rate of *C. puncticeps* suggests it is reaching its L_∞ . From the work of Kutty (1967) on the large scaled tongue sole, *C. macrolepidotus*, and extrapolation from the scale values it is evident that this species attains a length at one year old of ~ 16 cm with a subsequent yearly increment of 1 to 3 cm and an L_∞ of 25 to 28 cm according to sex. These results are, however, also based on small numbers.

Feeding

Evidence for a diel rhythm of feeding which would affect total daily food intake was obtained from day and night hauls made about every 3 h. The formalin preserved wet weight of the stomach contents (as a measure of food recently eaten) is plotted

against time in Fig. 3 as a percentage of the total formalin preserved wet weight for each fish. On each graph the time when a visual feeding threshold of light intensity would be reached at dusk and dawn is shown by a vertical arrow. This is the time when the light on the sea bed reached 0.1 mc, considered by Blaxter (1970) to be the best average estimate of a visual feeding threshold in fish generally. Below this light intensity fish might be expected to use senses other than vision to locate their food, since the eye will be in the dark-adapted state.

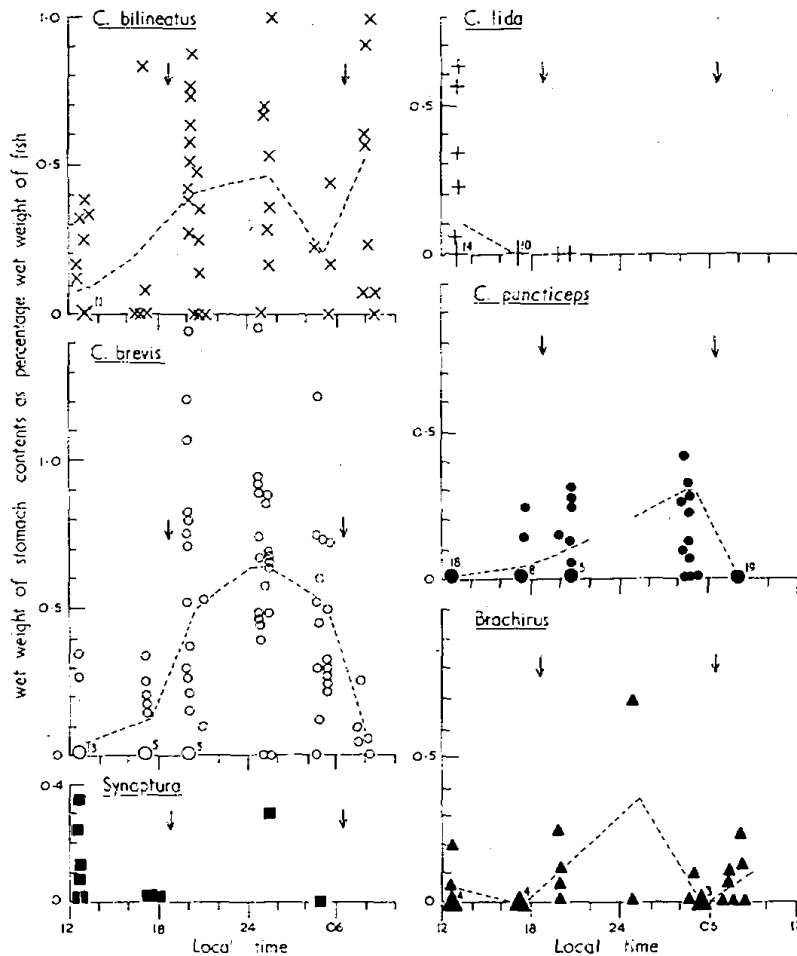


Fig. 3. Wet weight of stomach contents of individuals of six species given as a % of wet body weight for different times of the day and night: where a symbol represents more than one value, the number of fish is given beside it. The dashed line joins the mean for each sampling time. Arrows represent the time when the light intensity reaches the visual threshold on the sea bed in the sampling area.

All the *Cynoglossus* species adequately sampled fed mainly by night. *C. lida* and *Synaptura* showed signs of day-feeding but night-sampling was poor. *Brachirus* fed sparsely by day and night. The threshold light was reached at about 18.45 h at dusk and 06.30 h at dawn (local time), hence it may be assumed that feeding is mediated

in most species by stimuli other than visual. The conclusions regarding each species, the mean wet weight of food taken, and the main food organisms are set out in Table IV.

TABLE IV
Feeding results from 24-h experiment.

Species	Main feeding time	Wet weight of stomach contents/ wet weight of fish (mean values at feeding time) (%)	Animals taken as food
<i>Cynoglossus bilineatus</i>	Night	0.5	<i>Diopatra</i> , <i>Sabellaria</i> , corophids
<i>C. brevis</i>	Night	0.6	<i>Diopatra</i> , <i>Sabellaria</i> , <i>Lumbrinereis</i> , corophids, nemertines.
<i>C. lida</i>	?	0.3	<i>Sabellaria</i> , <i>Lumbrinereis</i> , corophids.
<i>C. puncticeps</i>	Night	0.2	<i>Sabellaria</i> , <i>Diopatra</i> , corophids, <i>Lumbrinereis</i> .
<i>Brachirus</i>	?Night & day	0.1	<i>Sabellaria</i> , nemertines, <i>Ceratonereis</i> .
<i>Synaptura</i>	?	0.15	<i>Sthenelais</i> (polychaete) <i>Lumbrinereis</i> , nemertines.

Other species of temperate water flatfish, have been examined for diel feeding rhythms. Verheijen & De Groot (1967) have summarized the studies on the plaice, *Pleuronectes platessa*, where gut contents, feeding activity and trawl catch data all suggest a diel rhythm with greater feeding activity by day. A reverse situation is found in the common sole, *Solea vulgaris*, which feeds actively at night, when trawl catches are greater (Kruuk, 1963). Furthermore, studies on the sole by De Groot (1969) show that it is mainly a chemoreceptive feeder, with polychaetes and molluscs predominating in the diet. The cynoglossids and possibly the solids in the present investigation show great similarities in feeding time and diet to the temperate sole. They appear to have abundant sensory areas on the ventral surface of the head and around the mouth which could be associated with the location and testing of food. These are especially prominent in *Brachirus*, so that there may be a dual mode of feeding.

LABORATORY WORK

METHODS

Live fish were only available from the beam trawl. Short hauls of about 20 min were used and the cod end of the net opened into a tank of sea water. It was difficult to keep

the water at sea-surface temperature and well aerated without a power supply on board. Transport to the laboratory took place in a rectangular fibre glass tank holding 38l of sea water. A survival of about 50 % could be expected by the subsequent day unless a large number of the crab *Neptunus pelagicus* were taken in the catch, when survival might be as low as 5 to 10 %. The high mortality in such mixed catches may have been due to both the weight and spines of the crabs and possibly to a toxic effect.

The fish were kept in a well-shaded laboratory with open windows, or outside in the shadow of a north-facing wall. The temperature ranged from 24–29 °C outside and from 25–29 °C inside over the experimental period. The maximum fluctuation in any one day never exceeded 2.5 °C and was usually about 1 °C. The main stocks of fish held in the laboratory were, therefore, kept at a mean temperature of 2 °C below that prevailing in the sea. Higher and lower temperatures were obtained by small heating units or a portable cooler and by the use of an air-conditioned room.

Most fish were kept in plastic tubs 36 cm in diameter and 13 cm deep or 45 cm in diameter and 18 cm deep. The usual water depth was 6 to 8 cm. The water was strongly aerated by diaphragm aerating pumps. There was a tendency for the fish, especially if crowded or at a higher temperature, to jump out at night. This necessitated gauze covers to the tubs or the use of an outer larger water bath to catch the fish. The sea water was collected in carboys from the sampling area and usually about a half of the water in each tub was changed per day.

*Respiration experiments*¹

The procedures used are described in detail by Edwards, Finlayson & Steele (1969). Respiratory rate was measured in a closed-circuit respirometer incorporating a Beckman oxygen electrode. Groups of fish closely matched for size were used and an experiment normally lasted up to 1 h. The respirometer was filled with air-saturated water and the fish allowed a period of acclimation before measurements were made. All fish used in the experiments had spent a period of 2 to 4 days in captivity at a temperature averaging 1 °C below sea temperature. Since these flatfish were reluctant to feed in captivity and since standard respiratory rate is known to be depressed by starvation (Beamish, 1964) it was considered unwise to use fish which had been starving for more than about 4 days: however, in the low temperature respiration experiments the fish did not feed. Care was taken to ensure that the oxygen level of the water in the respirometer did not fall below a critical level, since Hughes (1964) has shown that standard respiratory rate is increasingly depressed after the oxygen content of the water has fallen below a certain level. For *Cynoglossus* this level was found to be about 50 % of the oxygen content of water saturated with air; below this, asphyxiation rapidly occurred. The sea water used had a salinity of about 32 ‰ and an oxygen content of 6.0 mg/l at 28 °C as determined by the Winkler method.

¹ Oxygen uptake was measured and the values obtained are assumed to represent respiratory activity so the term respiration will be used when convenient.

Feeding physiology and biochemical composition

Attempts were made to feed the fish on a variety of food including shrimp, mussel, fish muscle, live gammarids, live adult *Artemia salina* (from a culture set up from eggs), and live tubicolous polychaetes. Eventually some fish were established on the live polychaetes and used for subsequent feeding and growth studies. These fish were kept individually in the smaller tubs with plastic netting covers and held in large water baths outside the laboratory (*i.e.* with a natural day-night cycle). The covers were needed both to retain the fish and to exclude red ants, mantis, and debris dropping from overhead trees. The fish were given daily weighed live meals of the tubicolous polychaete *Diopatra neopolitana* (removed from its tube) and the faecal matter collected. The fish were weighed under anaesthetic (MS222) at intervals of 4 to 11 days.

A few behaviour experiments were made to see whether the fish could eat moving food in the dark. Established feeders were held in the dark or light for periods of 5 to 17 h in tubs with known numbers of live *Diopatra* or live adult *Artemia* as food. Uneaten organisms were collected and counted at the end of each experiment.

Analyses were made of fish flesh, food, and faeces – protein by micro-Kjeldahl nitrogen, carbohydrate by the anthrone reaction, lipid after chloroform/methanol extraction, and ash after heating to 600 °C in a muffle furnace. All analyses were done in Aberdeen on dried material transported back in aluminium foil; for further details see Edwards, Finlayson & Steele (1969).

Starvation experiments

The fish were held at various temperatures without food and weighed, under MS222 anaesthesia, weekly. Some individuals were kept for at least three weeks in this way.

RESULTS

Respiration experiments

Standard oxygen consumption. This is defined as the oxygen consumption in the absence of activity, and is particularly easy to measure for flatfish which remain quiescent in respirometers. The results for the different species used are given in Fig. 4. The data may be put in the form $Q_{O_2} = aW^b$ as proposed by Winberg (1956), where Q_{O_2} is given in mg O₂ consumed/h, W is the live weight in g, and a and b are constants. There was very little difference between the results for the four species of *Cynoglossus* and they were pooled for analysis. Similarly *Brachirus* and *Synaptura* had comparable respiratory rates. The constants of the regression lines fitted to these data have the following values at 28 °C,

	a	b
<i>Cynoglossus</i> spp.	0.372	0.734
<i>Brachirus</i> and <i>Synaptura</i>	0.362	0.682

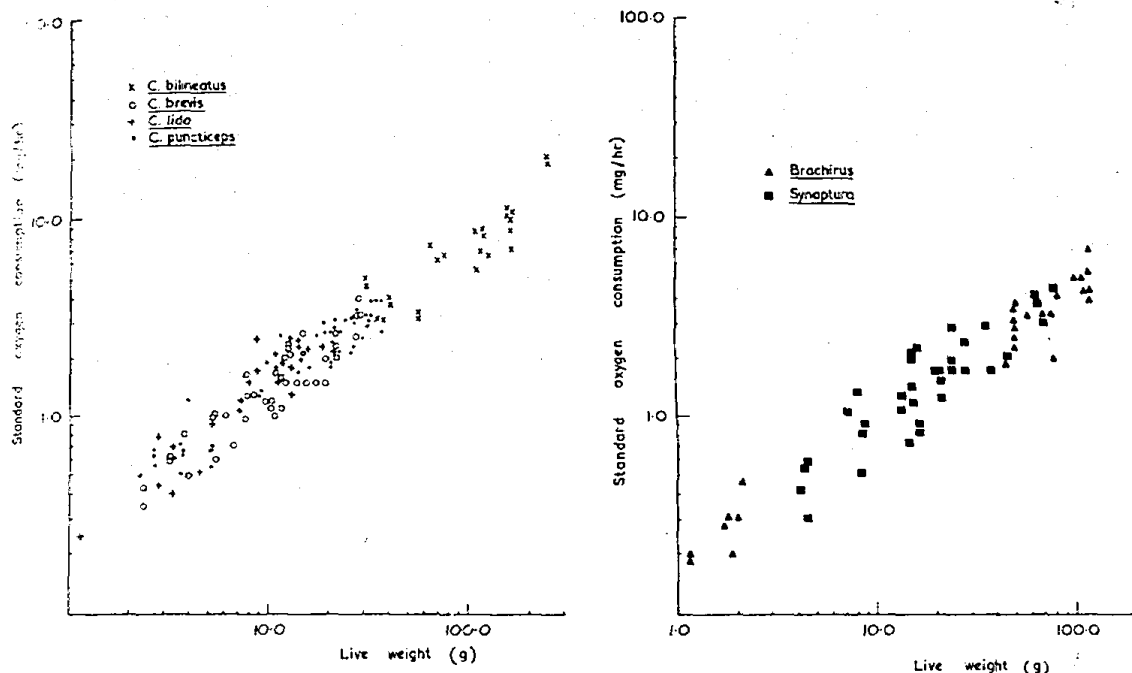


Fig. 4. Standard oxygen consumption in relation to live weight for *Cynoglossus* species, and *Brachirus* and *Synaptura*, all at 28 °C.

Effect of temperature on standard oxygen consumption. Groups of up to six *Cynoglossus* were kept in containers in a water bath and the temperature was progressively lowered from about 35 to 15 °C. It was necessary to complete the experiments within about two weeks, since the fish were not feeding and began to die after this time. The standard oxygen consumption was measured at intervals of 2.5 or 5 °C. All the results

TABLE V

Relationship of standard oxygen consumption in mg/kg/h to temperature in *Cynoglossus* spp.

Species	Mean weight (g)	Q ₁₀	Temperature, °C								
			15.0	20.0	22.5	25.0	27.5	30.0	32.5	35.0	37.5
<i>Cynoglossus brevis</i>	6.7	2.4	60	100	—	140	—	240	—	240	240
<i>C. brevis</i>	7.9	3.6	—	—	—	110	140	200	—	200	—
<i>C. brevis</i>	13.1	1.9	80	110	—	190	—	230	—	230	—
<i>C. puncticeps</i>	15.2	2.3	60	80	—	90	—	210	—	210	—
<i>C. puncticeps</i>	10.5	2.8	—	70	—	170	—	200	—	210	—
<i>C. puncticeps</i>	17.1	2.4	70	80	110	170	190	—	190	—	—
<i>C. puncticeps</i>	20.3	2.9	30	40	—	90	—	130	—	130	—
<i>C. puncticeps</i>	19.2	2.2	—	60	—	120	—	130	—	140	—
<i>C. puncticeps</i>	21.4	3.0	—	—	—	80	—	120	—	140	—
<i>C. puncticeps</i>	25.9	3.2	—	—	—	50	—	80	—	—	80
<i>C. puncticeps</i>	32.9	2.2	40	50	50	90	130	—	140	—	—

are given in Table V. Some of the results obtained are illustrated in Fig. 5, which shows that below 30 °C the standard oxygen consumption is dependent on temperature, but above 30 °C it becomes independent. Job (1969) reported a similar result for *Tilapia mossambica*. The mean Q_{10} for all fish over the temperature range 15 to 30 °C is 2.6 (Edwards *et al.*, 1970); temperatures above 37.5 °C or below 15.0 °C resulted in

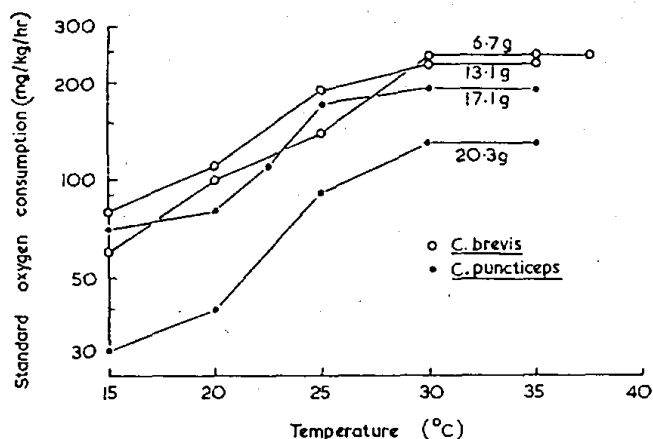


Fig. 5. Standard oxygen consumption of two *Cynoglossus* species at different temperatures.

rapidly increased mortalities. In its natural habitat in the Arabian Sea it is unlikely that *Cynoglossus* experiences temperatures differing much from 28–30 °C throughout the whole year. Experiments designed to test the rate of temperature acclimation of *Cynoglossus* when the temperature was lowered by intervals of 5 °C indicated that at temperatures below 30 °C it took at least 20 h for the respiratory rate to be reduced to its new level, but that most of the change occurred within 10 h.

Feeding physiology and biochemical composition

When fed on live *Diopatra* and *Artemia* it was found that *Cynoglossus brevis*, *C. lida*, and *C. puncticeps* would feed in the dark and light (Table VI). Assuming that the food organisms were equally available to the predatory activities of the fish there was a tendency for somewhat greater feeding activity by night; clearly they can take food in the absence of visual stimuli.

Analysis of protein, carbohydrate, and lipid content were made on all species freshly caught from the sea, to estimate the caloric content of the fish at the start of the feeding experiments. The results of these analyses are given in Table VII. Using the accepted caloric equivalent of 5.7 kcal/g dry weight for protein, 9.5 for lipid, and 4.2 for carbohydrate it was calculated that the average caloric content of freshly caught *Cynoglossus* was 4.95 kcal/g dry weight. For *Diopatra* it was 5.28 kcal/g dry weight and the faecal material produced was 1.38 kcal/g dry weight. On average the faecal material produced by the fish formed 19% of the dry weight of the food but only 4.96% of the energy content of the food, because of the high ash content of the

TABLE VI

Percentage food taken by different species *Cynoglossus* in the dark and light (10 or 15 food organisms offered per fish)

Species	Dark (D) or light (L)	Duration (h)	% <i>Diopatra</i> eaten	% <i>Artemia</i> eaten
<i>Cynoglossus bilineatus</i>	D	17	—	47
<i>C. brevis</i>	L	5	—	0, 13, 53, 80
	D	5	—	40, 100, 100
	L	7	—	33
	D	7	100	—
	D	17	100	100
<i>C. lida</i>	L	5	—	0, 53
	D	5	—	20, 73, 100
	L	5	—	93, 100
<i>C. puncticeps</i>	D	5	—	100, 100
	L	7	—	87
	D	17	40, 50	100

faeces. At the end of the particular feeding experiment in which the fish were sampled and the composition determined, the average caloric content of the fish was 4.70 kcal/g dry weight. The reduction from 4.95 kcal/g dry weight at the start was due to the fact that the fish were losing weight at the end of the experiment. Growth normally continued during the first and second week following introduction of the fish to the experimental conditions but thereafter weight loss occurred, although the fish were still feeding. After starvation experiments of about two weeks in the laboratory, the caloric content of *Cynoglossus* was reduced to about 4.65 kcal/g dry weight.

The results of the feeding experiments are given in Fig. 6, where the change of weight per week is plotted against food intake. The units used are in live weights, and although there is a wide scatter of points in the figure, possibly due to the inclusion of

TABLE VII

Biochemical analyses: (mg/100 mg dry wt.)

	Fresh				Starved			
	Protein	Carbo- hydrate	Lipid	Ash	Protein	Carbo- hydrate	Lipid	Ash
<i>Cynoglossus bilineatus</i>	77.45	0.47	5.21	16.77	77.99	0.47	5.43	15.51
<i>C. brevis</i>	69.65	0.46	6.54	23.35	73.41	0.61	4.38	21.57
<i>C. cynoglossus</i>	70.48	0.56	5.65	23.33	—	—	—	—
<i>C. lida</i>	72.30	0.57	9.42	17.73	67.05	0.81	13.28	18.82
<i>C. puncticeps</i>	77.98	0.54	6.08	15.43	63.55	0.35	2.76	33.33
<i>Brachirus</i>	80.64	0.68	5.13	13.58	79.18	0.65	2.95	17.24
<i>Synaptura</i>	82.31	0.69	3.22	13.79	72.84	0.55	5.20	21.43
<i>Diopatra neopolitana</i>	69.04	3.43	12.72	14.36	—	—	—	—
<i>Cynoglossus faeces</i>	14.50	0.63	3.11	81.78	—	—	—	—

fish of different sizes (3 to 29 g), there is an indication that about 25 % of the body weight is needed as food to maintain the weight constant over a period of a week. In terms of calories this is 23 % of the total caloric content of the fish, since the mean water content of *Diopatra* (79 %) is higher than that of *Cynoglossus* (75 %). The mean efficiencies of conversion of assimilated food into growth were between 11 and 12 %,

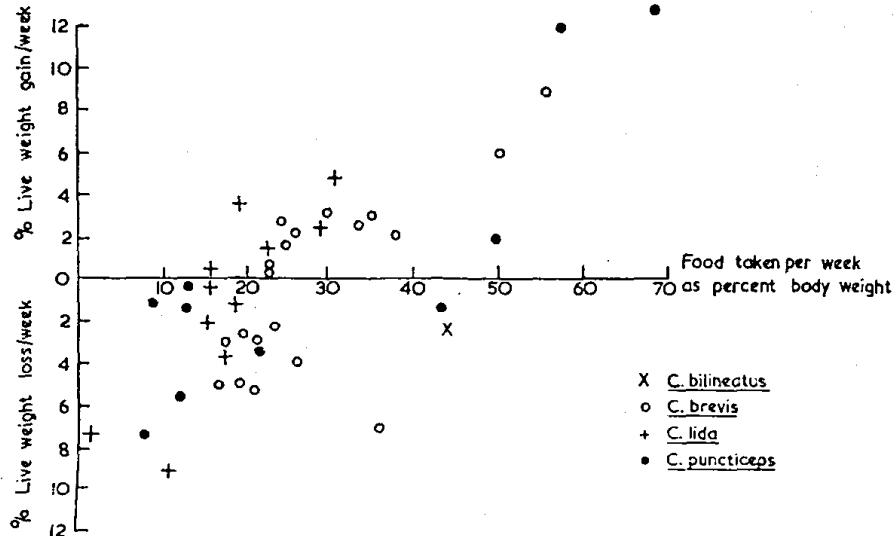


Fig. 6. Changes in live weight of *Cynoglossus*/week related to food taken/week as a % of the live weight.

and the highest observed was 23.8 % for a fish of 3.84 g. These efficiencies are considered to be low for juvenile fish, and may reflect the poor adaptation shown by *Cynoglossus* to experimental conditions; Pandian (1970) observed efficiencies as high as 50 % for temperate juvenile *Limanda limanda*.

To convert food material used for metabolism into oxygen consumed during respiration, an equivalent of 4.8 kcal of heat produced during the respiration of 1 g dry weight of food material was used (see Winberg, 1956; Paloheimo & Dickie, 1966); this would require the consumption of 1.420 g of oxygen (1 l at S.T.P.) on the basis of the usually accepted conversion. Brody (1945) has shown that this value changes very little with a variety of respiratory substrates.

In the analysis of the feeding experiment, the energy laid down as growth by the fish was subtracted from the total assimilated energy to give that used for metabolism (*M*). In the cases where a fish lost weight, the energy of the weight loss was added to that assimilated from the food to give the metabolic requirement. A loss of assimilated energy will occur through soluble nitrogenous excretion by the fish, particularly if urea is the principal component, but according to Winberg (1956) this is unlikely to exceed 7 % of the assimilated energy from the food.

In Table VIII the complete results of the feeding experiment are given as cal/h both for metabolism and rate of food assimilation. The difference between these quantities

TABLE VIII

Rate of metabolism and food assimilation in *Cynoglossus* spp. fed to excess on *Diopatra neopolitana* at 28 °C: (W_0 , live weight at the first weighing; W_1 , live weight after the number of days given in the column marked 'duration').

Species	Live W_0 (g)	Weight, W_1 (g)	Duration (days)	Metabolism (cal/h)	Food assimilation (cal/h)	
<i>C. brevis</i>	6.38	6.20	5	12.35	10.50	
	10.07	9.71	5	14.53	10.81	
	7.95	7.78	5	12.53	10.78	
	4.70	4.80	6	9.08	9.94	
	4.80	5.04	6	13.07	15.14	
	3.79	3.62	6	6.47	5.01	
	3.62	3.89	6	10.45	12.77	
	6.57	6.39	6	8.73	7.18	
	6.39	6.55	6	10.70	12.08	
	5.85	5.71	6	8.29	7.09	
	5.71	5.68	6	14.96	12.39	
	5.28	4.91	7	14.50	11.79	
	5.87	5.83	7	11.01	10.72	
	9.78	9.28	7	15.75	12.07	
	9.28	9.06	7	15.19	13.57	
	8.75	8.78	7	12.57	12.79	
	8.78	8.92	7	12.74	13.77	
	5.04	5.28	11	9.86	10.98	
	5.68	5.87	11	12.57	13.47	
	9.71	9.78	11	13.61	13.94	
8.45	8.75	11	12.26	13.67		
<i>C. puncticeps</i>	3.18	3.15	4	9.04	8.66	
	9.10	8.78	7	14.78	12.42	
	20.08	19.86	7	13.15	11.53	
	3.77	3.84	7	11.29	11.80	
	3.34	4.29	7	10.57	13.88	
	28.67	28.87	7	13.21	14.69	
	19.49	19.46	7	16.69	16.14	
	19.46	18.37	7	23.07	15.04	
	8.75	9.10	11	11.74	13.38	
	3.15	3.77	11	10.66	13.55	
	19.92	19.49	11	17.95	16.09	
	<i>C. lida</i>	10.74	10.74	5	10.84	10.84
		6.40	6.53	6	10.50	11.62
6.53		6.79	6	10.36	12.59	
10.29		10.59	6	10.17	12.75	
10.59		10.71	6	14.08	15.12	
10.69		10.56	7	13.67	12.72	
6.57		6.08	7	4.29	0.69	
10.39		10.00	7	14.25	11.38	
7.63		6.57	11	5.80	5.31	
10.74		10.39	11	12.15	10.50	
10.71	10.69	11	10.81	10.63		
<i>C. bilineatus</i>	3.93	3.86	5	11.61	10.88	

is the calories utilized in growth. In order to compare the effect of the rate of food assimilation on metabolism for all fish in the experiment the values given in Table VIII were divided by Q , or the standard respiratory rate converted to cal/h. The intercept value a (see p. 288), of 0.372 mg O_2 /h now becomes 1.258 cal/h, 4.8 kcal being equivalent to the consumption of 1420 mg of oxygen. The figure so obtained indicates the number of times that the metabolic rate has been raised above standard at 28 °C, and also the number of times the rate of food assimilation exceeds the standard metabolic requirement. The results are shown in Fig. 7. The growing fish can be seen to

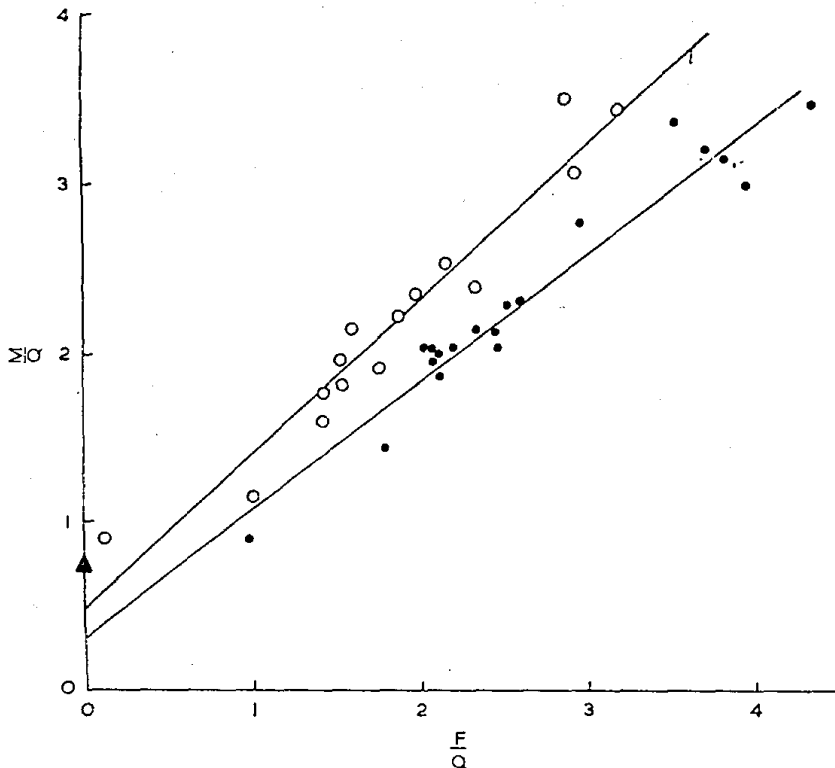


Fig. 7. *Cynoglossus* spp.: relationship of the metabolic rate (M) as cal/g dry wt/h divided by the measured standard oxygen consumption (Q) converted to cal/g/dry wt/h (y) and the rate of food assimilation (F) divided by the standard oxygen consumption (Q) as cal/g dry wt/h (x). \circ fish feeding but losing weight; \bullet fish increasing in weight; \blacktriangle a mean value for 39 starved fish ($F = 0$). The regression equation for the lower line is $y = 0.3173 + 0.7571x$ and for the upper line $y = 0.4578 + 0.9195x$.

have a lower metabolic rate than those losing weight at a particular feeding level, but only data for fish during their first week of weight loss are shown in the figure, since after this the results become very scattered towards higher levels of M/Q . Similar results have been obtained for plaice (Edwards, Finlayson & Steele, 1969). The explanation may lie in a greater activity of feeding fish which are losing weight though it was not possible to monitor this in the experiments. Included in the figure is a value for $F = 0$ from the starvation experiments (39 fish), which is seen to be slightly higher

than the extrapolated lines, and gives a respiratory rate for starved fish of about 80 % of the measured standard.

Starvation experiments

The results of the starvation experiments at room temperature (about 28 °C) are shown in Fig. 8. As expected there is a tendency for a higher percentage loss of weight

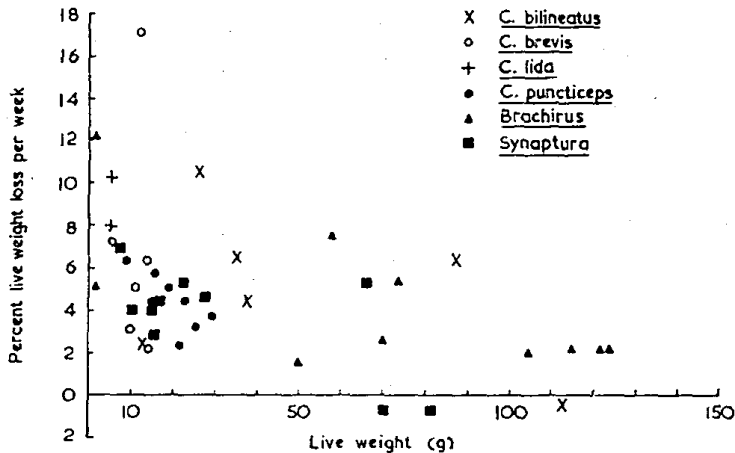


Fig. 8. Percentage loss of live weight/week of the different species related to the live weight at the first weighing.

with smaller fish which have a higher metabolic rate than larger fish. The loss in dry weight of each fish was converted into mg O_2 consumed/h using a caloric conversion of 4.8 kcal/g dry wt. All species used were considered together and the results plotted semi-logarithmically on the assumption that $Q_{O_2} = aW^b$. The intercept value, a , was 0.296 and the value of the exponent b was 0.683. Since approximately half the fish used were *Cynoglossus* and the others *Brachirus* and *Synaptura*, these values must be taken as a mean. They do, however, give support to the oxygen measurements and suggest that the respiratory rate of starved fish is about 80 % of that of freshly caught fish by comparison of the values of the intercept, a .

The data on rate of loss of weight during starvation at 22, 28 and 32 °C are shown in Fig. 9; the loss is highest at 32 °C, as expected. Three groups of *Cynoglossus puncticeps* were selected, each containing 4 fish of between 20 and 26 g mean live weight –

TABLE IX
Metabolic rate of *Cynoglossus puncticeps* starved at different temperatures.

Initial mean live wt., g	Temperature °C	Metabolic rate from wt loss, cal/h	Metabolic rate from Q_{O_2} , cal/h	Duration days
25.85	32	19.80	20.68	7
23.72	28	7.92	12.78	6
21.12	22	5.44	7.52	6

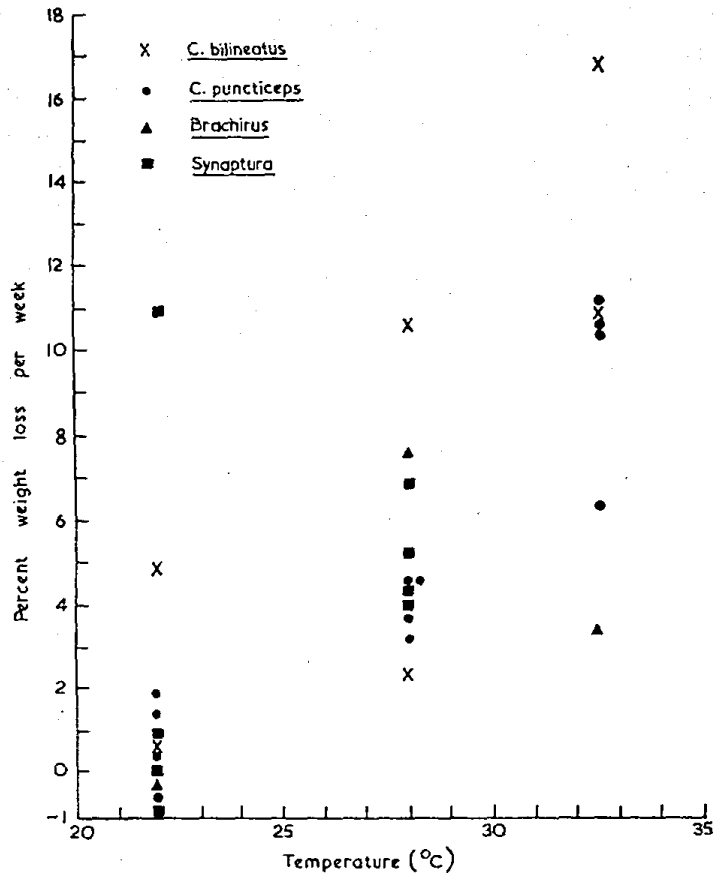


Fig. 9. Percentage loss of live weight/week related to temperature: the same fish were used (where they survived) at all three temperatures and no account is taken of absolute weight.

one from each experimental temperature. Their loss in weight was converted into calories and compared with that predicted from measurements of standard oxygen consumption (Q) using a Q_{10} correction of 2.6. The results are shown in Table IX. The agreement between the two estimates is fairly good, and shows that starvation has depressed the metabolic rate at each temperature.

DISCUSSION

The standard oxygen consumption of *Cynoglossus* at 28 °C is very similar to that of young plaice (*Pleuronectes platessa*) and common dabs (*Limanda limanda*) at 10 °C (Edwards, Finlayson & Steele, 1969). A comparison of the intercept values, a , shows 0.372 mg for *Cynoglossus*, 0.362 mg for *Brachirus* and *Synaptura*, 0.304 mg for *Pleuronectes*, and 0.449 mg for *Limanda*, though this latter was probably routine respiration. It was difficult to find other values for a for tropical fish in the literature, but interpolation in Fig. 1 (p. 72) of Scholander *et al.* (1953) yields a value of 0.43 mg of oxygen at 1 g live weight. These authors used different species of fish to obtain a

size range, but their values were about 1.2 times those quoted here for *Cynoglossus*. The exponent b for *Cynoglossus* and *Brachirus* and *Synaptura* of 0.734 and 0.682, respectively, compare with values for *Pleuronectes* and *Limanda* of 0.721 and 0.666 (Edwards *et al.*, 1969). These are slightly lower than the value of 0.8 proposed by Winberg (1956) and supported by Paloheimo & Dickie (1966). Scholander *et al.* (1953) quoted a value of 0.85 for tropical fish, but this was a composite value for several species.

Compensation of respiratory rate for fish living at different latitudes and hence water temperatures has been demonstrated by Scholander *et al.* (1953); at the temperatures of their respective environments the respiratory rates of arctic fish were two to three times lower than those of tropical fish, but on the basis of Q_{10} measurements this should have been seven to eight times. In much of the previous literature on tropical fish there is little information on activity levels during respiratory measurements, and measurements of standard respiratory rate are few. Kutty (1969) measured the respiratory rate of the mullet, *Liza macrolepis*, at 29 °C and at different swimming speeds, and extrapolated his measurements to zero swimming speed. In this way an estimate of standard oxygen consumption was obtained, and a figure of 50 mg O₂ kg/h was obtained for an 8.3 g fish. It is of interest to compare the measurements of Kutty (1969) with those of Tytler (1969). The latter author used the same method to determine the standard oxygen consumption of the haddock (*Melanogrammus aeglefinus*) at 10 °C and obtained estimates of 51–64 mg O₂ kg/h for fish of about 156 g weight. The similarity between these results despite the temperature and size difference is further evidence for temperature compensation, and also suggests a need for a more critical appraisal of activity level when comparing the respiration of fish from different latitudes.

The maintenance food values of 25 % of the live body weight/week for *Cynoglossus* agree well with those found for temperate fish (Birkett, 1969; Edwards, Finlayson & Steele, 1969): however, the value of 11–21 % for conversion efficiency for growing *Cynoglossus* is low compared with results for other fish (Gerking, 1955; Pandian, 1967, 1970; Birkett, 1969) where efficiencies of up to 50 % have been observed for juvenile fish. The poor adaptation shown by *Cynoglossus* to confinement in the laboratory, *i.e.*, its reluctance to feed and high excitability, may explain these low conversion efficiencies.

A comparison may be made between the natural growth rate of *Cynoglossus macrolepidotus* observed by Kutty (1967) and the growth of the North Sea sole, *Solea vulgaris*, observed by Bückmann (1943). The former attains 16 cm length at the end of the first year, 19 cm in the second, 21 cm in the third and 25 to 28 cm in the seventh year. The latter attains about 10 cm in the first year, 19 cm in the second, 25 cm in the third, and about 35 cm in the seventh year. The initial growth in *Cynoglossus* is greater than that of *Solea* but a marked reduction in growth rate occurs in the second year of *Cynoglossus* when spawning commences. Thereafter *Solea* has the faster growth rate since spawning occurs later in life, at about 3 to 4 years of age.

From the evidence presented in this paper and in the foregoing discussion it would not seem at all certain that the standard oxygen consumption of tropical fish is significantly higher than that of temperate counterparts at their normal environmental temperatures. The low oxygen-carrying capacity of tropical marine waters as a result of the high temperature must require a larger ventilation volume to be passed over the gills than is necessary for temperate fish, and an upper limit to the active respiration rate may be set by this. Indeed, the 'scope for activity' (Fry & Hart, 1948) may well be limited by the respiratory shortcomings of the fish. Additionally, limited availability of food in the habitat coupled with the rate of food intake may restrict the metabolic level to that range set by the scope for activity.

What may be deduced of the food required under natural conditions? This was estimated by the method of Winberg (1956) followed by Mann (1965). The calculation consists of doubling the metabolic requirement of the fish measured under standard conditions to give an estimate of the 'natural' metabolic rate. A correction is applied for energy loss in the excretory products and the energy required for growth is added to the total metabolic requirement. *Cynoglossus cynoglossus* attains a length of ~10 cm or 5.4 g live weight during its first year of life. The food required to produce this growth is ~25.6 g live weight (5.6 g dry weight) if the polychaete *Diopatra* is the food source. This implies a conversion rate of 20 % under natural conditions. (It should be noted that conversion rates of only 11–12 % were obtained in the feeding experiments, but it is considered that this was a response to the conditions of captivity.)

In conclusion it may be said that the results on the physiology of *Cynoglossus* (p. 288) are in reasonable agreement with those of temperate flatfish, indicating a marked compensation for temperature in the tropical fish. Such physiological differences as the earlier maturation of *Cynoglossus*, together with a longer spawning season, and also systematic differences such as more prolific speciation are accepted distinctions between temperate and tropical fish. A more detailed study of the blood of *Cynoglossus*, *e.g.*, haemoglobin content, haematocrit values, and cardiac rate, together with information on ventilation volume, efficiency of oxygen uptake by the gills, and the structure and area of the respiratory surfaces would further serve to amplify this work.

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APPENDIX

Mean total length in cm of *Cynoglossus* in different samples (size of sample in brackets).

Date	<i>C. cynoglossus</i>		<i>C. brevis</i>		<i>C. lida</i>		<i>C. puncticeps</i>	
	Sherthallai	Cochin	< 11	> 11	< 11	> 11	< 11	> 11
11/1	6.93 (80)							
14-15/1		7.90 (33)			9.46 (9)	11.75 (11)		
18/1	6.93 (100)							
20/1		8.10 (86)			10.23 (18)	12.79 (39)		
22/1			9.50 (3)	12.83 (4)			8.77 (15)	12.84 (10)
25/1	7.05 (100)							
27/1		7.50 (34)	9.34 (26)	13.51 (90)	10.1 (1)	12.64 (29)	8.19 (17)	14.71 (68)
4-6/2		7.60 (62)	8.90 (3)	13.74 (16)	10.00 (8)	13.20 (79)	8.58 (44)	14.19 (22)
8/2	7.45 (129)							
11-13/2			9.87 (3)	12.81 (16)	10.06 (8)	13.15 (22)	8.78 (18)	15.00 (59)
21/2	7.87 (134)							
26-27/2			8.40 (5)	14.27 (10)	8.97 (12)	13.21 (13)	8.68 (18)	14.47 (35)
7/3	7.70 (75)							
12/3		6.96 (54)			9.75 (21)	12.39 (21)	8.08 (12)	14.06 (7)
21/3	8.00 (74)							
4/4	7.93 (87)							
18/4	8.34 (92)							