Nutrition of the southern sea garfish *Hyporhamphus melanochir*: gut passage rate and daily consumption of two food types and assimilation of seagrass components*

D. W. Klumpp[1]** and P. D. Nichols[2]

[1] School of Botany and [2] Department of Organic Chemistry, University of Melbourne, Parkville, Victoria 3052, Australia

ABSTRACT: The southern sea garfish *Hyporhamphus melanochir* fed on the seagrass *Heterozostera tasmanica* for 13 h during daylight, ingesting an estimated 3 gut volumes of plant matter, equivalent to 500 kJ d^{-1} kg^{-1} dry wt. No cellulase was detected in garfish digestive tissues, and gut pH was near neutral, but the pharyngeal mill efficiently triturated the seagrass tissue. Seagrass frond was assimilated at an efficiency of 38 % (organic matter), 28 % (energy), 50 % (protein) and 76 % (lipids), these being equivalent to the total components available in seagrass cell contents. Nocturnally emergent crustaceans were preyed upon by garfish over a period of 6 h and were processed at half the rate of seagrass. The daily energy intake, and probably assimilation, from this source was 223 kJ kg^{-1} dry wt. Although the crustaceans consumed were only a third the quantity of seagrass, it was reasoned to be an essential source of protein, and at least as important as seagrass in satisfying the energy requirements of *H. melanochir*.

INTRODUCTION

Living seagrass fronds are considered to be of low nutritional quality in terms of digestibility and nitrogen-to-carbon ratio, when compared with algae or animal foods (Phillips and McRoy, 1980). Certainly only a minor proportion of seagrass production is grazed (Fenchel, 1972; Harrison and Mann, 1975; Ott and Maurer, 1977). Nevertheless, seagrass is a major part of the diet of a variety of animals, including fishes (Randall, 1967; Ogden, 1976), and little is known about the mechanisms of digestion or efficiency of utilization of ingested seagrass in these cases.

Garfish or halfbeaks, of the family Hemirhamphidae, have generally been described as herbivores, feeding mainly on the fronds of zosteracean seagrass (Thompson, 1957, 1959; Talwar, 1962; Collette, 1974). A more complex feeding pattern has emerged for the southern sea garfish *Hyporhamphus melanochir* (Valenciennes) which 'switches' from seagrass fronds during daylight to emergent benthic crustaceans, mainly amphipods, at night (Robertson and Klumpp, 1983). These authors propose that *H. melanochir* feeds preferentially on small crustaceans when these are available in the water column. The digestive system in hemirhamphids consists of a straight tubular alimentary canal without stomach or appendages (Suyehiro, 1942) and the ratio of gut-to-body length is only 0.5 (Robertson and Klumpp, 1983) which is atypical of a herbivore. Seagrass ingested by *H. melanochir* is thoroughly macerated (Robertson and Klumpp, 1983), presumably by the action of pharyngeal teeth that are present in all hemirhamphids.

The present study examines aspects of nutrition in *Hyporhamphus melanochir*, with particular emphasis on the digestion of seagrass and subsequent assimilation of its nutrient components. Measurement of the passage rate for animal and plant material down the gut is used to estimate the ingestion rates for each of these food types. We discuss the relative importance of seagrass and animal food to the nutrition of this fish.
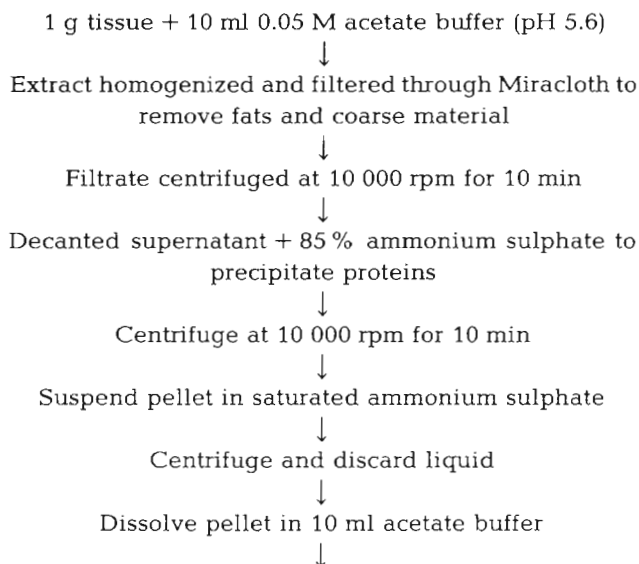
MATERIALS AND METHODS

Collection of samples

Hyporhamphus melanochir tissues and gut contents were obtained from the field at Duck Point in Corner Inlet (S.E. Australia) with methods previously described in a study of the diel feeding habits of this fish (see Robertson and Klumpp, 1983). The diel feeding study in Corner Inlet was made in mid November when water temperature averaged 17 °C. Although garfish are commonly reported as feeding on *Zostera*, it was established that *H. melanochir* in Corner Inlet consumes *Heterozostera tasmanica*.

Robertson and Klumpp (1983) have recorded the distinct and separate nature of ingested seagrass and animal material in the gut of *Hyporhamphus melanochir* at 3 h intervals of the diel feeding cycle. In the present study the rates of movement of these 'food zones' along the simple tubular gut are examined as a convenient measure of gut passage time under natural conditions. Ten fish were examined at each time interval. The number of gut volumes of food consumed per day for both food types is then calculated, and with the known mass of food in the gut, used to estimate the weight of seagrass and crustaceans ingested in a day.

Cellulase enzyme and gut pH analysis

Liver, spleen and alimentary tract tissues and gut contents from garfish freshly caught during the seagrass feeding phase were analyzed for cellulase enzyme activity. These tissues were maintained and the extractions made at 0 to 4 °C. The extraction procedure is summarized below:

1 g tissue + 10 ml 0.05 M acetate buffer (pH 5.6)

↓

Extract homogenized and filtered through Miracloth to remove fats and coarse material

↓

Filtrate centrifuged at 10 000 rpm for 10 min

↓

Decanted supernatant + 85 % ammonium sulphate to precipitate proteins

↓

Centrifuge at 10 000 rpm for 10 min

↓

Suspend pellet in saturated ammonium sulphate

↓

Centrifuge and discard liquid

↓

Dissolve pellet in 10 ml acetate buffer

↓

2.5 ml aliquot desalted on a Sephadex G25 disposable gel filtration column (PD-10)

↓

3.5 ml eluant

↓

+ 2 ml substrate (carboxy methyl cellulose 1 % solution)

↓

Incubation at 37 °C water bath for 3 h

↓

Analysis of reducing sugar byproducts by Somogyi-Nelson method and detection on a spectrophotometer at 520 nm.

The above procedure was repeated as the control without the addition of substrate, or with the enzymes deactivated by heat (100 °C) immediately following the addition of substrate. The procedure was checked by substituting active commercial cellulase enzyme for the tissue extract.

Fluid from the gut contents of fore-, mid- and hind-gut regions of freshly caught garfish was obtained by centrifugation and pH measured using a glass electrode.
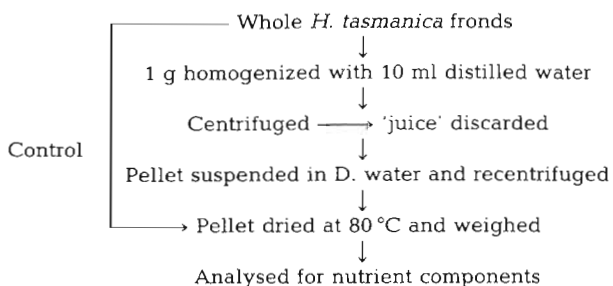
Nutrients in food and assimilation efficiency

The guts of 40 garfish, caught near the peak of the seagrass-feeding phase, were grouped in tens and the contents removed in 3 equal linear segments of fore-, mid- and hind-gut regions. Part of the fresh material was analyzed for total lipids by the method in Nichols et al. (1982). The remainder was air dried, ground in a Wiley Mill and divided into (a) that for direct determination of neutral detergent fibre (NDF), acid detergent (ADF) and lignin by the methods of Van Soest and Wine (1967); (b) that for oven drying (80 °C), and subsequent analysis for components: organic matter, energy and total nitrogen. Organic matter was determined by ashing in a muffle furnace (550 °C, overnight), energy with a Gallenkamp ballistic bomb calorimeter (CB-370) and total nitrogen by autoanalyser and the standard micro-Kjeldahl technique. The commonly used multiple of 6.25 for converting total nitrogen to protein is probably valid for animal tissues, but Harrison and Mann (1975) have shown that only 37.5 % of nitrogen in young *Zostera* fronds is associated with protein. *Heterozostera tasmanica* protein levels are therefore calculated from nitrogen data according to the formula:

% protein = % total nitrogen × 6.25 × 0.375

Tips of fronds (5 cm) from epiphyte-free *Heterozostera tasmanica* were collected concurrently with garfish gut

contents and analysed for nutrient components as described above. The proportion of components in the 'juice' of seagrass fronds was determined as follows:

```
                  ┌──────── Whole H. tasmanica fronds
                  │                   ↓
                  │  1 g homogenized with 10 ml distilled water
                  │                   ↓
                  │     Centrifuged ──────→ 'juice' discarded
 Control          │                   ↓
                  │  Pellet suspended in D. water and recentrifuged
                  │                   ↓
                  └──────→ Pellet dried at 80 °C and weighed
                                      ↓
                        Analysed for nutrient components
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The amount of components in seagrass 'juice' is then the difference in component content of control and extracted fronds. The proportion of organic matter in cell contents relative to plant mass can also be determined as the difference between percentage organic matter and ash-free NDF.

Several terms are used in fish nutrition studies to describe a single process and these are often ambiguous. An example is the use of assimilated, digested and absorbed nutrients to describe the difference between components in food and faeces. 'Digestibility' has been objected to by Pandian (1967) because digested foods are not necessarily assimilated or absorbed. The 'apparent digestibility coefficient' of Crampton and Harris (1969), is here referred to as assimilation efficiency (AE) and calculated as follows:

$$\% \text{ AE} = 100 - \left[\frac{\% \text{ lignin in food}}{\% \text{ lignin in gut content}} \times \frac{\% \text{ component in gut content}}{\% \text{ component in food}} \right] \times 100$$

Typically in this formula the components of food and faeces are compared. In the present study it was not possible to collect true faeces from the field or in the laboratory, therefore component utilization is examined in progressive segments of the gut, previously referred to as fore-, mid-, and hindgut. Lignin provides a natural marker to correct for the contribution of components from sloughed linings of the gut wall and the fishes' digestive secretions. It is assumed that hindgut material is representative of faeces and that lignin is not digested.

RESULTS

Gut passage time and daily food consumption

Seagrass, crustacean food, and empty regions formed distinct separate bands along the gut of *Hyporhamphus melanochir* (Fig. 1). The mean (n = 10) relative position of these bands were compared at successive 3 h intervals over 24 h in order to calculate
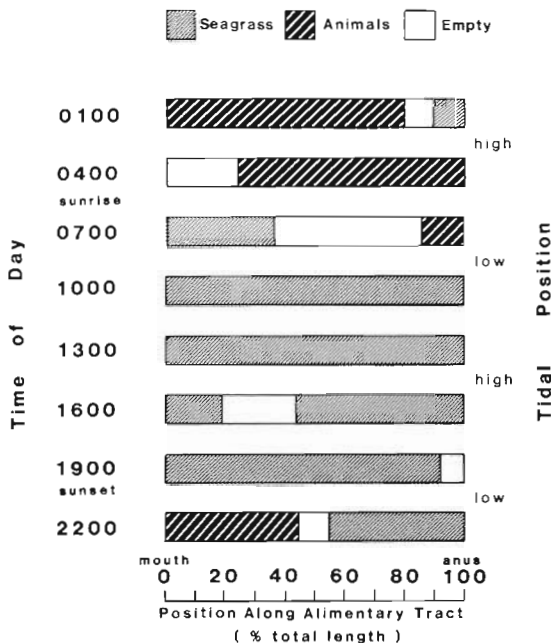

Fig. 1. *Hyporhamphus melanochir.* Mean (n = 10) position of food items (seagrass and crustaceans) and empty regions, along the alimentary tract at 3 h intervals of the diel feeding cycle

the rate of movement of these 2 food types. The most accurate measure of gut passage time was obtained over intervals when it was possible to measure the exact distance a 'food front' had travelled, e.g. for crustacean material between 22.00 h and 01.00 h and for seagrass material between 16.00 h and 19.00 h. Crustacean material occupied 45 ± 7 % of the gut at 22.00 h and 80 ± 14 % by 01.00 h which is a gut passage rate of 11.6 % h^{-1}. At 16.00 h seagrass material formed 2 bands separated by an empty space. The anterior band was 14 ± 3 % of the gut length at 19.00 h and 3 h later filled 92 ± 12 % of the gut, i.e. a rate of 26 % h^{-1}. Where a 'food front' was recognizable at one period only, the passage rate was calculated as the length of that food band divided by the maximum time interval of 3 h and is therefore a minimum rate. For example, between 07.00 h and 10.00 h ingested seagrass moved from 37 ± 17 % to 100 % of the total gut length which is a rate of 21 % h^{-1}. Over the sampling intervals 04.00 h to 07.00 h and 19.00 h to 22.00 h a maximum passage rate is calculated by assuming that the feeding interval commenced at sunrise (06.00 h) and sunset (20.00 h), respectively. Thus in these cases the calculated gut passage rates are 37 % h^{-1} for seagrass (37 ± 7 % of gut filled in 1 h) and 27 % h^{-1} for crustaceans (45 ± 7 % of gut filled in 2 h).

The above data are used to construct a feeding model (Fig. 2). Feeding was assumed to be continuous
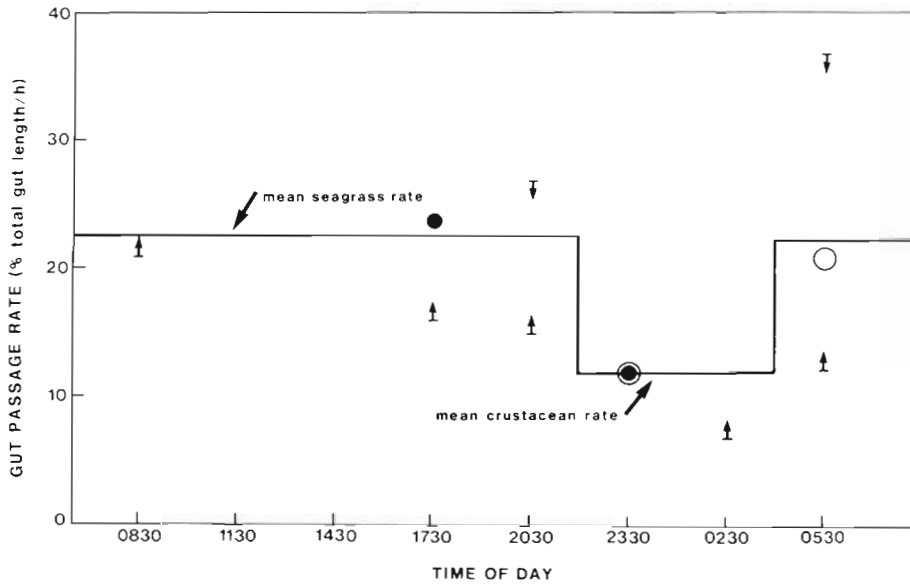
Fig. 2. *Hyporhamphus melano-chir.* Rate of food passage (sea-grass and crustaceans) along the gut at 3 h intervals of the diel feeding cycle. Gut passage rate shown as closed (seagrass) and open (crustaceans) circles when the exact distance of food passage could be calculated for a 3 h inter-val, and as arrows depicting max-imum ↓ and ↑ minimum rates when the distance of food passage was related to an estimated time interval

with food passing along the gut in a 'conveyor-belt' manner. The process operated at mean speeds of 22.5 % gut length h^{-1} and 12 % gut length h^{-1} during periods of seagrass and crustacean ingestion, respec-tively. Seagrass feeding was observed to commence between 04.00 h and 07.00 h (i.e. near sunrise). By 22.00 h the garfish had commenced feeding on crusta-ceans while seagrass had moved along 55 ± 7 % of the gut length at the rate of 22.5 % h^{-1}. The 'switch-over' in feeding is therefore calculated to occur around 19.30 h, i.e.

$$22.00 \text{ h} - \frac{55 \%}{22.5 \% \text{ h}^{-1}}$$

There was a break in seagrass feeding between 13.00 h and 16.00 h observed as an empty space 25 ± 6 % of the gut length and corresponding to a time interval of 1 h, i.e.

$$\frac{25 \%}{22.5 \% \text{ h}^{-1}}$$

Thus garfish fed upon seagrass for a total of 13 h at a gut passage rate of 22.5 % h^{-1}; this is equivalent to 3 gut volumes of food d^{-1}.

Ingested crustaceans occupied 45 ± 7 % of the gut by 22.00 h, and for the purpose of the model, commence-ment of feeding on crustaceans is calculated to be 20.00 h, i.e.

$$22.00 \text{ h} - \frac{45 \%}{22.5 \% \text{ h}^{-1}}$$

This is consistent with an observed cessation in feed-ing between the 'switch' from seagrass to crustaceans. Crustaceans were preyed upon between 20.00 h and 22.00 h at a passage rate of 22.5 % h^{-1} and subse-quently at the rate of 12 % h^{-1}. By 04.00 h feeding on

crustaceans had ceased and the gut was 25 % empty in the foregut region. Crustaceans were therefore con-sumed until 02.00 h, i.e.

$$04.00 \text{ h} - \frac{25 \%}{12 \% \text{ h}^{-1}}$$

Feeding for 2 h at 22.5 % h^{-1} and 4 h at 12 % h^{-1} is equivalent to a combined consumption of 1 gut volume of crustacean material per day. The crustacean feeding period of 6 h was followed by another non-feeding period of 3.5 h, preceding the 'switch-over' to seagrass food.

The gut of *Hyporhamphus melanochir* was 90 to 100 % full by volume at all sampling periods except at 04.00 h, 07.00 h and 16.00 h when fullness decreased to between 50 and 75 % (Fig. 1). An analysis of var-iance (Newman-Keuls multiple range test) showed that the total weight of food in the gut (Fig. 3) at 04.00, 07.00 and 16.00 h was significantly lower than at other times ($F_{[0.05], 7,72} = 6.55$). Dry weight (mg) of either food type in full guts was not significantly different, and was linearly correlated (r = 0.95) with dry weight of fish (g) according to the regression y = 1.1 + 12.5 wt. The fish examined ranged in size from 12 to 40 cm length to caudal fork (LCF) and 1.2 to 52.0 dry wt., with a mean weight of 3.4 g. Thus the average fish had 40 mg food in a full gut. The daily consumption of food was therefore 120 mg (3 gut volumes) of seagrass and 40 mg of crustaceans.

Digestion of seagrass

Green seagrass tissue in the foregut had been thoroughly macerated by the pharyngeal plates. The ingested seagrass consisted mostly of 5 cm lengths of

Table 1. Nutrient components in the entire fronds and extractable 'juice' of seagrass *Heterozostera tasmanica* plus the assimilation of these nutrients by the southern sea garfish *Hyporhamphus melanochir*

Nutrient component	Nutrient content of whole seagrass frond (mean ± SD; n = 6)[*]	Proportion of nutrients in seagrass 'juice' (% of whole frond)[**]	Assimilation efficiency (%) (mean ± SD; n = 10)		
			Food to hindgut	Foregut to midgut	Midgut to hindgut
Organic matter	77.8 ± 1.2	37.8	38 ± 2	34 ± 3	14 ± 4
Energy	14.4 ± 0.3	24.2	28 ± 1	31 ± 4	14 ± 1
Protein from total N	6.9 ± 0.7	67.0	50 ± 7	41 ± 8	16 ± 1
Lipid	4.5 ± 0.4	nd	76 ± 1	nd	nd
Ash-free NDF	49.9 ± 3.3	–	0	0	0
Ash-free ADF	42.2 ± 1.1	–	0	0	0
Lignin	12.2 ± 1.1	–	–	–	–

[*] Data expressed as kJ g^{-1} dry wt for energy, and percent dry matter for other nutrients
[**] Extracted 'juice' was approximately 50 % of total plant mass. nd: not determined; NDF: neutral detergent fibre; ADF: acid detergent fibre

tangled fronds in which a high proportion of cells had been ruptured. The food material in different segments of gut was similar in general appearance and retained green pigmentation. The foregut material was usually mixed with mucous secretions while the hindgut material appeared drier and fibrous. The pH varied from 6.5 to 6.7 in the foregut, 6.9 in midgut, and 6.6 to 7.0 in the hindgut. Analysis for cellulase enzyme activity was negative for all tissues tested.

Assimilation of nutrients from seagrass

Young fronds of *Heterozostera tasmanica*, the main plant food of garfish in Corner Inlet, comprised 78 % organic matter of which 38 % was contained in the extractable 'juice' (Tab. 1). The 'juice', which is possibly the most relevant food of the garfish, contributes 24 % to the total energy of 14.4 kJ g^{-1} in seagrass fronds. The majority of protein (67 % of 6.9 %) was found in the 'juice' portion of seagrass fronds. The garfish assimilated 38 % of organic matter, 28 % of energy and 50 % of protein from whole seagrass fronds, indicating that the 'juice' components were apparently assimilated with 100 % efficiency. Lipid content was 4.5 % in whole fronds, and although there are no comparative data on lipids in 'juice', there was a high assimilation (76 % efficiency) of lipids from seagrass. The total fibre content (NDF) of *H. tasmanica* was 50 %, of which hemicellulose (NDF-ADF) was 7.7 % and cellulose (ADF-lignin) was 30 %. No assimilation of seagrass fibre by garfish was detected. The absorption of nutrients along the gut shows that most assimilation (70 %) occurs between the fore- and midgut regions.
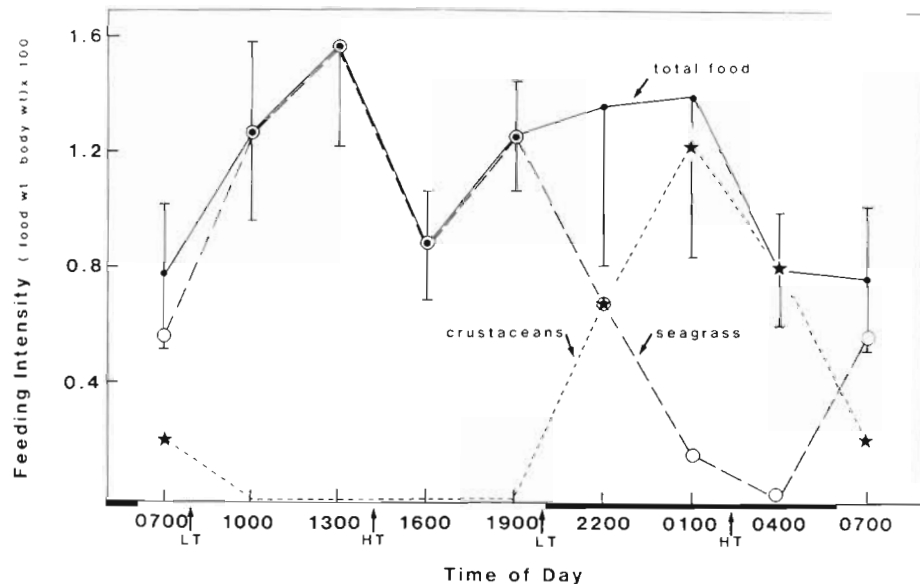

Fig. 3. *Hyporhamphus melanochir*. Mass of food in the gut in relation to body weight, i.e. feeding intensity, at 3 h intervals of the diel feeding cycle. Data presented as amounts of seagrass (open circles) and crustaceans (stars) and the total mass (mean ± SD) of both food types (closed circles) in the gut; sunrise and sunset indicated by end and beginning respectively of a thickened x-axis; high (HT) and low (LT) tide also shown

Table 2. Comparison of gut passage time (GPT) and gut passage rate (GPR) in stomach-less fish from a variety of feeding habits

Species	Body length LCF (cm)	RLG (gut: body length)	Feeding habits	GPT (h)	GPR (cm h^{-1})[•]	Source
Tautogolabrus adspersus cunner (Labridae)	15–20	0.8–1.0	Carnivore on planktonic crustaceans	10–14	1.1	Chao 1973
Monacanthus chinensis leatherjacket (Monacanthidae)	8.2–21.6	0.9	Omnivore on amphipods, seagrass (fed on animals)	7.5 (from 13.4% h^{-1} GPR)	1.0–2.6	Conacher et al. (1979)
Belone belone garfish (Exocetidae)	5.0–5.5	0.5	Carnivore on crustaceans	3.8	0.7	Rosenthal and Paffenhöfer (1972)
Ctenopharyngodon idella white amur	40–55	2.25	Herbivore on freshwater vegetation	8	13.6	Hickling (1966)
Scarus spp. parrot fish (Scaridae)	30.8	1.3–1.6	Herbivore on coral, algae and seagrass	4–6	8–10	Smith and Paulson (1974)
Hyporhamphus melanochir			Herbivore on seagrass	4.4	1.8	Present study
Southern sea garfish (Hemirhamphidae)	15	0.53	Carnivore on crustaceans	8.3	0.9	

[•] Data have been normalized to standard gut length from LCF and RLG data, where $GPR = \dfrac{LCF \times RLG}{GPT}$

DISCUSSION

The main limitation to the utilization of plant food by fish is the penetration of plant cell walls, since fish possess the necessary complement of enzymes (Beauvalet, 1933; Ishida, 1936; Fish, 1960; Hickling, 1966; Moriarty, 1973; Payne, 1978) for the digestion and assimilation of nutritious cell contents. A further deterent to herbivory in fishes, for which little information is available, is the presence of toxic substances in plants (Ogden and Lobel, 1978; Nicotri, 1980). Fish do not possess an enzymatic mechanism for the digestion of plant cell walls, e.g. cellulase (review by Kapoor et al., 1975); however, alternative mechanisms are found in fish. These are (1) the lysis of cells in an acidic (pH 2 to 4) stomach medium (Fish, 1960; Moriarty, 1973; Bowden, 1976; Lobel, 1981); (2) mechanical action of the mouthparts or the gizzard (Al-Hussaini, 1947; Hicking, 1966; Lobel, 1981). The stomachless fishes, with representatives in 15 families including the Hemirhamphidae, typically possess a pharyngeal mill (Chao, 1973) and a gut pH of 7.0 ± 2.0 (Ishida, 1936; Barrington, 1957; Gohar and Latif, 1961). An acidic gut would be superfluous, and indeed impede the action of enzymes such as amylase, invertase, lipases and the tripsin-like proteases which show optimum activity around neutral pH (Fish, 1960; Karlson, 1968). The above enzymes have been recorded in stomachless fish (Chesley, 1934; Fish, 1960; Hickling, 1966; Moriarty, 1973) and are likely to be important in the digestion of seagrass in the gut of *Hyporhamphus melanochir* (pH 6.5 to 7.0).

The current methods for estimating food consumption in fish are mostly derived from studies on fish that possess a defined stomach and consume discrete meals, which are then evacuated at exponential rates (Elliot, 1972; Thorpe, 1977; Elliot and Persson, 1978). The limited data available on the feeding of *Hyporhamphus melanochir* do not justify a more complicated model of food consumption than that proposed (Fig. 2), and this is essentially that of Bajkov (1935). The garfish has a simple straight tubular gut (Suyehiro, 1942) and feeds almost continuously, with food passage rate being nearly constant for the ingestion of a particular food type. The main limitation of this proposed model is the uncertainty of gut passage rate, or even that ingestion is actually taking place, when no comparison of food markers was possible. This was a particular problem during the daylight feeding on seagrass, e.g. 10.00 h to 13.00 h (Fig. 1), where it was assumed that food was being ingested at the mean calculated rate. This assumption seems safe since the gut remained full in terms of food volume and weight during these periods (Fig. 1 and 3).

The ratio of gut length to body length (RLG) in fish is frequently used as a general guide to feeding habits (Suyehiro, 1942; Al-Hussaini, 1947; Hickling, 1966; Kapoor et al., 1975; Van Dyke and Sutton, 1977) being generally less than 0.1 for carnivores, greater than 3.0 for herbivores and intermediate in omnivores. The same trend is evident in our summary of comparative data on stomachless fish in Table 2 although the garfish would be incorrectly defined as a carnivore. Gut passage rate (GPR) is perhaps a more sensitive indicator than RLG for feeding in omnivores, e.g. garfish, and is considerably faster for plant than for animal food. In fish, GPR is found to vary with both food quantity (Tyler, 1970; Elliot, 1972; Flowerdew and Grove, 1979; Tseitlin, 1980) and quality (Rozin and Mayer, 1964; Lee and Putnam, 1973; Grove et al., 1978) and usually shows an increase with an increase in ration size. For example, a continuous supply of different food types to carnivorous garfish *Belone belone* (Exocetidae) resulted in a GPR for zooplankton that was 57 to 64 % slower than for *Tubifex* (Rosenthal and Paffenhöfer, 1972). It is not certain whether food quality or quantity were responsible for these observed differences since the capture rate, and hence ingestion, of *Tubifex* is expected to be higher than for mobile zooplankton. The gut passage time (GPT) averaged 3.8 h for *B. belone* (5 to 5.5 cm) consuming crustaceans (Rosenthal and Paffenhöfer, 1972) which is equivalent to a GPR of 0.7 cm gut h^{-1} (Table 2) calculated from a gut: LCF ratio of 0.5 (Al-Hussaini, 1947). This compares favourably with a GPT of 8.3 h, or GPR of 0.9 cm gut h^{-1}, for the closely related *H. melanochir* (15 cm LCF) consuming crustaceans (Tab. 2). The GPT for *H. melanochir* consuming seagrass was 4.4 h or 2 cm gut h^{-1} GPR, i.e., twice the rate of crustaceans. These differences in GPT are probably a function of ingestion rate. Seagrass is available to *Hyporhamphus melanochir* as an unlimited, static food resource, whereas the dominant crustacean prey are expected to be evasive, less abundant, and vulnerable to predation during a limited period when they emerge into the water column above the seagrass beds at night (Robertson and Howard, 1978; Robertson and Klumpp, 1983; Fig. 1 and 3). A difference in nutritive qualities of seagrass and crustacean food may also contribute to the observed differences in GPR. The dilution of food quality with inorganic material has been shown to increase ingestion and egestion rates in fish, i.e. to result in less time to empty the gut (Rozin and Mayer, 1964; Lee and Putnam, 1973). The presence of other non-digestible materials, such as seagrass fibre, may be expected to have a similar effect on GPR in *H. melanochir*. It was calculated that a garfish of 3.4 g dry weight ingests 120 mg (i.e. 3.5 % of body weight) of seagrass d^{-1}. This is equivalent to 1.7 kJ energy of which 0.5 kJ (or 147 kJ kg^{-1} dry weight) was assimilated. Crustacean food

was ingested at the rate of 40 mg d^{-1} (i.e. 1 % of body weight) and assimilated at an assumed efficiency of 85 to 98 %. Using the data on energy content of amphipods from Conacher et al. (1979) we can predict that the daily crustacean diet of garfish provides 0.64 to 0.74 kJ of assimilated energy. The assimilated energy from both food types is then approximately 1.2 kJ d^{-1}, or 353 kJ kg^{-1} dry wt d^{-1}, nearly 60 % of which is derived from the crustaceans. The fanbellied leatherjacket *Monacanthus chinensis* – one of the important consumers of seagrass and micro-crustaceans in Australian seagrass beds – has been estimated to consume daily 152 kJ energy kg^{-1} wet weight (Conacher et al., 1979). The garfish by comparison consumes 180 kJ energy on a wet weight basis (dry : wet ratio = 0.25). The difference is expected because garfish are highly active, fast swimming fish, which feed almost continuously, compared with leatherjackets, which are cryptic inhabitants of the seagrass canopy being active during only part of the day.

Growth is a component of the energy balance of garfish for which data are available. Growth rates in *Hyporhamphus melanochir* from South Australia have been determined by Ling (1958) from field data on age and length frequency distribution. Our data agreed closely with Ling's calculated length to weight relationship (log wt = 3 log L − 5.6) and was used to estimate successive annual growth rates over the first 5 yr, for which data are available. Fish of year Class I, II, III, IV and V had lengths of 9.5, 16.5, 22.5, 27.2 and 32.6 cm. The growth rates are 4.1, 19.0, 37.3, 74.0 and 128 g wet wt yr^{-1}, corresponding to an energy content of 16, 76, 149, 296 and 512 kJ, calculated from a garfish mean energy content of 4.1 kJ g^{-1} wet wt (unpubl. own data). The average-sized fish of the present study (15.5 cm, year Class II) therefore has required 76 kJ energy for its preceding year of growth. We estimate the intake of such a fish to be, at maximum, 909 kJ yr^{-1} of which 445 kJ yr^{-1} is assimilated. This represents a gross growth efficiency of 8 % and a net growth efficiency of 17 % which is within the range reported for fish under natural conditions (Mann, 1965; Conover, 1978). Assuming that our estimates of energy consumption and assimilation are accurate, the garfish has a surplus of 369 kJ energy, i.e., 83 % of assimilated energy, available for metabolism during the second year of growth.

Data are not available on the metabolic energy requirements of garfish or related species. The regression of basal metabolic energy requirement to fish weight at 20 °C, R = 35.8 $Weight^{0.81}$, as proposed by Winberg (1956), and derived mainly from fresh water fish studies, can be used as a guide to the energy requirement of garfish. The respiratory rate value in the above regression was adjusted for a water temperature of 17 °C using the table of Winberg (1956) as quoted in Grodzinski et al. (1975, p. 127). Under these conditions a garfish of average weight (13.6 g wet) is calculated to require 222 cal or 0.9 kJ energy d^{-1} for basal metabolism, and twice this amount if active (Winberg, 1956; Mann, 1969). Such a demand exceeds our measured estimate of assimilated energy by 50 %. Mann (1965) discusses the limitations of the Winberg formula and points out that, whereas the regression coefficient varies little from 0.8, the respiratory rate value can range widely between species from the theoretical 35.8 cal g^{-1} wet weight d^{-1}.

The nutrient content of seagrass is considered to be low in comparison with other vascular plants (Birch, 1975). However, Lobel and Ogden (1981) noted that seagrasses had the highest nutrient quality in terms of energy and protein content when compared with algae of a coral reef lagoon. Similarly a study of herbivore food preference by Nicotri (1980), in which *Zostera* and 17 different algae are compared, found that *Zostera* ranked 3rd in terms of organic matter and energy but only 13th in terms of nitrogen. Energy levels in seagrasses range from 12 to 18 kJ g^{-1} dry wt (McRoy, 1970; Birch, 1975; Conacher et al., 1979) with 14.4 kJ g^{-1} in *Heterozostera tasmanica* of the present study. A C : N ratio of less than 17 : 1 is considered necessary in animal nutrition (Russell-Hunter, 1970), but seagrasses and most macrophytic algae exceed this (Mann, 1972; Harrison and Mann, 1975). Seagrasses are reported to have a nitrogen content of between 0.7 and 4.8 % (Vinogradov, 1953; Burkholder et al., 1959; Birch, 1975; Harrison and Mann, 1975; Murray et al., 1977), with 2.9 % recorded in the present study. It has already been noted that only a third of this nitrogen is associated with protein in *Zostera* (Harrison and Mann, 1975).

The consumption of crustaceans by *Hyporhamphus melanochir* must be important in maintaining a balanced intake of nitrogen since the protein content of zooplankton is relatively high (40 to 80 %; Mayzaud and Martin, 1975) and the published estimates for nitrogen assimilation efficiency in carnivorous fish are around 90 % (Buckley and Dillmann, 1982) compared with 50 % assimilation of seagrass nitrogen by *H. melanochir*. Also the crustacean food of *H. melanochir* is energy-rich (19 kJ g^{-1} in amphipods from an Australian seagrass bed; Conacher et al., 1979) compared with seagrass of which only 3 kJ g^{-1} is actually available as cell contents (Table 1). Seagrass energy was assimilated at 28 % efficiency in *H. melanochir* and this is at the lower end of the range (20 to 60 %) reported for herbivorous fish (Mathaven et al., 1976; Van Dyke and Sutton, 1977; Conacher et al., 1979; Lobel and Ogden, 1981). Assimilation of energy in carnivorous fish is estimated to be 85 to 98 % (Beamish

et al., 1975). Thus, on a weight for weight basis, the crustacean diet of *H. melanochir* will provide a richer source of available energy and protein than seagrass.

The southern Australian garfish seems adapted for utilizing rich food resources of a seagrass bed. The feeding strategy of this fish is based on the grazing of seagrass, a vast resource of relatively low nutritional quality. Ingested seagrass is passed through the gut in the relatively short time necessary to fully extract nutrient components, such as simple sugars, from the cell contents. The small crustaceans that swarm above the seagrass canopy at night form a limited but highly nutritious resource exploited by the garfish. In turn, the faeces produced by abundant garfish feeding on seagrass are probably of major importance to the detrital food web and in the recycling of nutrients within the seagrass bed.

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