Ontogenetic Diet Shift and Feeding Activity in the Temperate Reef Fish *Cheilodactylus fuscus*

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The red morwong, *Cheilodactylus fuscus*, is a large and conspicuous temperate reef fish of south-eastern Australia and is a popular target of spearfishers as well as an indicator species of bioaccumulation for water quality authorities. *C. fuscus* is a benthic carnivore, feeding on crustaceans, polychaetes and molluscs. Amphipods and other small benthic crustaceans (tanaids, cladocerans, cumaceans and mysids) constitute over 60% of the diet of juvenile fish (<200 mm standard length, SL), but only 35% of the adult diet (200 to 390 mm SL), and <20% of large adult diet (360 to 500 mm SL, which were obtained from spearfishing competitions). Adult and large adult fish consume significantly greater proportions of brachyurans, molluscs and echinoderms than juveniles. Juveniles occur over turfing algae in the upper sub-tidal region to depths of five metres, and feed continuously throughout the day, with bite rates of up to 16 per minute and high gut fullness (60–100%) throughout the day. Conversely, adults occur in deeper sub-tidal habitats (between five and 18 metres), rarely feed during the day (<4 bites per minute) and adult gut fullness declines from >50% in the early morning to <18% by early afternoon. Ontogenetic and diel factors as well as habitat choice influence the diet of this cheilodactylid. The crepuscular nature of feeding in adults of this species is in contrast to several other cheilodactylids which feed during the day.

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INTRODUCTION

Temperate reefs provide a habitat for a diverse assemblage of fishes which obtain food and shelter from the rocky reef. High densities of attached organisms and numerous interstitial animals provide an important food source for benthic feeding carnivorous reef fishes (Russell 1983). These fishes are the most speciose, and often the most abundant group of temperate reef fishes (Berry et al. 1982; Jones 1988; Holbrook et al. 1990). On the rocky reefs of north-eastern New Zealand, Russell (1983) found 36 of the 44 species examined to be carnivores, with 29 benthic feeders, and 7 species considered to be open water feeders (Russell 1983). This pattern is repeated in other temperate reef fish assemblages, with benthic feeding carnivores being the dominant group on temperate reefs of California (Kotrshcal and Thomson 1986; Holbrook et al. 1990) and South Africa (Berry et al. 1982).

Many fish undergo an ontogenetic shift in diet which may encompass changes in the mean size of prey (Leum and Choat 1980; Schmitt and Holbrook 1984) and even in the dominant prey categories and trophic status (Werner and Gilliam 1984). On rocky reefs of north-eastern New Zealand, 11 of the 13 species for which dietary information exists show widely differing diets as juveniles compared to adults (Jones 1988 and references therein). Diets may also vary seasonally in relation to seasonal changes in prey abundance (Bell 1979; Jones 1988; Gillanders 1995), or may vary geographically (Jones 1984; Cowen 1986; Gillanders 1995).

The temperate reef fishes of New Zealand have been relatively well studied (reviewed by Jones 1988) and these studies provide some insight into the feeding ecology of Australian temperate reef fishes because of the overlap in species and family distributions. While there have been comparatively fewer studies on the diets and feeding behaviour of Australian temperate reef fishes, those that have been conducted show similar trends in feeding behaviour such as ontogenetic shift in diet (Gillanders 1995) and feeding rates (Cappo 1980), and seasonal changes in diet (Bell et al. 1978; Bell 1979; Gillanders 1995).

The family Cheilodactylidae (Perciformes) is distributed throughout the southern hemisphere and parts of Japan. It is well represented in Australia and New Zealand, being common inhabitants of temperate reefs. Most cheilodactylids are diurnally active benthic carnivores, consuming mainly gammaridean amphipods, decapod crustaceans, polychaetes and molluscs (Godfriaux 1974; Bell 1979; Leum and Choat 1980; Cappo 1980; Russell 1983; Sano and Moyer 1985; Wöhler and Sánchez 1994). Ontogenetic changes in feeding behaviour have been observed in several species including *Cheilodactylus spectabilis*, found on New Zealand and southern Australian reefs (Leum and Choat 1980); *C. nigripes*, found off southern Australia (Cappo 1980, 1995); and *C. bergi*, a demersal species from the south-east coast of South America (Wöhler and Sánchez 1994).

The red morwong (*Cheilodactylus fuscus*) is a large (up to 650 mm total length), conspicuous and abundant, temperate rocky reef fish. While not a commercially important species, it is a popular spearfishing target (Lincoln Smith et al. 1989) and has been used by local authorities as an indicator species of organochlorine and heavy metal bioaccumulation (Lincoln Smith and Mann 1989). In a study on the diet of large adult red morwong obtained from spearfishing competitions, Bell (1979) identified the species as a benthic carnivore and observed seasonal changes in diet. This study only examined stomachs (not the entire gut), of which 93% were between empty and half full, and did not investigate diel feeding periodicity, or the diet of juveniles. Bell (1979) postulated that there was little feeding during the day and concluded that further work was required on the diet of juveniles. No evidence of crepuscular peaks in feeding activity was reported for a similar species, *Cheilodactylus spectabilis* (Leum and Choat 1980), and has not been reported in studies on temperate reef fishes in California (Ebeling and Bray 1976).

The objectives of this study were to firstly investigate the feeding ecology of *C. fuscus* and compare this with the results of Bell (1979), and secondly to investigate the presence of any ontogenetic or diel shift in diet by comparing the diet of three different size groups of *C. fuscus* at three different times of day.

MATERIALS AND METHODS

Field procedure

Specimens of *C. fuscus* used for gut analysis (97 in total) were collected by hand-spear whilst using SCUBA from various sites in the eastern region of Sydney Harbour (mostly Middle Head and Quarantine Bay) between January and April 1993 (see Lowry and Suthers 1998 for site details and map). Fish were divided into size groups before analysis. Juvenile fish (n=20) were those <200 mm with undeveloped gonads (Schroeder et al. 1994) and an average standard length (±S.E.; range) of 155.5 mm (±3.6; 120–185) and weight of 67.6 g (±4.5; 30.8–112.4). Adult fish (n=52) were those from within Sydney Harbour, averaging 307 mm SL (±7.5; 202–390) and 569 g (±40.6; 140–1099). The sites selected for collection of fish were typical of the red morwong habitat, consisting of a boulder field, flat rock and kelp cover between 0 and 20%, in depths of 2 to 12 m. Fish were sampled during three diel periods: 0600 to 1000 h (11 juveniles, 26 adults), 1000 to 1400 h (6 juveniles, 10 adults) and 1400 to 1800 h (3 juveniles, 16 adults). Fish were placed on ice, and upon returning to shore the weight and standard length were measured before the entire intestinal tract (gut) from the stomach to the anus was removed and fixed in 10% formalin for sorting in the laboratory (see below).

The intestinal tracts (guts) of an additional 25 large adult specimens were obtained from spearfishing competitions. These competitions were held along the Sydney coast (Manly to Cronulla) and the south coast of NSW (Jervis Bay) between August 1992 and March 1993 (Lowry and Suthers 1998). Competitors leave shore at 0900 h and collect fish from inshore rocky reefs along the open coast before returning at 1300 h to have their fish "weighed in". Once fish had been weighed, the guts of specimens of *C. fuscus* were removed and preserved in 10% formalin. Because more points are awarded for larger individuals, the guts collected from spearfishing competitions were from larger fish than the adults sampled in Sydney Harbour (see above), averaging 418 mm SL (±8.2; 363–498) and 1273 g (±66.4; 850–1680).

Feeding behaviour

Adult and juvenile fish were observed at sites in Sydney Harbour and off Clovelly, approximately 10 km to the south of the Harbour along the open coast (see Lowry and Suthers 1998). Fish were observed during the day using SCUBA from a distance of 5 to 10 m with most observations lasting four to five minutes. Juveniles that were feeding and constantly moving were sometimes only observed for 30 seconds, while the behaviour of adults that were stationary for long periods was monitored for up to 6 minutes. During the observation period the number of bites made at the substratum was counted and then this was converted to number of bites per minute. Generally juveniles were not disturbed by observation and fed continuously, while adults tended to be more wary if approached to within 5 m. A correlation was performed to determine whether the number of bites per minute at the substrata was related to the period of time the fish was observed. This relationship was not significantly different from zero ($r=0.10$, $p=0.46$).

Laboratory procedure

A gut fullness ratio (C/F) was devised for use in later gut analysis. This was calculated by dividing the weight of the gut content (C) by the weight of the entire intestinal tract when full (F). Guts had a C/F value of approximately 0.8 when full, 0.4 when half full and <0.15 when empty. All guts containing food were used to determine the general diet but only guts from adults sampled in the early morning, from juveniles and from the spearfishing competitions, were used in the comparison of the diets for the different size classes. These guts ranged from half full to full (C/F of 0.4 to 0.8) with no significant difference (One-way ANOVA, $P=0.10$) in C/F values between the three size groups. The gut contents were rinsed through three sieves of 1 mm, 300 μm and 100 μm mesh sizes. The three size fractions were then drained, weighed and their volumes were measured by displacement of water in a measuring cylinder. The 1 mm and 300 μm fractions were then analysed using the points method (Pollard 1973; Hyslop 1980) and the occurrence method (Hyslop 1980). Only half of the large samples were analysed and the results were doubled to give abundances of the prey categories.

The points method provides a subjective estimate of the volume of different prey categories in the diet (Hyslop 1980). In this method of gut analysis each food category present in individual guts is assigned points based on a subjective estimate of its volume. If gut fullness is taken into account, each gut is assigned a weighting factor and then the points for each stomach are adjusted accordingly (Hyslop 1980; Harris 1985). Points for each food type are then summed over all guts examined and the results expressed as a percentage of the total number of points allocated to all food types, i.e. percentage volume (Hynes 1950; Pollard 1973; Hyslop 1980). While the points method is less accurate than more exact techniques (Pollard 1973; Hyslop 1980), it provides a means of more rapidly analysing larger volumes of material. The occurrence method simply expresses the number of stomachs containing a particular prey category as a percentage of all stomachs containing food (Hyslop 1980).

In this study an estimate of the volume of each prey category was made in a way similar to that of Choat and Clements (1992) and Gillanders (1995). The separate fractions (1 mm and 300 μm) were spread evenly over a 100 point, 10 mm grid in a Petri dish. Prey items falling on each point were identified and recorded giving a percentage proportion, or points out of 100, for each category. Whole prey items and fragments falling upon each of the 100 grid points were counted and placed into the taxonomic categories listed in Table 1. To take into account gut fullness, each gut was weighted according to the value of its gut fullness ratio and the total points for each gut were then multiplied by its weighting factor. To determine the consistency of this method eight samples were replicated and no significant differences (t-tests on major prey items, all $p>0.05$) were obtained between initial and replicated analyses. The weight and volume of the 100 μm fraction were determined, but because this fraction consisted mostly of flocculate matter and a small amount of crustacean remains it was not analysed further. While the results of the points method can be used to calculate the exact volume of particular prey items (in ml) from the volumes of the size fractions (see above), the results for this study are presented as percentage volumes obtained from the points method analysis.

The volume of each prey item was compared among groups (juvenile, adult, large adult) using a one way ANOVA and Scheffe's post-hoc test. Probability levels for rejecting the null hypotheses were adjusted by the number of prey-item comparisons made on the particular set of data ($P<\frac{0.05}{n}$). Normality was inspected from the frequency distribution, and homogeneity of variances was tested using Cochran's test. When necessary prey item points data were transformed using a $\log_{10}(x+1)$ transformation.

RESULTS

General diet

Gut analysis results for all fish with guts containing food (n=81) showed *C. fuscus* to be a benthic carnivore consuming mostly crustaceans, with smaller amounts of polychaetes, molluscs and echinoderms (Fig. 1, Table 1). The predominant crustaceans in the diet were gammaridean amphipods (average volume >30%), and brachyurans (10%). Other small Crustacea (comprising tanaids, cladocerans, cumaceans and mysids), as well as isopods, contributed 13% of the overall diet by volume. Polychaetes were the second most abundant prey item by volume after crustaceans (14%). Gastropod snails and bivalves were the most abundant molluscs by volume (4.5%), while limpets, chitons and abalone occurred in minor proportions. The echinoderm group consists of both echinoids (mostly juvenile *Centrostephanus* sp.) and ophiuroids. Algae was also present in the diet, but only in small, incidental amounts.

In terms of the level of occurrence of these major prey items in guts containing food (Table 1), amphipods and molluscs occurred in 100% of fish, isopods in 94%, brachyurans in 87% and tanaids in 51%. Polychaetes and algae occurred in 99% and 86% of guts respectively. The mean number of food items per gut was found to be 12.2 (standard error = 1.4), with the lowest number of items in any one gut being 3 (in a juvenile) and the greatest 18 (in an adult).

Ontogenetic variation in diet

Most of the 30 prey groups identified in the diet of *C. fuscus* occurred in all three size groups examined, except abalone and barnacles which were not consumed by juveniles. Some differences between the groups were observed in the occurrence of certain items. The larger molluscs (chitons, abalone and limpets), crabs, echinoderms and algae all occur in fewer juvenile guts than both adult groups, while small crustaceans (ostracods and tanaids) occur more in the diet of juveniles than in the diet of adults (Table 1). The differences in the diets of the three size groups were more obvious when comparing the proportion by volume of dietary items between the three groups (Fig. 1). Juvenile gut contents had significantly more amphipods (1 way ANOVA, P<0.001), small crustaceans and tanaids (P<0.001) than adult or large adult *C. fuscus*. Conversely, both adult groups consumed a significantly larger proportion of brachyurans and anomurans (approximately 14%) than juveniles (1%; P<0.001), as well as a greater proportion of echinoderms (1% in juveniles compared with 6% in adults and 7% in large adults, P<0.05) and molluscs (4% in juveniles compared with 7% in adults and 13% in large adults, P<0.01).

Some differences were also found between the diets of adult and large adult fish. Adult fish consumed a significantly greater volume of amphipods than large adult fish (approximately 31% versus 19%, P<0.001), and adults also consumed significantly more isopods (12%) than both juveniles and large adults which consumed similar proportions (3% and 5% respectively). The difference in diet between adult and large adult fish could be due to geographic variation in diet rather than size, as the adult fish came from Sydney Harbour while large adult fish came from a range of coastal regions outside the harbour. To investigate the possibility of geographic variation, we compared the diets of the eight largest adult fish from Sydney Harbour (335 to 390 mm SL), to the eight smallest specimens from the spearfishing competitions (360 to 400 mm SL). There was no significant difference in the volume of amphipods in the diet of similar sized adult and large adult fish (P=0.77), while the difference in isopods was still significant, albeit less so (from P=0.001 to P=0.05). No substantial geographic effects in diet were found amongst fish sampled from different sites in Sydney harbour or amongst fish collected from different spearfishing competitions.

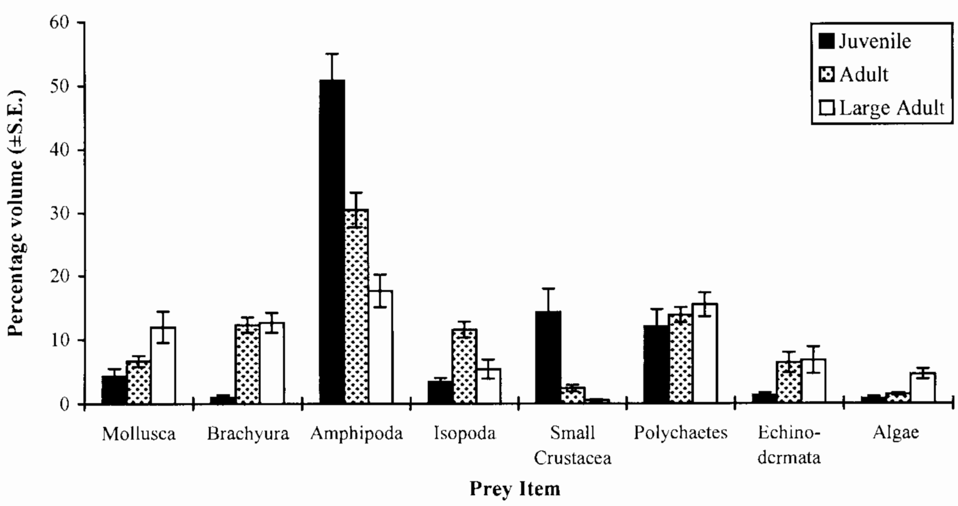

Figure 1. Mean percentage volumes (± standard error) of major prey items in the diets of juvenile (<200 mm standard length, SL), adult (200 to 400 mm SL) and large adult red morwong (350 to 500 mm SL).

TABLE 1

Percentage volume (vol.) of all prey items for the three size classes and the general diet of *C. fuscus* with percentage occurrence (occ.) in brackets. Juveniles, SL<200 mm, n=20; Adults from Sydney Harbour, 200–400 mm SL, n=26; Large adults from spearfishing competitions, 350–500 mm SL, n=25. Mean values for gut fullness (C/F ± standard error) are given for each size class.

Prey items	Juvenile		Adult		Large adult		Overall
	vol.	occ.	vol.	occ.	vol.	occ.	vol.
Mollusca	4.06	(80)	6.75	(96)	13.19	(96)	8.05
limpets	0.23	(30)	0.68	(54)	4.52	(74)	1.79
abalone	0	(0)	0.71	(35)	1.07	(43)	0.62
other gastropods	1.94	(80)	2.26	(96)	1.59	(96)	1.95
chitons	0.15	(20)	1.09	(58)	2.09	(70)	1.14
bivalves	1.74	(75)	2.01	(92)	3.92	(96)	2.55
Crustacea	70.1	(100)	59.37	(100)	40.46	(100)	56.37
Brachyura	1.07	(55)	12.17	(100)	13.11	(100)	9.27
Anomura	0.01	(5)	1.02	(46)	0.79	(35)	0.66
other decapods	0.14	(10)	1.41	(31)	0.46	(35)	0.73
Amphipoda	50.92	(100)	30.73	(100)	18.6	(100)	32.65
Isopoda	3.38	(90)	11.6	(100)	5.08	(91)	7.12
Cirripedia	0	(0)	0.05	(12)	1.71	(43)	0.57
Cladocera	3.11	(90)	2.09	(62)	0.19	(26)	1.77
Tanaidacea	9.65	(80)	0.18	(27)	0.31	(52)	2.96
Cumacea	0.89	(50)	0.04	(8)	0.01	(9)	0.28
Mysidacea	0.86	(20)	0.09	(8)	0	(0)	0.28
Other	0.06	(10)	0	(0)	0.19	(17)	0.08
Polychaeta	12.27	(95)	13.91	(100)	16.35	(100)	14.23
Echinodermata	1.25	(55)	6.32	(81)	7.60	(70)	5.27
Echinoidea	0.05	(5)	0.33	(38)	2.96	(57)	1.10
Ophiuroidea	1.2	(55)	5.99	(81)	4.64	(70)	4.17
algae	0.71	(50)	1.44	(100)	4.73	(100)	2.29
Ascidiacea	0.37	(15)	0.2	(35)	1.05	(35)	0.52
Hydrozoa	0.06	(10)	0.11	(15)	0.24	(22)	0.14
Bryozoa	0.07	(10)	0.36	(58)	2.04	(83)	0.82
Anthozoa	0	(0)	0.02	(4)	0.1	(17)	0.04
Sipuncula	0	(0)	0.15	(12)	0.07	(13)	0.08
Porifera	0.04	(5)	0.02	(8)	0.13	(26)	0.06
Pycnogonida	0	(0)	0.03	(8)	0.02	(4)	0.02
sediment	1.68	(90)	2.87	(92)	4.21	(100)	2.96
digested material	9.16	(95)	8.16	(92)	9.19	(83)	8.78
unidentified	0.23	(20)	0.14	(27)	0.57	(48)	0.30
Gut fullness	0.60±0.02		0.62±0.01		0.56±0.03		0.59±0.01

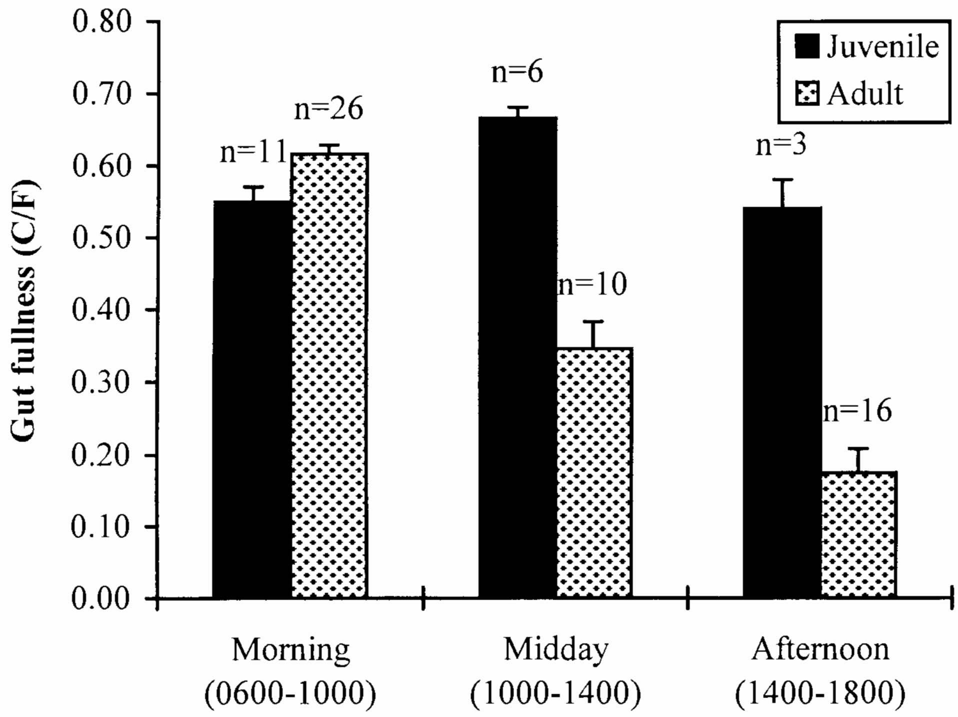

Figure 2. Gut fullness (mean C/F ± standard error) of juvenile and adult red morwong during morning (0600–1000 h), midday (1000–1400 h) and afternoon (1400–1800 h) sampling.

Juveniles and both groups of adult red morwong also displayed differences in the mean number of prey items consumed. Juveniles had an average of six prey items (range 3 to 9) while large fish had an average of nine prey items (range 7 to 13) in their intestinal tract.

Feeding periodicity and feeding behaviour

The gut fullness of juveniles sampled from Sydney Harbour were more than half full across the three diel sampling periods; morning (0600 to 1000 h), midday (1000 to 1400 h) and afternoon (1400 to 1800 h) (Fig. 2). The gut fullness ratio of juveniles sampled from the middle of the day was significantly greater, although only slightly, than C/F values from morning and afternoon samples ($p=0.03$). Adult fish sampled from early morning through midday to late afternoon were also found to have significantly different gut fullness ratios ($P<0.001$), with guts progressing from 60–90% full in the morning (C/F 0.54 to 0.77), to 0–50% during midday (C/F 0.10 to 0.50) (Fig. 2). Of the midday guts that did contain food, the foregut (stomach and beginning of intestine) was usually empty. Fish sampled late in the afternoon were, with one exception, found to be virtually empty (C/F value of approximately 0.15). The one exception to the empty guts of these late afternoon adults was a large juvenile of 210 mm SL with no gonad development whose inclusion in the afternoon sample elevated the mean C/F ratio for this period (approximately 0.20, Fig. 2).

In general, *C. fuscus* feeds by biting and sucking at the rock or algal turf with its large papillate lips, and then filtering sand and other unwanted material through the gill

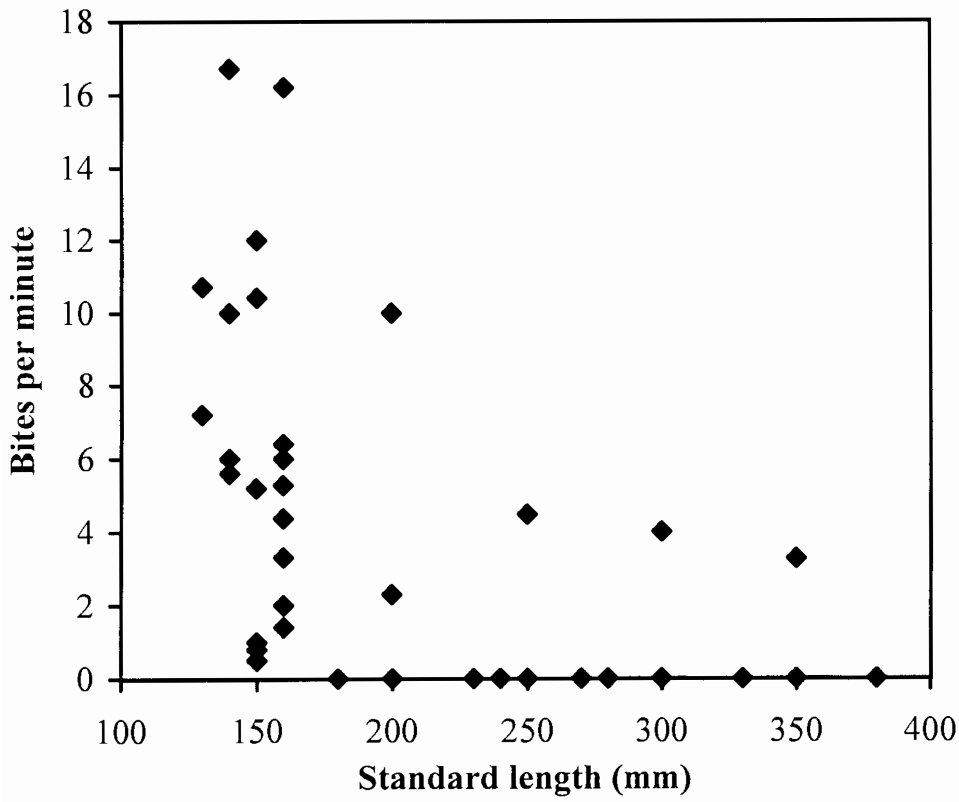

Figure 3. Number of bites at the substrata per minute for fish during daylight hours, relative to estimated standard length (n=26 juveniles, n=26 adults).

rakers and operculum. Juveniles display a different feeding behaviour to adults by feeding throughout the day, during which time adults are generally inactive. The number of bites per minute as a function of estimated length shows that juveniles feed significantly more than adults through the day (Fig. 3) ($P<0.001$).

DISCUSSION

General diet

Cheilodactylus fuscus is one of the larger and more important benthic feeding carnivores of temperate reefs in southeastern Australia. The main dietary components of all three size classes were amphipods, polychaetes, crabs, molluscs and echinoderms. We found a higher proportion of amphipods and a lower proportion of polychaetes, crabs and molluscs compared to that found by Bell (1979), which can be largely attributed to the significantly different diets among juveniles (<200 mm SL), adults (200 to 390 mm SL), and large adults (360 to 500 mm SL). Bell (1979) collected only large adults from spearfishing competitions which ranged from 275–415 mm SL (Bell 1979), while we found that the proportion of amphipods significantly declined even from adults to large adult fish. Inclusion of juveniles and smaller adults in dietary analysis raises the proportion of amphipods and lowers the proportions of crabs and molluscs compared to Bell's (1979) study. Another factor leading to differences between the two studies may be the amount of the gut examined. Bell (1979) examined only the stomachs (14% of gut) of which 93% were half full to empty and this may have underestimated the importance of the more common prey items in the diet. By examining the entire gut when nearly full, from adult fish collected in the early morning in this study, the majority of prey items taken during the feeding period are still present. We observed an occurrence of 100% for amphipods and crustaceans in the diets of fish regardless of size, while Bell (1979) observed an occurrence of 79% for amphipods and 89% for crustaceans.

The general diet of *C. fuscus* is similar to that recorded for other cheilodactylid fish with similar habitats. These include the banded morwong (*C. spectabilis*) from New Zealand (Leum and Choat 1980), the magpie perch (*C. nigripes*) from southern Australia (Cappo 1980), and two species from Japan (*C. zonatus* and *C. zebra*, Sano and Moyer 1985). All of these species inhabit shallow coastal regions and have diets in which amphipods dominate, and crabs, polychaetes, molluscs and echinoderms compose varying proportions of the remaining diet. These species also employ the same feeding technique as the red morwong, taking bites from algal turf, rocks and sediment then separating prey items from unwanted material. Leum and Choat (1980) found *C. spectabilis* to be a non-selective feeder, feeding on particular substrata rather than on prey items themselves. Cappo (1980) observed similar feeding behaviour in *C. nigripes* and this would appear to be true for most shallow water cheilodactylids. Our results show that adult red morwong prey on large molluscs which are most probably taken selectively from bare rocky substrate surrounding algal turf. Leum and Choat (1980) occasionally observed this behaviour in *C. spectabilis* in New Zealand.

Feeding periodicity of adults

Adult fish had full guts in the early morning which were progressively emptied throughout the day to be almost completely empty by mid-afternoon (1500 h). This implies that adults feed either nocturnally or in crepuscular peaks in activity, supporting inferences made by Lowry and Suthers (1998) who tracked adult *C. fuscus* carrying implanted radio tags. Radio-tagged fish showed significant increases in activity at 0400 to 0600 h and 1700 to 1900 h, in microhabitats well away from the normal boulder-associated habitats in which they rest during the day.

These findings contrast with feeding in other cheilodactylids. Leum and Choat (1980) found that *C. spectabilis* feeds diurnally and observed no dawn or dusk feeding peaks. Since *C. spectabilis* occupies a similar niche to that of *C. fuscus* (McCormick and Choat 1987; McCormick 1989) it is peculiar that the two species should display such markedly different feeding behaviour. Observations of *C. nigripes* throughout the day and night showed this species to also be diurnally active, sheltering in crevices and caves during the night and feeding during the day (Cappo 1980). Larger specimens of this species were found to be active earlier in the morning and later in the afternoon than smaller individuals (Cappo 1980). Both *C. zebra* and *C. zonatus* have been found to feed diurnally with the greatest amount of foraging occurring during the morning and decreasing gradually through the day with social interactions increasing greatly at dusk (Sano and Moyer 1985). While feeding in these species has been observed to begin again after sunset, data have not been collected on foraging activities through the night. *C. zonatus* has been observed "sleeping" between 2000 and 2200 h (Sano and Moyer 1985). The jackass morwong (*Nemadactylus macropterus*), a schooling species which occurs in deeper shelf waters up to 240 m (Gomon et al. 1994), feeds mostly at night, ingesting and voiding food within 24 hours (Godfriaux 1974).

Size-specific differences in diet and feeding

Juvenile *C. fuscus* consume a greater proportion of small crustaceans, in particular amphipods, while adults consume a greater proportion of large prey items such as brachyurans, molluscs and echinoderms. A similar difference has been documented for *C. spectabilis* (Leum and Choat 1980) and *Nemadactylus macropterus* (Godfriaux 1974). In some cases these changes in the diet of *C. fuscus* appear to be progressive depending on the age or size of the fish. In addition to a shift in diet, juveniles were observed to feed diurnally and those sampled throughout the day all had full guts, in contrast to the adults. Ontogenetic changes in feeding behaviour were also observed in *C. spectabilis*. Adult and juvenile *C. spectabilis* both feed during the day but juveniles spend considerably more time feeding than adults (Leum and Choat 1980). *Cheilodactylus nigripes* juveniles also were observed to feed only during the day, and to feed more frequently than adults (Cappo 1995).

An investigation into the ontogeny of prey selection of black surfperch (*Embiotoca jacksoni*) indicated that the mechanism causing ontogenetic diet shift was a group of interacting factors including morphological constraints (e.g. gape limitation), foraging behaviour, habitat selection and prey availability (Schmitt and Holbrook 1984). While consumption of large prey by juvenile *C. fuscus* is probably limited by gape, small crabs, molluscs and echinoderms do occur in their foraging habitat and are eaten (Table 1) but only in very small proportions. Juveniles of the limpet *Patelloida latistrigata* are commonly found around 5 mm length (Moran 1985) and densities of adult limpets of other species have been found around 14 m^{-2} in the shallow subtidal region (Fletcher 1987).

The main factors mediating ontogenetic diet changes in *C. fuscus* are probably those of habitat selection and resultant prey availability with morphological constraints also playing a role. As with several other temperate reef species (*C. spectabilis*, Leum and Choat 1980; *Pseudolabrus celidotus*, Jones 1984; *Achoerodus viridis*, Gillanders 1995), *C. fuscus* exhibits a size based depth distribution (pers. obs. Lowry 1997). Juveniles occur in shallow marginal zones (to depths of five metres) characterised by a greater abundance of foliose algal turf and the kelp *Ecklonia radiata*, compared to the adult habitat in deeper water (10 to 20 m) amongst large boulders and less algal turf.

The benthic fauna of coralline algal turf can include high densities of amphipods (1040 per $0.01m^2$), ostracods (220 per $0.01m^2$) and polychaetes (130 per $0.01m^2$) but low densities of ophiuroids (Choat and Kingett 1982). They found that two species of fish feeding on this substrate (*Chrysophrys (Pagrus) auratus* and *Upeneichthys porosus*) had diets made up of these items in similar proportions (e.g. 55% amphipods, 4% polychaetes and ostracods for *U. porosus*). With increasing depth, there tends to be a decrease in the abundance and biomass of prey (crabs and shrimp), as well as a decrease in the amount of algal turf, associated with a decrease in light (Larson 1980). It may be that shallow (0 to 5 m) sub-tidal temperate regions support a greater biomass of prey for micro-carnivores than deeper (10 to 20 m) areas. Therefore juvenile *C. fuscus* may forage in the sub-littoral zone because this region provides a plentiful food source consisting of small prey items, in addition to providing protection from predators. Risk of predation is often an important factor mediating age specific patterns in habitat use (Schmitt and Holbrook 1985), and juvenile fish have often been found associated with habitats of greater structural complexity (i.e. shelter) than adults (Ebeling and Lauer 1985; Carr 1989; Holbrook et al. 1990; Levin 1991). Interactions of food abundance and predation risk have also been found to determine habitat selection by juvenile fish (Werner and Hall 1988).

Upon reaching a length of about 200 mm there was a shift in habitat use by *C. fuscus* which was reflected in diet and an accompanying change in feeding behaviour. They move to deeper regions where larger prey items (crabs, molluscs, echinoderms) are taken to replace the small crustaceans that are not as plentiful at depth. A similar ontogenetic movement into deeper water has been observed in *C. spectabilis* (Leum and Choat 1980;

McCormick 1989). *C. fuscus* differs significantly from other cheilodactylids in that adults appear to feed in crepuscular peaks (or possibly through the night), while other cheilodactylids (especially *C. spectabilis*) feed during the day and are inactive at night. These ontogenetic and diel influences on *C. fuscus* diet need to be incorporated into sampling designs of future studies. In particular, bioaccumulation studies may be confounded by the use of different size classes, which have different diets.

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