M. I. McCormick

Ontogeny of diet shifts by a microcarnivorous fish, *Cheilodactylus spectabilis*: relationship between feeding mechanics, microhabitat selection and growth

Abstract The mechanisms leading to ontogenetic shifts in prey selectivity are examined for the temperate microcarnivore *Cheilodactylus spectabilis* (Cheilodactylidae) in north-eastern New Zealand. These fish prey on invertebrates associated with benthic turf and foliose algae, using a suctorial feeding mode combined with oral sorting. All sizes of fish feed in the same shallow-water habitat using the same feeding mode. Dietary analysis revealed that while all sizes of fish consumed similar taxa, the relative proportion of taxa consumed reflected fish size. Juveniles consumed mainly gammarid amphipods while large adults targeted ophiuroids, with an abrupt shift from feeding predominantly on amphipods at 250 mm standard length. This dietary shift loosely coincided with the onset of sexual maturity and a change in growth trajectory, although dietary trends did not differ between sexes. Both juveniles and adults were found to select particular taxa from the available turf micro-fauna, with juveniles consuming smaller sizes of amphipods than adults. Microhabitat use was also found to change ontogenetically. Detailed observations on feeding mechanics suggested that size-related changes in suctorial force allowed the exploitation of a broader range of microhabitats with increasing fish size.

Introduction

Ontogenetic shifts in diet are the norm for demersal fishes. A variety of potentially interacting factors may account for the prevalence of these shifts. The almost universal occurrence of complex life-cycles in fishes

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means that dramatic changes in diet and foraging techniques are often associated with settlement into the reef population (e.g. Mahon and Neilson 1987). After settlement, size- and age-related morphological differences can lead to changes in foraging ability and, in turn, differential exploitation of a food resource (e.g. Werner and Gilliam 1984; Luczkovich et al. 1995). Habitat and microhabitat use can change with ontogeny (e.g. Helfman 1978; Werner and Hall 1988; Clements and Choat 1993), being a function of changing food requirements and biological interactions such as intraspecific competition (e.g. Holbrook and Schmitt 1992) and risk of predation (e.g. Holbrook and Schmitt 1988a, b; Olson et al. 1995). Likewise, activity schedules of fish may change with age (e.g. Blaber 1976; Helfman 1978; Clements and Choat 1993), which can influence the prey available for harvest. Studies that examine the basis of ontogenetic diet shifts seldom study more than one of these potential mechanisms.

Although mechanisms have been postulated to account for size- or age-related differences in diet within a species, field populations have rarely been investigated in detail to evaluate the processes involved (Holbrook and Schmitt 1984). Fish development involves changes in physical structure and physiology that facilitate behavioural change (Noakes and Godin 1988). Changes may include increased length and absorptive potential of the alimentary tract (Montgomery 1977), and changes in osteology that alter mouth orientation, strike mode, and gape (Luczkovich et al. 1995). Accompanying these changes, species often undergo dramatic niche shifts involving diet, habitat use and interspecific interactions (Bergman and Greenberg 1994). From an ecological perspective this means that individuals of the same species at different life stages can be as functionally separate as different species. An understanding of how a species utilizes its food resource, and how that changes ontogenetically, is prerequisite to any examination of the impact of a predator on the structure of a prey assemblage.

I examined the dynamics of ontogenetic diet shifts in a large microcarnivore, *Cheilodactylus spectabilis*

(Pisces: Cheilodactylidae), on the north-eastern coast of New Zealand. These fish are a common component of the fish assemblage, particularly in shallow, topographically complex areas (Leum and Choat 1980; McCormick 1989a), and are one of a large group of species that feed on invertebrates within algal turf and holdfasts. I investigated whether diet changes with fish size or sex, and explored the mechanisms by which partitioning of the benthic food resource occurs. Information on size-related feeding mechanics and diel foraging patterns has been used to interpret prey-size selectivity. Diel patterns of foraging and microhabitat selectivity are examined. Since diet shifts can have energetic and growth implications, the coincidence of diet shifts with growth is explored in relation to energy-partitioning.

Materials and methods

Sampling and study location

Cheilodactylus spectabilis were collected from three locations on the outer edge of the Hauraki Gulf, north-eastern New Zealand, over four seasons during April 1984 to February 1985. In three of these seasons, major collections were made from one locality (Hen Island), with a supplementary sample from Little Barrier Island (autumn). Due to adverse weather, the summer (1985) sample was collected from Tokatu Point, some 35 km south of Hen Island. All collections were made with SCUBA using a speargun in 1 to 25 m water depth. Standard length, sex, maturity stage (through histological sections of gonads) and weight were recorded for each fish.

Observations of foraging behaviour (details below in subsection "Diel and depth-related patterns of feeding and microhabitat preferences") were conducted in the Cape Rodney to Okakari Point Marine Reserve. Behaviour schedules were obtained for fish on Tabletop Reef, a strip of heterogeneous rocky reef swarded with the brown alga *Carpophyllum* sp. (shallow) and the laminarian *Ecklonia radiata* (deep). This location has been described in detailed previously (Leum and Choat 1980; McCormick and Choat 1987; MacDiarmid 1991).

Diet assessment

The alimentary tracts of all fish collected were dissected-out immediately after capture and stored in 10% buffered formalin. The alimentary tract was typical of a benthic microcarnivore, with a short oesophagus leading to a small sac-like stomach with four associated caecae, followed by a long intestine and muscular rectum.

Gut-contents analysis was confined to the anterior third of the alimentary tract, from the base of the oesophagus to the first bend of the intestine. Prey items from this region exhibited little of the digestive deterioration that hampered identification of amphipods and polychaetes in the posterior intestine and rectum. Items were initially placed into one of 22 categories that were later pooled into nine broad taxonomic categories due to the rarity of many prey items (eight of these are given in Fig. 1; the ninth was a miscellaneous category). Percent volumetric occurrence of each prey category was obtained by scoring the identity of food items on 100 regularly spaced intercepts along eight random transects through a dish of diluted gut contents.

Preliminary cluster-analyses (average linkage, centroid and Ward's hierarchical cluster analyses: SAS 1987) of the dietary information were used to determine whether individuals separated into distinct groups by diet. Broad groupings of fish were found based on fish standard length (SL). Hence, for subsequent analyses involving fish size, data were grouped into size classes that had been previously found to be ecologically meaningful (McCormick and Choat 1987; McCormick 1989 a, b). These categories were: A, ≤250 mm SL; B, >250 ≤ 350 mm SL; C, >350 ≤ 450 mm SL; D > 450 mm SL. For gut analyses, the latter two size classes were combined, since insufficient fish of the largest size class were collected.

Multivariate analysis of variance (MANOVA, Tabachnick and Fidell 1989) was used to test the hypothesis of no difference in diet among the three size classes of fish. Canonical discriminant analysis (CDA) was used to identify and display the nature of the significant differences among the size classes determined by MANOVA. CDA identifies a number of trends in the data set (canonical variates)
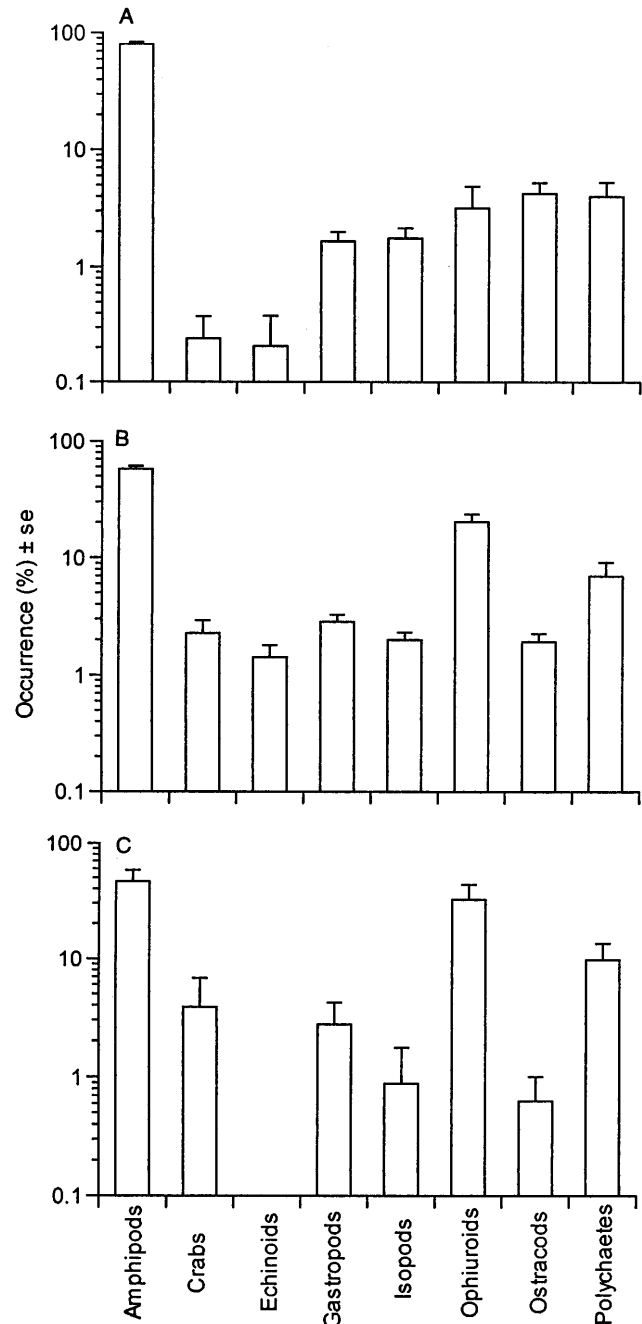

Fig. 1 *Cheilodactylus spectabilis*. Comparison of volumetric occurrence of major dietary items among three size classes (**A** ≤ 250 mm; 250 < **B** ≤ 350 mm; **C** > 350 mm standard length)

that maximally discriminate among the identified groups (in this case, size classes) and sequentially explain less of the variance in the data set. Trends in the original variables (i.e. dietary categories) are represented as vectors given by correlations of these variables with the canonical variates (also known as total structure coefficients). These vectors are plotted on the first two canonical axes, together with treatment centroids and their 95% confidence limits (Seber 1984). The strength or importance of each of the original variables in discriminating among groups is displayed graphically as the length of these vectors. The assumption of multivariate normality was validated prior to analysis.

A principal-components analysis (on the correlation matrix) was undertaken to examine the main trends in variance in the diets of the fish. To determine whether these dietary relationships changed over the four seasons or with fish size (expressed as Size Classes A to C) a fixed two-factor analysis of variance (ANOVA) was conducted on the first and second principal components. These components have the advantage of being linear, normally distributed, and independent by definition. It should be stressed that these ANOVAs do not represent strict hypothesis tests, and are only suggestive of possible trends in the data. Bivariate plots of the first three principal-components axes were checked visually for curvilinearity of relationships prior to interpretation, since parabolic relationships have been associated with percentage data and can hamper description of trends in variability by ordinations (Aitchison 1983).

Feeding structures and foraging techniques

Characteristics of the head of *Cheilodactylus spectabilis* were examined that potentially determine the prey consumed. The view adopted here is that a fish utilizes food resources available in the environment according to the opportunities made possible by its anatomical structure. Detailed field observations were made on the feeding and foraging techniques. Material for osteological and myological examination was prepared by controlled maceration in boiling water. Observations of the jaw articulation and movement of the buccal elements were made on fresh material. Buccal cavity expansion during feeding was estimated by the volumetric difference in the buccal cavity between a relaxed and fully expanded state (representative of the start and end of a bite sequence, respectively). It must be noted that the attribution of function to particular muscle groups in the absence of kinematic analyses is speculative. Nevertheless, in the light of published information on taxa with similar feeding morphologies (e.g. Richard and Wainwright 1995), and the general nature of the functional description undertaken here, I feel justified in making the interpretation on foraging technique embodied in the present study.

Feeding selectivity

To examine food-item selectivity, samples of the benthic prey were collected at the same time and location as fish collected for the summer sample. Sampling of benthic items on the turf was by an air-lift suction sampler, which sampled a confined circular area 15 cm in diameter (177 cm^2). Extensive trials had shown this sampler to collect 100% of the small benthic crustacea from coralline turf beds (Sylvester 1986). Four replicate benthic samples from the coralline turf were collected from two sites separated by 20 m. Coralline turf had been observed to be the favoured feeding substrata for *Cheilodactylus spectabilis* (see fourth subsection of "Results"). All samples were stored in 10% buffered formalin prior to examination. The percent occurrence (by volume) of benthic items was calculated and compared with prey composition. Because preliminary investigation had shown that amphipod crustaceans were an important part of the diet of *C. spectabilis*, the mean length of amphipods was calculated for each benthic sample and compared with that found in the guts of fish from the same location.

Gill rakers have been found to be important in the selection of particle size in planktivorous fish and those fish that process food

by winnowing (Lazzaro 1987). To investigate the role of gill rakers in food selectivity, the relationship between mean gill raker spacing and amphipod size was examined. The left first gill arch was removed from all fish from the summer sample, and the distance between gill rakers was measured using an ocular micrometer ($n = 5$ per arch). The length of a random sample of 20 amphipods from the gut contents of each fish was measured using an ocular micrometer.

Diel and depth-related patterns of feeding and microhabitat preferences

The diel and depth-related pattern of foraging behaviour for each of the three size classes, plus the largest individuals in the population (> 450 mm SL), were examined using scan field observations with SCUBA during monthly fish censuses of Tabletop reef, a strip of reef extending from the intertidal to the reef edge (27 m depth) and encompassing ~35 000 m^2 (detailed in McCormick 1989a). Fish size was estimated visually as detailed by McCormick and Choat (1987). The behaviour of individuals the instant they were first seen was recorded as one of four behavioural categories: (a) foraging (head oriented toward substratum, pectoral fins outstretched and often beating, moving slowly across substratum in search of prey; also involves biting and winnowing food); (b) swimming (actively moving with head not oriented towards substratum); (c) resting (stationary, not foraging); (d) interacting (this category was very rare and will not be examined further here).

Activity schedules were constructed from the behavioural observations pooled over a 12 mo period. For each size class, 100 behavioural observations were used to calculate the percent occurrence of the three main behaviours (a, b, c) for each of three times (morning, 05:30 to 09:30 hrs; midday, 11:30 to 13:30 hrs; afternoon, 16:30 to 20:00 hrs) and three depths (shallow, 0 to 9 m; mid, 9 to 17 m; deep, 17 to 23 m). Collecting behavioural data in this way has the advantage of obtaining a good overview of behaviour in the general population that is not strongly biased by individual variation in activity patterns, which are usually high. However, the method is prone to overestimating the occurrence of swimming, since this is the escape or startle response in most fish species. This bias is believed to be small for *Cheilodactylus spectabilis* as the species shows little response to diver presence.

The diel patterns in bite rate and microhabitat selectivity were determined for *Cheilodactylus spectabilis* by replicate field observations of the three size classes of fish (a, b, c) at Waterfall reef in the Marine Reserve (see Fig. 1 of Kingett and Choat 1981). All size classes of fish were observed to feed at this study site. Bite rates (number of bites per minute) of five randomly chosen fish of each size were recorded during each of three time periods: morning (06:00 to 10:30 hrs); midday (11:30 to 14:00 hrs); afternoon (15:30 to 19:30 hrs). Bite rates were recorded over five 1-min periods randomly chosen within a 20 to 90 min total observation period. The microhabitat to which each bite was directed was recorded during these 5 min periods. Foraging microhabitats on the turf algae and broken-rock habitat were classified into four groups: coralline turf; rock crevice; holdfast (*Carpophyllum* sp. bases and *Ecklonia radiata* haptera); and algal thallus.

Growth

Growth of *Cheilodactylus spectabilis* was examined to assess whether ontogenetic changes in diet coincided with changes in growth. Sagittal otoliths were removed from all fish collected, and then fractured, charred over a low flame, and ground to produce a transverse section through the nucleus. The otoliths were immersed in cedar oil and viewed by reflected light with a black background. This resulted in light-coloured opaque zones and dark hyaline zones. Three counts of completed opaque zones were made for each otolith. Replicate counts of otoliths were made in random order to avoid bias. If replicate ring counts differed, otoliths were cleaned, polished, and re-counted. Rings were not validated as annual, but

two pieces of information suggest that a single hyaline and opaque pair are formed annually. Firstly, opaque marginal increments were only found in specimens from the spring sample; secondly, the size of fish aged at 1 yr corresponded to the size of individually identifiable fish whose growth had been followed in the field since recruitment. Von Bertalanffi growth curves were fitted to male and female growth relationships, and growth parameters were estimated.

Results

Diet assessment

The diets of all sizes of *Cheilodactylus spectabilis* were similar in gross taxonomic composition, with all sizes consuming virtually the same range of invertebrate taxa and relying heavily on gammarid amphipods, ophiuroids and polychaetes (Fig. 1). The proportional contribution of each prey category varied considerably among individuals within a size class. This high variability is in part due to fish in the larger size classes targeting specific prey items. For instance, the gut of one 350 mm SL female contained 23 limpets (*Cellana stellifera*) and 2 chitons (*Acanthochitona* sp. and *Rhyssoplax* sp.) ranging from 8 to 23 mm length.

Amphipods comprised between 0 and 98% of the gut contents (mean 63%). Of these, amphipods 79% were gammarids, 3% talitrids, 3% stenothoids or stegalocephalids and 1% each of lysianassids, podocerids, pontogenids and caprellids. The remaining 11% were unidentified.

The diet differed significantly among the three size classes of fish (Fig. 2). Small fish had proportionally more amphipods and ostracods in their diet than fish >250 mm SL. In contrast, fish >350 mm SL (Size class C) had proportionally more ophiuroids and crabs. There was a strong negative relationship between the occurrence of ophiuroids and amphipods in the guts of fish ($p < 0.0001$, $r = 0.769$; Fig. 3).

When these dietary components are examined with respect to fish length, there is evidence of a threshold effect (Fig. 4). Ophiuroids seldom occurred in the diets of fish <250 mm SL, with diets instead being dominated by amphipods. This appeared to abruptly change at 250 mm SL, when ophiuroids prominently featured in the diet of many individuals.

A principal-components (PC) analysis identified two main trends in the variance of the diet of *Cheilodactylus spectabilis* (Table 1). Firstly, a negative relationship between the occurrence of amphipods and the occurrence of ophiuroids in the gut, as noted above (PC 1, 25% total variation). Secondly, a co-occurrence of echinoids and isopods in the diet (PC 2, 17.7% variation). As previously noted, an ANOVA revealed that the first relationship (PC 1) differed among size classes (Table 2). The relationship differed among seasons (Table 2), with regression coefficients showing that the relationship between amphipod and ophiuroid occurrence was weaker during the summer ($r^2 = 0.39$, $p < 0.003$) than during the other three seasons (r^2:0.65 to 0.74). Furthermore,
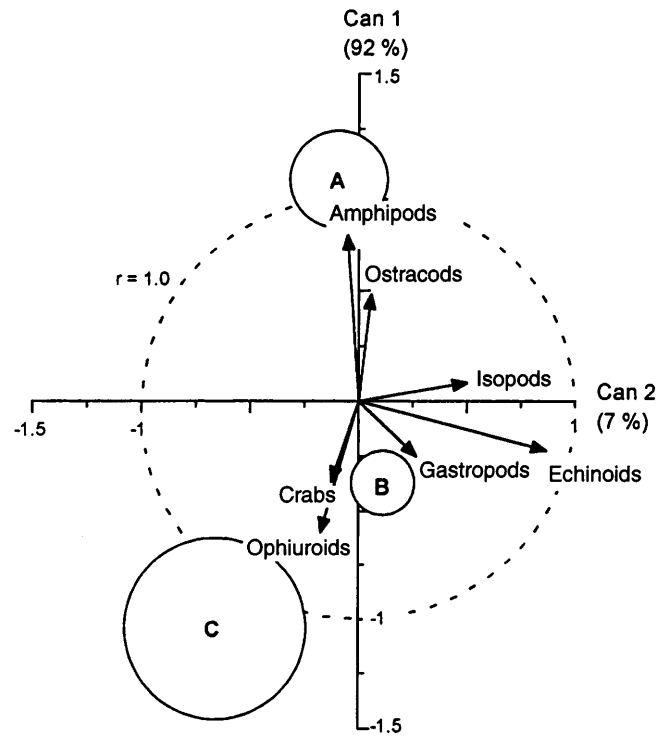

Fig. 2 *Cheilodactylus spectabilis*. Comparison of diets of three size classes (*A, B, C*, as per Fig. 1 legend). Canonical discriminant-analysis reveals differences in contribution of eight prey types to diets. Contribution of polychaetes to difference among size classes was so small that it is not shown. Mean centroids of size classes and 95% confidence limits are plotted. Superimposed on axes (canonical variates, *Can*) are direction and importance (indicated by vector length) of trends in prey-item contribution to diet. These vectors represent correlation of variables with canonical variates and are plotted in relation to location of an absolute correlation ($r = 1$). Multivariate analysis-of-variance revealed significant difference in diet composition among size classes (Pillai's trace $= 0.36$, $F = 2.65$, *df* 16, 194, $p = 0.001$)
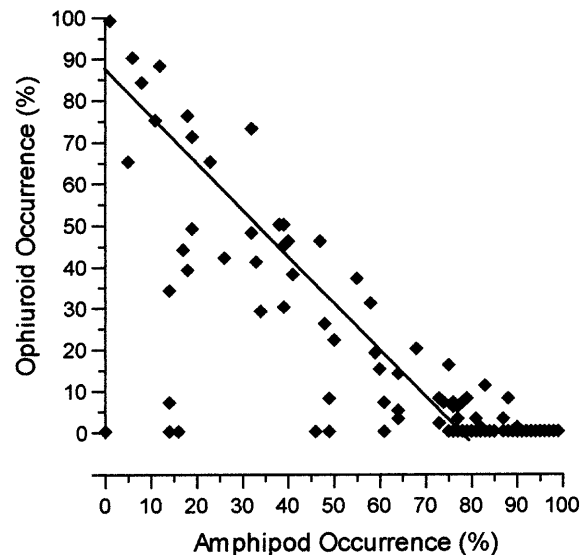

Fig. 3 *Cheilodactylus spectabilis*. Relationship between occurrence of ophiuroids and amphipods in diet ($r^2 = 0.769$, $p < 0.0001$, $n = 106$)
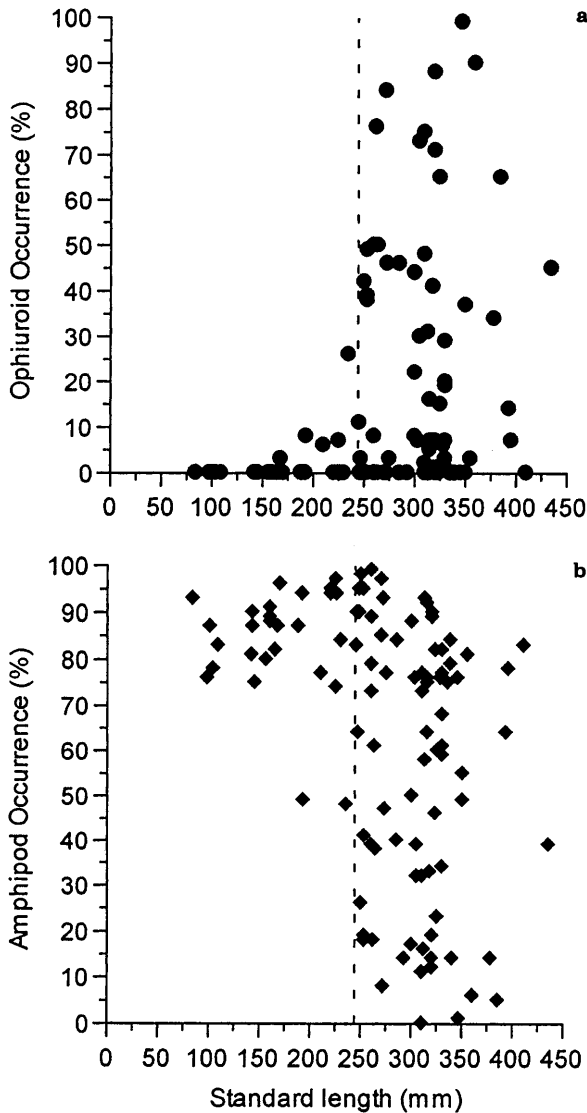
Fig. 4 *Cheilodactylus spectabilis*. Occurrence of ophiuroids (**a**) and amphipods (**b**) in guts as a function of fish length

Table 1 *Cheilodactylus spectabilis*. Eigenvectors of principal-components (*PC*) analysis examining trends in variance of dietary components. Percentage of total variance accounted for by first two components is given [* Dietary categories that contributed most to components (only those > 70% of maximum eigenvalue have been interpreted)]

Variable	PC 1 (25.3%)	PC 2 (17.7%)
Amphipods	0.667*	−0.107
Crabs	−0.222	0.436
Echinoids	0.000	0.658*
Gastropods	0.245	0.162
Isopods	0.134	0.479*
Ophiuroids	−0.554*	−0.155
Ostracods	0.073	−0.293
Polychaetes	−0.336	0.003

amphipods in the winter sample. The second trend (PC 2: co-occurrence of echinoids and isopods) differed among size classes in a similar way to that shown in Fig. 2, where trends in Canonical Variate 2 are largely driven by the co-occurrence of echinoids and isopods. Tukey's tests suggested that the co-occurrence of these two food items was commonest in the mid-sized fish (Size class B). There is a suggestion that this relationship may differ among seasons ($p = 0.053$, Table 2), with Tukey's tests suggesting that the relationship may be stronger in spring.

There was no difference in diet between male and female *Cheilodactylus spectabilis*. A MANOVA on a similar size range of males and females found no significant difference in the occurrence of the eight food categories for any of the size classes, pooled over seasons (sex:Pillai's trace = 0.070, $F = 0.703$, df 8, 75, $p = 0.688$; sex × sizeclass:Pillai's trace = 0.209, $F = 1.110$, df 16, 152, $p = 0.351$). An analysis of variance of the first principal component revealed that the negative relationship between the occurrence of amphipods and ophiuroids did not differ between the sexes ($F_{1,86} = 0.07$, $p = 0.790$).

analysis shows that this relationship changed for a given size class among seasons (Table 2, size–season interaction). However, this was more an artefact of a small sample size than being biologically meaningful. Specifically, means comparisons (Tukey's HSD) suggest that the contribution of amphipods and ophiuroids to the diets of fish > 350 mm SL differed between winter and summer. Examination of the raw data suggests this was driven by three fish that had fed predominantly on

Feeding structures and foraging techniques

During foraging, the down-tilted head is oriented to the feeding substratum by the sweeping action of the large palmate pectoral fins. Long fin-rays act as stabilisers, preventing lateral roll during feeding. These fins have a dual purpose of manoeuvring the fish to an appropriate feeding site and acting as a pivot around which intense feeding episodes are centred. Once the pectoral fins have

Table 2 *Cheilodactylus spectabilis*. Main relationships between prey items in gut identified by principal-components analysis (non-transformed correlation matrix) and compared among three size classes over four seasons by analysis of variance. Data are probabilities of wrongly rejecting null hypothesis of no difference in dietary trend (for size classes, seasons and their interaction)

Principal component	Relationship	Size class	Season	Size class × season
1	Ophiuroids ∝ - amphipods	0.005	0.005	0.014
2	Echinoids and isopods	0.017	0.053	0.873

oriented the mouth towards the target site, a sharp flick of the caudal fin propels the feeding apparatus into the algal or rock substratum. This force moulds the thick fleshy lips (typical of cheilodactylids and tropical plectorhynchids) to the contours of the feeding substratum, thereby concentrating the suction force in the small area bounded by the lips. At the same time, the algal material is raked by fine teeth that line the premaxillae and dentary.

Prey is brought into the mouth by a powerful suctorial force produced by the rapid expansion of the buccal cavity. The speed of this movement causes an audible crack. The buccal cavity is expanded by the combined movement of the operculum, palate and hyoid complex. With the lowering of the mandible, there is an associated contraction of the muscle joining the dorso-anterior edge of the operculum to the neurocranium. This causes the operculum to rotate upward and anti-clockwise around its pivot on the hyomandibular knob. At the same time, the muscles of the palate contract. By doing so the suspensorium, which forms the roof of the buccal cavity, is pulled dorsolaterally. Lastly, the hyoid (of which a large "tongue" forms a major part) is pulled posterioventrally by the constriction of the large hypaxial and associated muscles. These three movements combine to expand the buccal cavity to about seven times its volume when constricted.

Once material is in the mouth, debris is sorted from edible prey items. This is done by rhythmical and sequential contraction of the hyoid complex, operculum and branchial muscles. Water is drawn through the mouth, past the gill rakers on the first gill arch, and out through the operculum, carrying with it particles sufficiently small to pass unhindered through the gill rakers. These include sand, arthropod moults, harpacticoid copepods and the juvenile stages of many amphipod species. Larger material trapped within the buccal cavity is sorted by a combination of water circulation and the action of a large ridged tongue. Heavier, inedible material is forced to the front of the buccal cavity, where it is held by the hyoid ridge until being ejected from the mouth at the end of feeding. Smaller particles are carried past the ridge and accumulate at the rear of the buccal cavity. This winnowing process is very efficient, and no sediment was found in the guts of any of the fish sampled.

Feeding selectivity

The benthic samples collected concurrently with the summer fish sample had a similar assemblage of invertebrate fauna to that found in the guts of *Cheilodactylus spectabilis*. Fish and benthos did, however, significantly differ in the percent occurrence of the various invertebrate categories (MANOVA, Pillai's trace = 0.954, $F = 52.89$, df 8, 20, $p = 0.0001$). A CDA revealed that the reason for this difference was the low number of gastropods and ostracods in the diet compared to the numbers in the turf substratum (Table 3, Fig. 5). The

Table 3 *Cheilodactylus spectabilis*. Mean percentage taxonomic composition of diet and of turf samples collected by air-suction pump

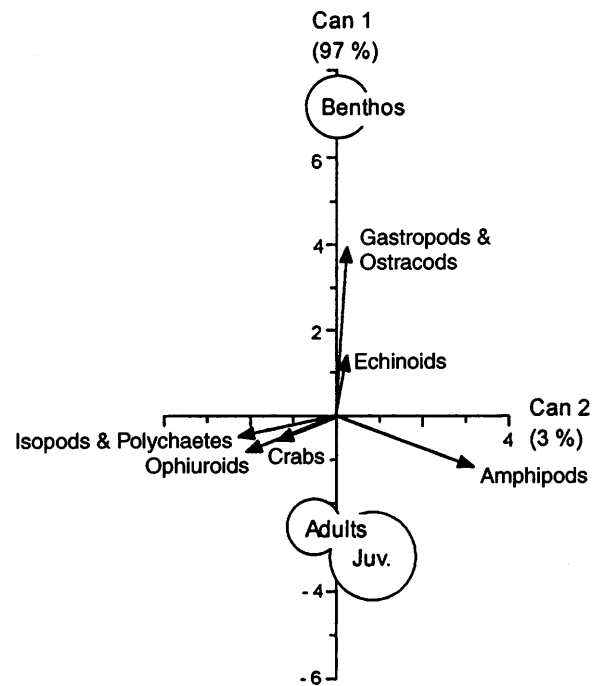| Variables	Fish diet	Turf samples
Amphipods	58.23	45.00
Crabs	4.70	0.25
Echinoids	0	0.13
Gastropods	2.50	28.60
Isopods	0.75	0.25
Ophiuroids	12.91	0
Ostracods	1.23	10.90
Polychaetes	18.5	10.50

Fig. 5 *Cheilodactylus spectabilis*. Comparison of invertebrate fauna associated with turf substrata and diets of juvenile s (<250 mm standard length) and adults (>250 mm standard length) collected from same site. Canonical discriminant-analysis reveals position of mean centroids and 95% confidence limits with respect to trends in original variables

difference in taxonomic composition between the fish diets and benthic samples (97% of the total variability) overshadowed the difference between juvenile and adult diets (3%).

Size classes of *Cheilodactylus spectabilis* differed substantially in the sizes of amphipods they consumed. The mean amphipod size in the guts of fish <250 mm SL was significantly smaller than in larger individuals [1.71, 2.29 mm, respectively; Student's $t = -5.25$, df 54, $p < 0.001$, log $(x + 1)$ transformed]. This predator–prey size relationship may be a consequence of the strong correlation between gill raker gap and standard length ($r^2 = 0.43$, $p < 0.001$). A strong relationship between the inter-raker distance on the first gill arch and the mean size of prey items consumed could be expected,

given the oral winnowing amphipod size consumed described in the foregoing subsection.

However, there was no relationship between amphipod size consumed and the distance between gill rakers ($r^2 = 0.07$, $p > 0.05$). The mean amphipod length was consistently larger than the gill raker gap (mean ratio of amphipod size to raker gap = 2.96). Body width or depth of the prey may set the lower boundary for prey retention, and had these dimensions been measured there might have been a stronger relationship between amphipod size and gill raker gap. However, it is probable that inter-raker distances increase with the degree of buccal cavity expansion, and therefore the inter-raker distance measured in this study may significantly overestimate actual retention probabilities.

An examination of how other body variables correlate with the mean prey size yielded interesting results (Table 4). Those body characteristics that correlate strongest with standard length also have the strongest relationship with amphipod size consumed. This suggests that the mean size of prey consumed is a function of the fish's overall body size rather than of any specific part, such as inter-raker distance. Only large sizes of *C. spectabilis* preferentially consumed amphipods that were larger than the average size of those present in the turf (Table 5). This difference in the size of amphipods consumed as a function of fish length may be due to suctorial force. Having a larger buccal cavity and associated hypaxial and palate musculature, large fish can exert a greater suctorial force than smaller individuals. Similarly, the initial impact with the substratum and subsequent raking of the dentary over the feeding surface could dislodge more large amphipods from the substratum.

Diel and depth-related patterns of feeding and microhabitat preferences

The occurrence of individuals foraging when first observed differed markedly among size classes and with

Table 4 *Cheilodactylus spectabilis*. Correlations of body morphology with mean length of amphipods consumed (morphological variables were measured as detailed in Fig. 1 of McCormick 1989a) (*SL* standard length; *nt* no test)

Fish morphology	Correlation coefficient with:	
	fish length (SL)	amphipod length
Standard length	nt	0.65
Amphipod length	0.65	nt
Snout angle	−0.06	0.06
Cheek depth	0.98	0.69
Pectoral fin length	0.87	0.50
Anal fish depth	0.96	0.72
Eye diameter (max.)	0.97	0.71
Snout width	0.89	0.47
Snout length	0.96	0.73
Head length	0.99	0.67

Table 5 *Cheilodactylus spectabilis*. Comparison of length of amphipods found in guts of juveniles (i.e. < 250 mm SL) and adults and those found in turf samples collected from same site

Sample	Mean (*df*) amphipod length (mm)	Student's *t*-statistic	*p*
Juveniles	1.59 (*116*)	1.77	0.079
Adults	2.11 (*116*)	7.52	0.0001
Turf	1.45		

time of day (Fig. 6). There was a trend for larger individuals to feed less and rest more than smaller size classes. In all fish there was a dawn and dusk peak in
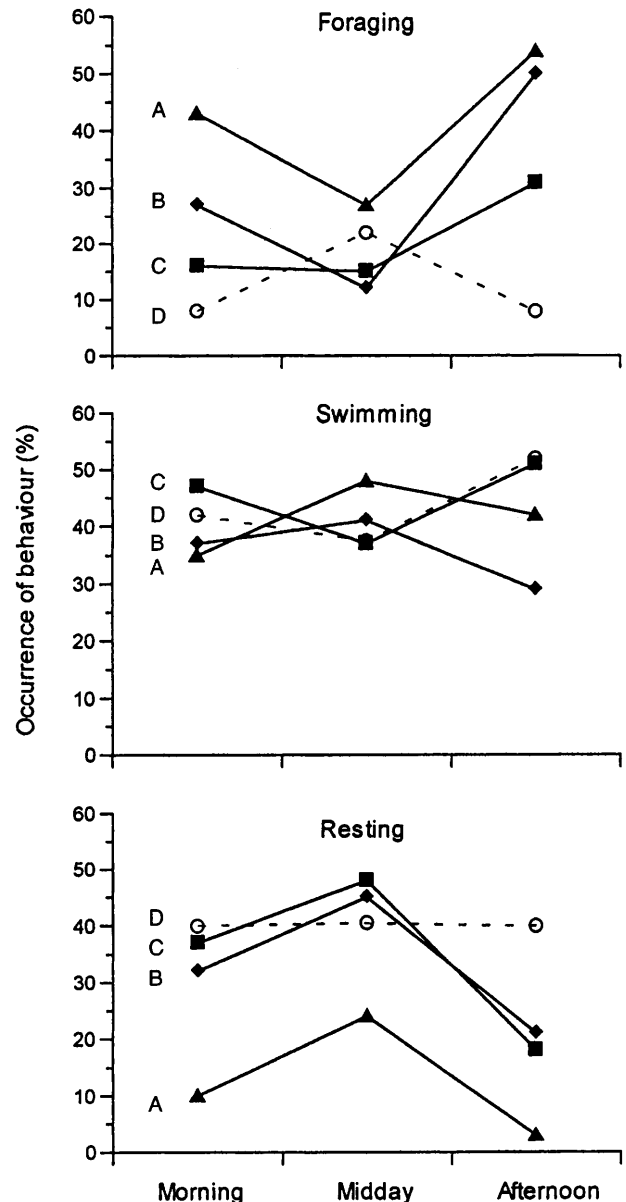

Fig. 6 *Cheilodactylus spectabilis*. Diel patterns of behaviour determined from 100 behavioural observations of each size class for each size × time combination (*A* ≤ 250 mm; *B* > 250 ≤ 350 mm; *C* > 350 ≤ 450 mm; *D* > 450 mm standard length)

general activity (swimming and foraging combined). However, this became less accentuated with increasing fish size. A crepuscular peak in foraging was displayed by the two smallest size classes (A and B), while the largest fish (D) exhibited an opposite pattern, with most feeding occurring at midday (Fig. 6).

Behaviour changed markedly as a function of depth for fish < 450 mm SL (Fig. 7). In these fish, ≃50% more foraging occurred in the shallows than at mid depths, while < 10% foraged in depths below 17 m. There was an increase in the number of fish found swimming with increasing depth for all size classes.

Patterns of resource-use differed among size classes of fish on a microhabitat scale (Fig. 8). Fish < 250 mm SL fed almost exclusively on the flat faces of boulders and rockflats. Feeding was concentrated on areas of dense coralline turf that trapped large amounts of sand. Virtually all bites required winnowing. Large individuals (> 350 mm SL) had two main feeding modes. The majority fed from crevices that dissected the turf flats. These accumulated sand and debris, and consequently bites from these substrata required winnowing of separate prey items from inedible material. Often a number

of bites were required to fill the large buccal cavity before winnowing commenced. A second group of individuals concentrated on areas of more heterogeneous microtopography; including haptera of the laminarian kelp *Ecklonia radiata*, beds of the brown algae *Carpophyllum* sp., algal holdfasts and associated turf. Large prey items such as chiton, ophiuroids and polychaetes were common in these areas (author's personal observation).

Feeding rates differed markedly among size classes (Fig. 9; Table 6). Bite rates per minute decreased with increasing size. Analysis also suggests that bite rate varied with time of day, with feeding more intense in the morning and afternoon than at midday for all size classes (Table 6).

Growth

In this long-lived species, males grow much faster than females and reach a larger maximum size (Fig. 10). Growth of the sexes diverged at ∼280 mm SL, with the females showing a marked leveling off of growth after

Fig. 7 *Cheilodactylus spectabilis*. Depth-related patterns of behaviour for four size classes (**A** to **D**, as in legend to Fig. 6) determined from behavioural observations of 100 fish of each size class at each depth
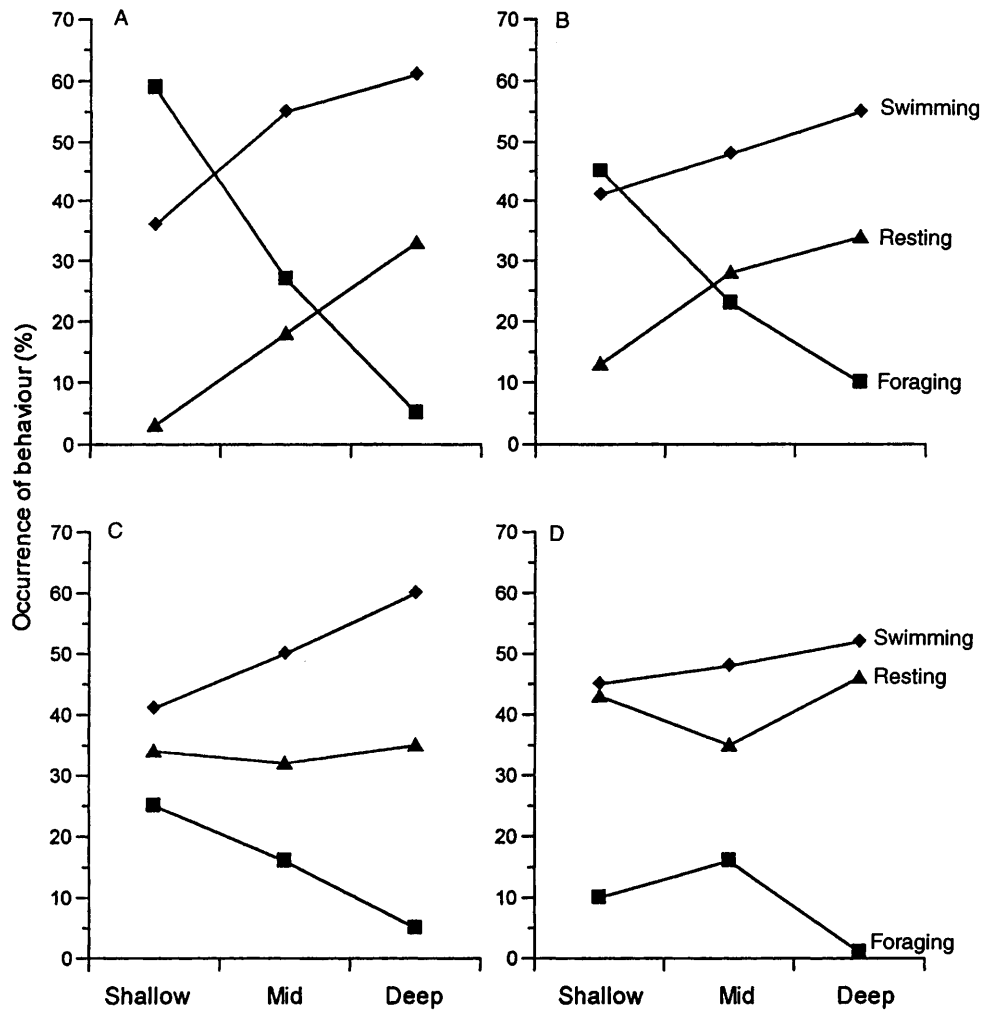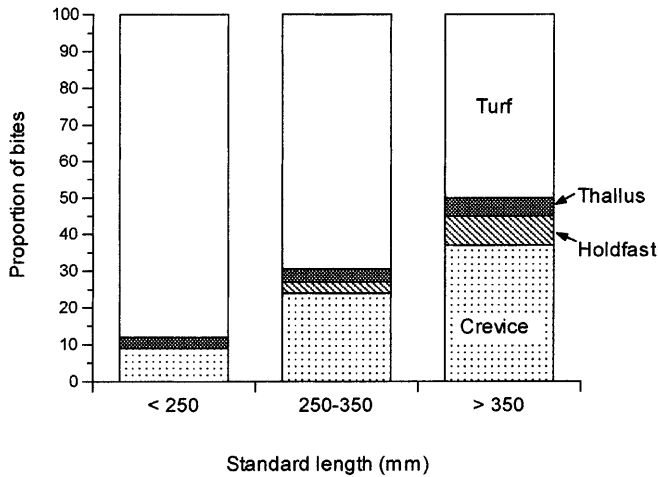
Fig. 8 *Cheilodactylus spectabilis.* Pattern of microhabitat selectivity in foraging as a function of size
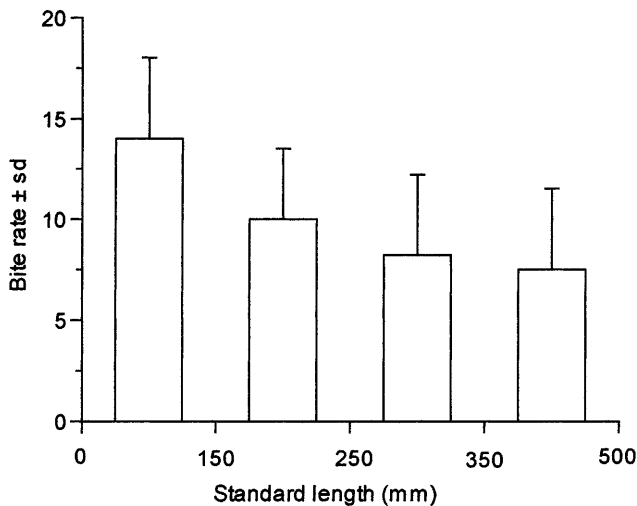

Fig. 9 *Cheilodactylus spectabilis.* Comparison of bite rates (bites per min) for four size classes

this size (Fig. 10). Males continued their linear growth phase for an additional 150 mm SL, and could reach sizes of 320 mm SL after 3 yr.

Discussion

The ontogenetic shift that occurs in the diet of *Cheilodactylus spectabilis* is partly driven by structural changes in feeding apparatus and morphology that open up new and unexploited feeding opportunities. The size of the feeding structure alone can enable the exploitation of differing food sources and influence food selectivity (Stoner and Livingston 1984; Wainwright 1988; MacNeill and Brandt 1990). For *C. spectabilis*, the increases in the size of the buccal cavity, hyoid complex and associated musculature lead directly to an increase in the suction primarily used to capture prey. This allows large fish to exploit more complex microtopography such as algal holdfasts, where ophiuroids and polychaetes are common.

Diet shifted dramatically at 250 mm SL from predominantly amphipods to ophiuroids. Interestingly, this coincides with the start of gametogenesis in both sexes (McCormick unpublished data). Gonad histology indicates that females have fully developed ovaries at ~250 mm SL, while males may mature later at ~300 mm SL (McCormick 1989b). This size also coincides with a marked slowing of the growth and a movement of males into deeper water (McCormick 1989a). A change in diet at approximately the time of sexual maturity is not uncommon. MacNeill and Brandt (1990) found that shifts in prey coincided with the transition from juvenile to sexually maturity in the clupeid *Alosa pseudoharengus*, and suggested that diet shifts were an adaptation to the increased requirements for gamete production. Energetics have also been used to explain the switch between algal food types from reproductive to non-reproductive seasons in the surgeonfish *Acanthurus nigrofuscus* (Fishelson et al. 1987). For *Cheilodactylus spectabilis*, there appears to be a strong temporal link between initial maturity and a slowing of growth, but whether this necessitates the abrupt shift in dietary focus remains unclear.

Interestingly, sex did not influence the diet of *Cheilodactylus spectabilis* or the timing of ontogenetic shifts in prey composition, despite the fact that males had an extended period of rapid growth and frequented the deeper regions of the reef (McCormick 1989a). Although few studies distinguish between sexes of fish in ecological analyses of foraging, it is likely that gender-based difference in diet are commonplace. Distribution patterns and behaviour are often gender-specific (e.g. Robertson and Warner 1978; Moyer et al. 1983), and gender-differences in foraging patterns have been demonstrated for some fish species (e.g. Hoffman 1983; Gillanders 1995). Part of the reason why the male habitat-shift and difference in energy requirements are not expressed in the

Table 6 *Cheilodactylus spectabilis.* Comparison of bite rates during three times of day (morning, 06:00 to 10:30 hrs; midday, 11:30 to 14:00 hrs; afternoon, 15:30 to 19:30 hrs) and four size classes of fish ($SL \leq 150$ mm; $SL > 150 \leq 250$ mm; $SL > 250 \leq 350$; $SL \geq 350$ mm). Data log $(x + 1)$-transformed

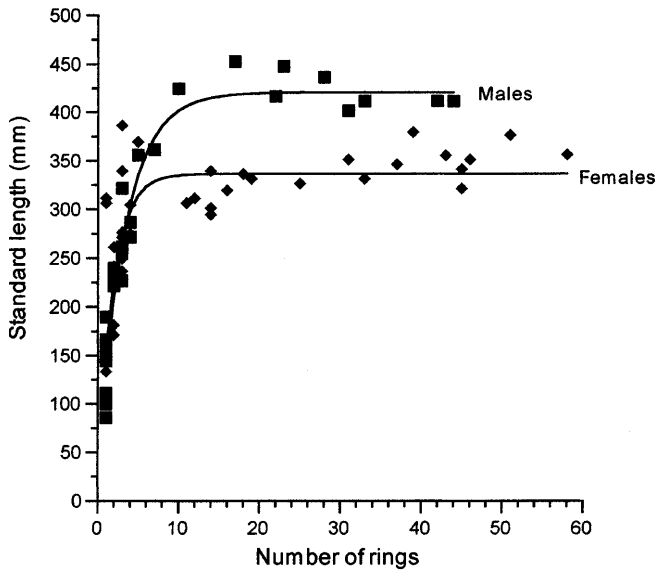| Source	(df)	Mean square	F	p
Time	(2)	0.630	3.99	0.02
Size	(3)	4.385	27.74	0.0001
Time × size	(6)	0.257	1.63	0.15
Residual	(228)	0.158		

Fig. 10 *Cheilodactylus spectabilis.* Growth of males and females, showing a divergence growth at ~280 mm standard length (SL). Von Bertalanffy growth models were fitted to males and females separately (males: $L_\infty = 420.9$ mm SL, $K = 0.30$, $T_0 = -0.303$; females: $L_\infty = 337$ mm SL, $K = 0.523$, $T_0 = -0.187$; where: L_∞ = maximum length obtained; K = growth constant; T_0 = x-axis intercept)

diet of *C. spectabilis* is that males have large home ranges and feed most intensively in the shallow portions of the reef inhabited by the juveniles and females.

Ontogenetic dietary shift in *Cheilodactylus spectabilis* does not appear to be associated with the migration of males offshore. However, within the shallow broken-reef habitat (McCormick and Choat 1987) where all sizes of fish feed, individuals did display microhabitat preferences during foraging that were size-related. These differences in microhabitat selection appear to be made possible by increasing head size and associated musculature, and ultimately appear to account for ontogenetic dietary changes. It appears that juvenile *C. spectabilis* do not possess the suction force to remove ophiuroids and polychaetes from the interstices of crevices and algal holdfasts. Differences in foraging patterns at this small spatial scale have seldom been found to be important in determining ontogenetic dietary trends. Holbrook and Schmitt (1984) found that juveniles and adult surfperches (*Embiotoca jacksoni*) selected between foliose algae or algal turfs and were able to differentiate the quality of individual patches (prey density) within each algae type. In this instance, however, habitat choice was found to be driven by a mechanical requirement (adults winnowed while juveniles picked) and by the need for shelter from predators, which is met by foliose algae.

Despite the differences in the size of the prey captured by juveniles and adults, the taxonomic composition of the prey items remained very similar. This is surprising given the ontogenetic change in feeding morphology and use of foraging substrata. Dramatic dietary shifts often

accompany use of different microhabitat for foraging (e.g. Werner and Hall 1977; Bowen and Allanson 1982). This suggests that, in the present study, the prey composition among the foraged substrata was similar. Many of the taxa present in the diets of juvenile and adult *Cheilodactylus heilodactylus spectabilis* are known to be highly abundant on laminarian and fucoid algae (Kingsford and Choat 1985; White 1989). One implication of this prey-size difference is that, although juveniles and adults feed on the same prey, their different feeding mechanics and substrata foraged means that they are effectively not directly exploiting the same resource. This would reduce the intensity of competition if food became limiting at any stage. The only other study to find ontogenetic differences in prey size without changes in gross taxonomic composition was of the Californian black surfperch *Embiotoca jacksoni* (Schmitt and Holbrook 1984).

The present study found that *Cheilodactylus spectabilis* consumed prey in proportions that differed from those present in the algal turf, suggesting some degree of selectivity. Amphipods tended to be selected, while gastropods and ostracods were consumed much less than would be expected had fish been feeding non-selectively. Sylvester (1986), in a comparative study of demersal fish-feeding in the Leigh Marine Reserve, found no evidence that *C. spectabilis* consumed some amphipods in preference to others species. The most common species present in the turf, *Gammaropsis typica*, *Podocerus karu*, and *Ischyocerus longimanus*, were consumed in proportion to their abundance. However, while *C. spectabilis* does not appear to select among amphipod species, the present study found that adults (>250 mm SL) preferentially consumed amphipods that were larger than the average size of those present in the turf.

It is commonly expected that for planktivores and winnowing benthic microcarnivores the mean prey size will be strongly related to the distance between gill rakers (e.g. Hessen et al. 1988; Eggold and Motta 1992; Langeland and Nøst 1995). Theoretical models of retention efficiencies predict that gill rakers operate as passive sieves, retaining only those particles that are larger than the spacing between gill rakers (e.g. Drenner et al. 1978). However, this rarely occurs under normal feeding conditions (e.g. Langeland and Nøst 1995). Evidence for *Cheilodactylus spectabilis* illustrates a huge discrepancy between mean amphipod size and the mean gap between gill rakers, with much lower retention than would be predicted by inter-raker distance. For the white crappy *Pomoxis annularis* Wright et al. (1983) found that inter-raker distance increased with buccal cavity expansion, and that inter-raker distances measured on moribund fish may overestimate retention probabilities dramatically. For the bream *Abramis brama*, Hoogenboezen et al. (1991) also found that the inter-raker distance within and among gill arches in the branchial sieve changed throughout the feeding action. This appears to be the case for *C. spectabilis* also: during

feeding, the seven-fold increase in the volume of the buccal cavity distorts the distance between rakers, allowing the passage through the operculum of amphipods that are larger than would be predicted from inter-raker distance.

A number of factors have not been assessed that may contribute to the changes in diet observed among size classes of *Cheilodactylus spectabilis*. Exposure of individuals to predation has been shown to be an important determinant of microhabitat use in both freshwater and marine fishes (e.g. Holbrook and Schmitt 1988 a, b; Werner and Hall 1988), and may influence the patterns documented in the present study. This is particularly true of recent recruits, for which predation may be an important determinant of space use. Such individuals are highly territorial among like-sized conspecifics, and this results in a restriction of the microhabitats available for foraging. Regardless of the mechanisms underlying ontogenetic changes in space use, this study has shown that ontogenetic diet changes are substantially affected by size-related morphological changes which open up new opportunities to exploit extensions of the same resource (subtle microhabitat shifts). It appears that although all fish feed on exactly the same prey taxa, the different size classes of fish effectively partition the food resource by utilising different sizes of prey items and by progressively shifting emphasis to larger prey taxa with increasing size. The abruptness of the dietary shift, that loosely coincides with the onset of maturity, is puzzling, and points to release from some as yet unexplored foraging constraint.

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