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Opportunistic utilization of mysid shoals by surf-zone teleosts

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ABSTRACT: The utilization of dense concentrations of the mysid *Mesopodopsis slabberi* by nearshore teleosts associated with a surf-exposed sandy beach in southern Africa was investigated during a 24 h study. Five species, namely *Lithognathus mormyrus, Liza richardsoni, Monodactylus falciformis, Pomadasys olivaceum* and *Sphyraena africana,* fed extensively on this resource. Mysids also featured in the diets of the other teleosts examined. Foraging activity did not appear to coincide with periods of increased prey availability. This may be a reflection of the patchy distribution of both predators and prey or, alternatively, it may indicate that mysids were consumed outside the beach/surf-zone system. Temporal differences in habitat occupancy probably reduce the likelihood of interspecific competition over food. Comparison of the mean contribution of mysids to the diet estimated during this 24 h study with that obtained from long-term studies suggests that the dietary importance of highly motile prey items such as mysids may, in the past, have been overlooked. Opportunistic utilization of superabundant prey items, when readily available, may be of immense importance to teleosts frequenting highly dynamic environments.

INTRODUCTION

Dense concentrations of mysids have been observed in association with sandy beaches along the eastern seaboard of southern Africa (Cockcroft 1979, Wooldridge 1983). The dominant mysid species found inshore, *Mesopodopsis slabberi,* has an average density of approximately 1000 m^{-3} and densities in excess of 15 000 m^{-3} have been recorded (Wooldridge 1983). Several studies have shown that this organism is an important prey item of teleost fish (Lasiak 1982, 1983, 1984a, Smale 1983, 1984, Smale & Kok 1983, Buxton et al. 1984). These studies summarize data obtained from either monthly or quarterly collections made over a 1 to 3 yr period. Lasiak (1983) has shown that the contribution of *M. slabberi* to the diet of surf-zone teleosts fluctuates considerably. This variability probably reflects the gregarious behaviour of the mysid and can therefore be attributed to the presence or absence of mysid shoals in the vicinity of actively foraging fish.

The present paper describes the feeding habits of the fish assemblage associated with an exposed sandy beach over a single 24 h period in January 1979. A concomitant study (Cockcroft 1979) on surf-zone zooplankton indicated the presence, particularly after dark, of large concentrations of *Mesopodopsis slabberi* just outside the breakers. The opportunistic utilization of this 'superabundant' food resource by surf-zone teleosts during this 24 h period is compared with the apparent contribution of mysids ascertained from long-term studies.

METHODS

The 24 h study was carried out in the surf-zone off King's Beach, Port Elizabeth, South Africa (33° 56' S, 25° 39' E). This is the least exposed beach in Algoa Bay. It is subjected to continuous moderate wave action; the waves have an average breaking height of 0.7 m and break 50 to 100 m offshore at an average depth of 2 m (McLachlan 1980). Physical, chemical and biological features of this area have been extensively studied and are summarized in McLachlan (1983a, b).

Fish were collected by seine netting within the surf-zone; details of the netting procedure are given in Lasiak (1984b, c). At 3 h intervals 3 hauls were made through the surf, with a coarse-meshed seine net (60 mm stretched mesh) 60 m long and 2 m deep.

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Sampling began in the late afternoon and continued through to 1800 h the next day. Thus 9 separate collections were taken over the 24 h period. The catch from each seine haul was sorted by species, counted, and the individual fish were weighed and measured. Subsamples of each species, from each of the collections, were retained for stomach contents analysis. The entire alimentary canals of these fish were removed and stored in 10 % formalin.

Stomach contents were extracted and sorted into broad taxonomic categories. The more abundant prey organisms were identified to the lowest taxonomic level possible. Following the recommendations of Berg (1979) and Hyslop (1980), 2 methods of stomach contents analysis were adopted: frequency of occurrence and gravimetry. The gravimetric contribution of prey items was determined on both a wet and dry basis. Dry mass estimates were made after 24 h exposure to 60 °C, and wet mass estimates were made after excess moisture was removed by blotting. Variations in the mean wet weight of stomach contents relative to the total wet weight of individual fish were used to examine temporal fluctuations in the feeding intensity of some species.

Morisita's (1959) index of association

$$C_\lambda = \frac{2\sum x_i y_i}{\sum x_i^2 + \sum y_i^2} \quad (1)$$

was used to estimate both dietary and temporal overlap. In the case of dietary overlaps, x_i and y_i represent the proportion of the ith prey item consumed by species x and y respectively. In the estimation of temporal overlap, x_i and y_i represent the percent contribution of species x and y to the catch. Species from which less than 10 stomachs were analysed were omitted in the estimation of dietary overlaps.

RESULTS

Catch composition

A total of 3314 fish representing 25 species were caught during the 24 h study. On a numerical basis, 4 species predominated, accounting for 90 % of the total catch. These were the pinkie *Pomadasys olivaceum*, the southern mullet *Liza richardsoni*, the streepie *Sarpa salpa* and the sand steenbras *Lithognathus mormyrus*. None of these was present throughout the entire 24 h period. The most prevalent species were *L. richardsoni*, *P. olivaceum* and the blacktail *Diplodus sargus* which were caught in 8 of the 9 sampling sessions. Of the 25 species recorded 14 were caught irrespective of the day/night cycle, 5 species were nocturnal, 2 diurnal and the remaining 4 were too scarce to classify. Further details of the catches are given in Lasiak (1984b).

Feeding habits

The dietary habits of the dominant species are summarized in Table 1. In terms of both frequency and gravimetry the mysid *Mesopodopsis slabberi* was the major prey item consumed by *Liza richardsoni*, *Lithognathus mormyrus*, *Monodactylus falciformis*, *Pomadasys olivaceum* and *Sphyraena africana*. Between 60 and 98 % of the food eaten by these fish were mysids. Smaller quantities of *M. slabberi* were consumed by

Table 1. Feeding habits of the dominant teleosts caught during a 24 h study at King's Beach. F: frequency of occurrence; G: percentage contribution of prey items on a wet gravimetric basis; N: number of stomachs analysed; Ah: *Argyrosomus hololepidotus*; Ds: *Diplodus sargus*; Lm: *Lithognathus mormyrus*; Lr: *Liza richardsoni*; Mf: *Monodactylus falciformis*; Po: *Pomadasys olivaceum*; Ps: *Pomatomus saltatrix*; Ss: *Sarpa salpa*; Sa: *Sphyraena africana*

Prey item	*Ah* N = 18		*Ds* N = 17		*Lm* N = 21		*Lr* N = 121		*Mf* N = 19		*Po* N = 122		*Ps* N = 113		*Ss* N = 35		*Sa* N = 30	
	F	G	F	G	F	G	F	G	F	G	F	G	F	G	F	G	F	G
Sediment							25.6	4.9										
Unidentified			23.5	19.5														
Algae			11.8	32.8					5.3	0.1					31.4	87.2		
Polychaetes			5.9	0.8														
Sipunculids			5.9	14.8														
Isopods									15.8	2.1								
Amphipods									15.8	4.2								
Megalopas									5.3	0.5								
Mesopodopsis slabberi	11.1	0.9	11.8	0.8	85.7	97.8	57.9	95.1	73.7	89.6	95.1	92.8	7.7	24.7	34.3	12.8	71.9	59.8
Macropetasma africanus	66.7	17.7			4.8	2.2			15.8	6.5	1.6	3.3						
Cephalopods			17.6	18.8									7.7	< 0.1			3.3	2.6
Teleosts	50.0	81.4	5.9	12.5					15.8	0.8								

the other dominant teleosts. The streepie *Sarpa salpa* was essentially a herbivorous species consuming vast amounts of rhodophytes associated with small offshore reefs and the harbour breakwater. Algae were also an important dietary component in the generalist-feeder *Diplodus sargus*. Small pelagic teleosts were the major prey items of the top predators *Argyrosomus hololepidotus* and *Pomatomus saltatrix*.

Dietary overlaps between species (Table 2) varied from < 0.01 to 1.00. High overlaps were evident amongst fish that predated heavily on *Mesopodopsis slabberi* and also between the top 2 predators. Morisita's (1959) index of association was also used to evaluate the temporal co-occurrence of these fish (Table 3). Overlap values varied between < 0.01 and 0.87. Thus, *Pomatomus saltatrix* co-occurred with *Argyrosomus hololepidotus, Diplodus sargus, Monodactylus falciformis* and *Sarpa salpa; M. falciformis* was found in association with *A. hololepidotus* and *D. sargus;* and *S. salpa* co-occurred with *A. hololepidotus*. There was little temporal overlap between the teleosts that consumed large quantities of mysids.

Table 2. Dietary overlaps between the dominant teleosts caught off King's Beach, Port Elizabeth, South Africa, based on Morisita's (1959) index of association. Abbreviations as in Table 1

	Teleost species							
	Ds	*Lm*	*Lr*	*Mf*	*Po*	*Ps*	*Ss*	*Sa*
Ah	0.22	0.02	0.01	0.03	0.06	0.93	< 0.01	0.52
Ds		0.01	0.01	0.02	0.02	0.33	0.57	0.17
Lm			1.00	0.99	1.00	< 0.01	0.14	0.81
Lr				0.99	1.00	< 0.01	0.14	0.82
Mf					1.00	0.01	0.14	0.84
Po						0.05	0.15	0.84
Ps							< 0.01	0.52
Ss								0.12

Table 3. Temporal overlaps between the dominant teleosts caught off King's Beach, Port Elizabeth, South Africa, as indicated by Morisita's (1959) index of association. Abbreviations as in Table 1

	Teleost species							
	Ds	*Lm*	*Lr*	*Mf*	*Po*	*Ps*	*Ss*	*Sa*
Ah	0.55	0.01	0.29	0.80	0.02	0.87	0.83	0.09
Ds		0.07	0.47	0.78	0.15	0.75	0.45	0.40
Lm			0.05	< 0.01	0.49	0.19	0.06	< 0.01
Lr				0.20	0.11	0.55	0.17	0.12
Mf					0.04	0.78	0.64	0.06
Po						0.22	0.10	0.13
Ps							0.74	0.08
Ss								0.15

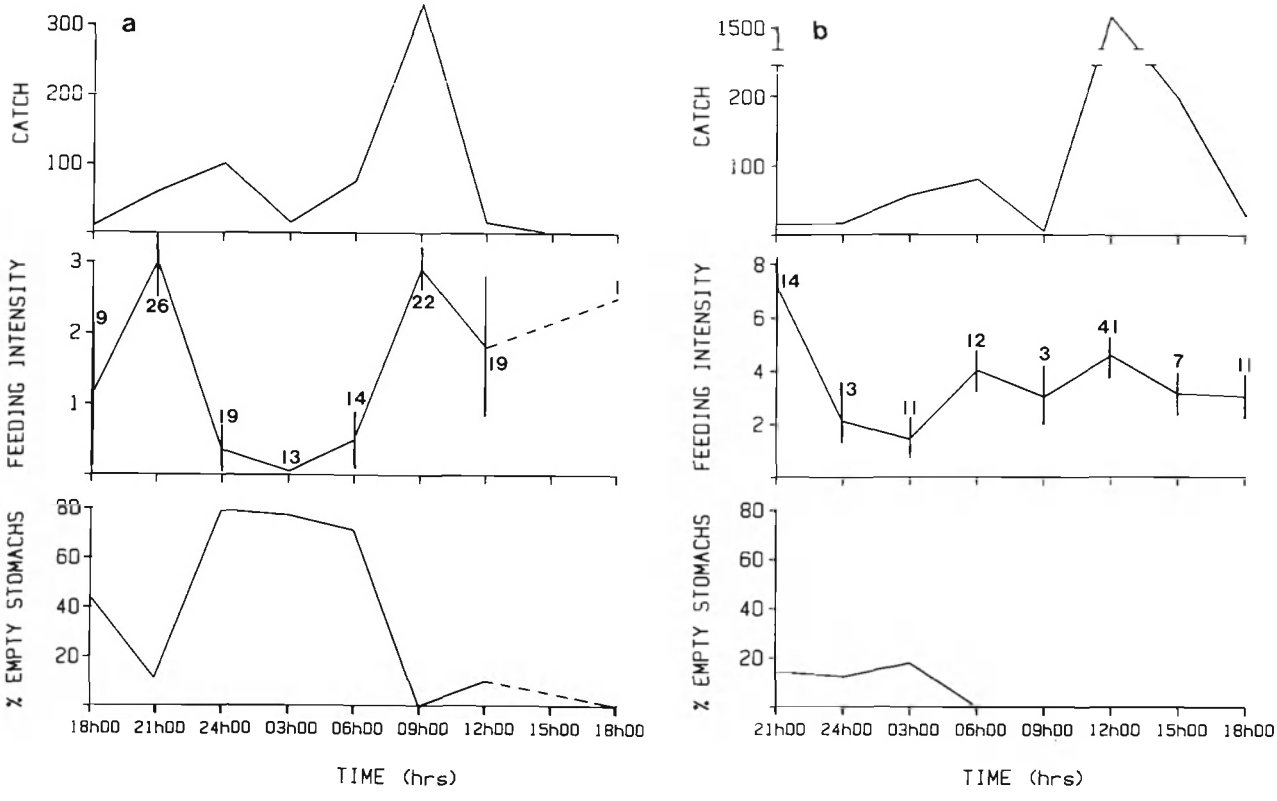

Fig. 1. Diel changes in catch, feeding intensity and % empty stomachs observed in (a) *Liza richardsoni* and (b) *Pomadasys olivaceum* at King's Beach, Port Elizabeth, South Africa. Numbers of stomachs examined; vertical bars: standard deviations

Diel changes in the occurrence and feeding intensity of *Liza richardsoni* and *Pomadasys olivaceum* are shown in Fig. 1. Two peaks in the feeding intensity of the southern mullet were discernible, both coincident with mid-ebb tide. Fish caught at these times had highly distended stomachs containing large quantities of densely packed *Mesopodopsis slabberi*. On a gravimetric basis this mysid accounted for over 80 % of the stomach contents (Fig. 2). Relatively little food was present in mullet stomachs between 2400 and 0600 h as indicated by the low feeding intensity and high proportion of empty stomachs. There was no correlation between the diel feeding and abundance patterns of *L. richardsoni*. Large numbers of freshly consumed *M. slabberi* were found in the stomachs of all *P. olivaceum* caught between 0600 and 1800 h (Fig. 2).

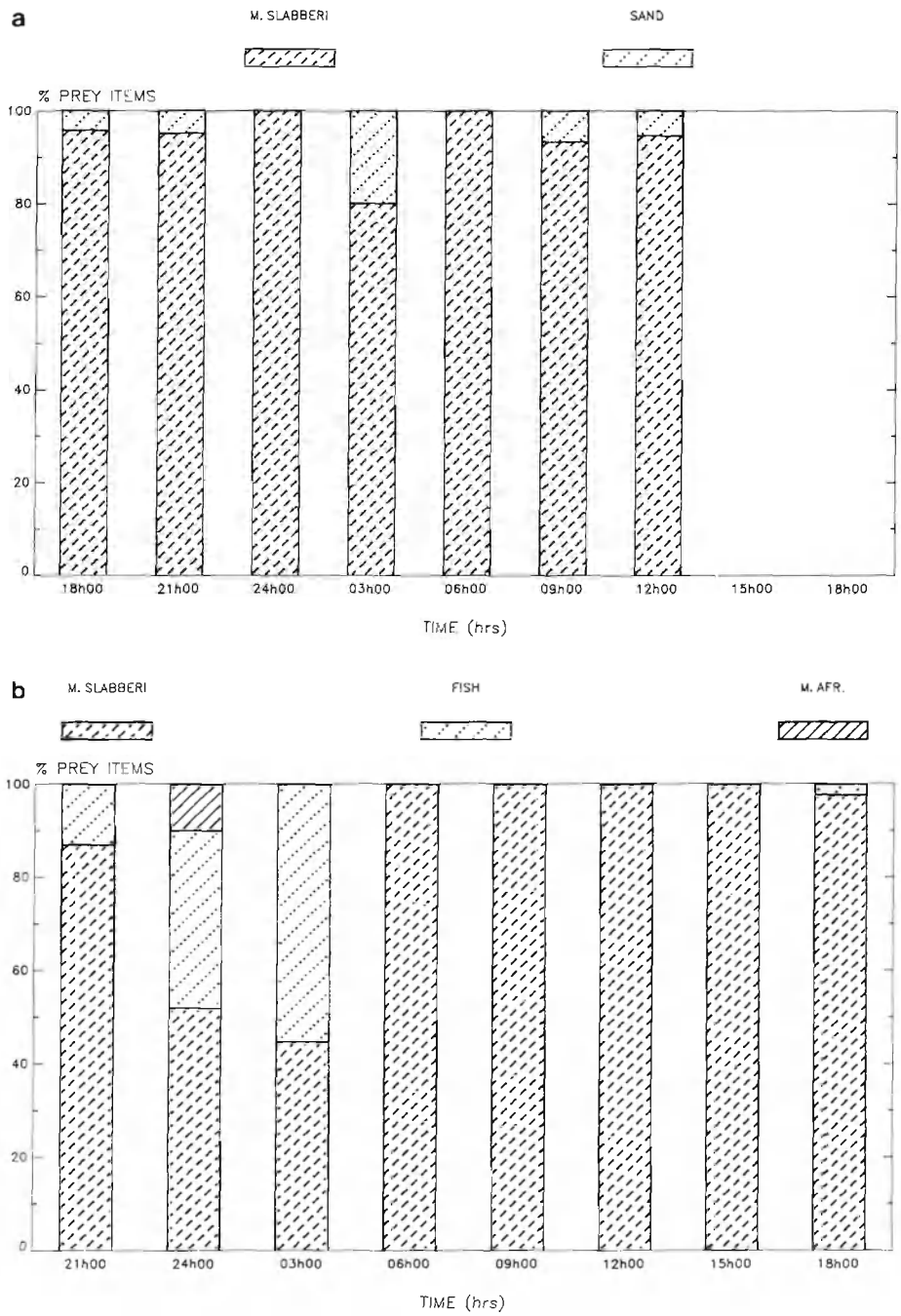

Fig. 2. (a) *Liza richardsoni* and (b) *Pomadasys olivaceum*. Diel changes in dietary intake determined by the relative gravimetric contribution of prey items including the mysid *Mesopodopsis slabberi* and swimming prawn *Macropetasma africanus*

Feeding intensity was lowest at night. There was no relationship between feeding intensity and abundance of *P. olivaceum*.

DISCUSSION

Motile faunal assemblages associated with surf-exposed beaches are not discrete entities, they are in constant flux. Being an 'open' system, import and export of planktonic organisms to and from the surf zone takes place. Inshore current systems and wave action determine the availability of these organisms as potential prey items. The mysid *Mesopodopsis slabberi* is the major component of the zooplankton assemblage. Considerable temporal and spatial fluctuations in the standing stock of this organism have been recorded in Algoa Bay (Cockcroft 1979, Wooldridge 1983). These fluctuations reflect the lack of substrate specificity and high motility of this mysid (Wooldridge 1983). Zooplankton studies carried out by Cockcroft (1979) in association with the present study indicated the presence of large mysid shoals off King's Beach between 2100 and 0300 h, thereafter the number of *M. slabberi* caught was negligible. The King's Beach fish assemblage is itself highly dynamic (Lasiak 1984b, c). Although some species regularly frequent this habitat it is not known whether any can be considered 'true residents'. There appears to be continual exchange of individuals and species with adjacent areas on-, off- and alongshore.

It has been suggested that prey availability, both in quantity and quality, may be a major factor influencing the structure of fish assemblages (Helfman 1978). Comparison of fish feeding activity with the availability of *Mesopodopsis slabberi*, however, indicated that many of the teleosts caught between 2100 and 0300 h were not actively foraging. These fish may have been using King's Beach as a refuge site. Shallow coastal waters are thought to be relatively free of predators (Lenanton 1982, McDermott 1983). Furthermore, the increased turbidity characteristic of surf zones may decrease the foraging effectivity of piscivorous predators (Lasiak 1986). Although *M. slabberi* was apparently scarce after 0300 h (Cockcroft 1979), many of the teleosts caught between 0600 and 1800 h had stomachs distended with large quantities of undigested mysids. This discrepancy probably reflects the patchy distribution of both predators and prey coupled with inadequate sampling methodology. Alternatively, the mysids may have been consumed outside the beach/surf-zone limits. In addition to stomach contents analysis, visual observations of foraging activity are needed to establish whether or not the surf zone acts as an important feeding ground.

All the dominant teleosts caught during the 24 h study consumed mysids. On a gravimetric basis > 90 % of the prey items eaten by the teleosts *Lithognathus mormyrus*, *Liza richardsoni*, *Monodactylus falciformis* and *Pomadasys olivaceum* were *Mesopodopsis slabberi*. The contribution of this mysid to the overall diet of these fish based on monthly sampling over a 27 mo period (Lasiak 1982, 1984c) is given in Table 4. From this it is apparent that *M. slabberi* was not of such over-riding importance in the diets of *L. richardsoni* and *P. olivaceum* and it was only a minor prey item of *L. mormyrus* and *M. falciformis*. Even so, the long-term study (Lasiak 1982) indicated that on some occasions *M. slabberi* was the predominant prey item consumed by these and other surf-zone teleosts. This mysid accounted for more than 90 % of the total food complement eaten by *L. richardsoni* on 4 occasions and by *P. olivaceum* on 7 occasions.

Table 4. Contribution of the mysid *Mesopodopsis slabberi* to the diet of some common surf-zone teleosts, as ascertained from monthly collections made over a 27 mo period. N: number of stomachs examined; a: frequency of occurrence in stomachs; b: percentage gravimetric contribution to total stomach contents; c: number of occasions mysids made up >90 % of the mass of stomach contents

Fish species	N	a	b	c
Lithognathus mormyrus	80	5.0	2.2	–
Liza richardsoni	100	81.0	62.8	4
Monodactylus falciformis	214	18.6	2.3	–
Pomadasys olivaceum	554	23.3	38.9	7

The prevalence of *Mesopodopsis slabberi* in the stomachs of the southern mullet *Liza richardsoni* was somewhat unexpected. The 'natural' diet of this mullet consists largely of sediment particles, decaying plant detritus and associated microbenthos (Masson & Marais 1975, Marais 1980). These resources are not available to mullet frequenting surf-exposed beaches, where turbulence prevents the deposition of detrital material (McLachlan et al. 1981). Romer & McLachlan (1986) have recently shown that *L. richardsoni* makes extensive use of the surf diatom *Anaulus birostratus* as a primary food source. They suggest that grazing of surf diatoms by mullet may be widespread along much of the South African coast. However, surf diatom accumulations do not build up or persist off all beaches, and neither are mullet restricted to these diatom-rich areas. Mullet frequenting beaches where diatom blooms are absent must seek alternative food supplies. The consumption of mysids by *L. richardsoni* was previously considered to be a deviation from the 'natural diet' (Marais & Erasmus 1977, Romer & McLachlan 1986). However, the data presented in this paper suggests that the mysids' dietary importance may have been overlooked.

Opportunistic utilization of 'superabundant' food resources by teleost fish is well documented (McFarland 1963, Odum 1968, Murdock et al. 1975, Keast 1978, McDermott 1983). The sharing of such resources by co-occurring species results in high dietary overlaps as observed during this study. However, these are not necessarily indicative of interspecific competition (Zaret & Rand 1971, Keast 1977), which occurs only when feeding demands of the fish exceed the biomass of prey items available. Interactions between co-occurring species do not only involve food resources. Niche segregation may be achieved through temporal, spatial and/or behavioural differences in habitat utilization. Results from the present study suggest that potential interspecific competition over *Mesopodopsis slabberi* is avoided by temporal differences in habitat occupancy. Modde & Ross (1983) have proposed temporal partitioning of resources by surf-zone teleosts to be a viable strategy preventing competition, since wave action and alongshore current movement would result in the replenishment of zooplankton resources. However, other studies in unpredictable environments indicate that resource partitioning does not play a role in structuring communities (Matthews & Hill 1980, Thorman & Wiederholm 1986).

Such opportunistic utilization of food resources is probably of immense importance to teleosts frequenting physically-stressed environments, such as surf-exposed beaches. Long-term studies that summarize data on feeding habits may overlook the significance of opportunism. The surf zone is not only a physically dynamic habitat; many of the associated faunal assemblages are themselves highly dynamic. Short-term variations in wind strength and direction and their subsequent effects on surf conditions probably play a major part in the control and interaction of these assemblages (Lasiak 1984b, c, McLachlan 1983a). To fully evaluate trophic relations between surf-zone teleosts and their motile food resources, a sampling strategy which takes both temporal and spatial variability into account is required. The energetic significance of this trophic plasticity, in terms of absorption, conversion and growth efficiencies, needs to be examined.

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