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Influence of season, ontogeny and tide on the diet of the temperate marine herbivorous fish *Odax pullus* (Odacidae)

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Abstract. The diet of the temperate marine herbivorous fish *Odax pullus* (Pisces: Odacidae) was examined using gut-content analysis followed by principal-component analysis and analysis of variance. Fish were collected near Leigh, on the northeast coast of New Zealand, from February 1983 to September 1984. The data were categorised by size of fish, season, and state of tide. A major ontogenetic shift in diet was observed. Juveniles fed on animal material (crustaceans and gastropods), epiphytic rhodophytes, and some phaeophyte material. Adults fed almost exclusively on two phaeophyte taxa, the laminarian *Ecklonia radiata* and the fucoid *Carpophyllum* spp. Dietary selection was evident at the level of particular plant components; the diet of larger fish in spring samples was dominated by fucoid reproductive receptacles. There was no direct evidence of a tidal influence on diet composition of *O. pullus*, although the relative proportions of *E. radiata* and *Carpophyllum* spp. ingested by adult fish appeared to vary with tidal state. The volume of gut contents varied seasonally for all size classes, although the timing of peak annual food intake varied among size classes. Tidal state did not influence the volume of the gut contents. The ontogenetic and seasonal trends evident in the diet of *O. pullus* appeared to be related to a number of factors, including relative gut length, gonad development, ontogenetic changes in feeding anatomy and seasonal changes in algal composition.

Introduction

Dietary selectivity by marine herbivorous fishes has received considerable attention in recent years. Several factors have been shown to account for patterns of food selectivity in a number of tropical and temperate species (Horn 1989). Much of this work has focussed on the influence of algal secondary metabolites on food choice (e.g. Hay and Fenical 1988, Hay et al. 1988, Wylie and Paul 1988, Irelan and Horn 1991). Other studies have examined dietary selectivity in relation to the nutritional requirements of the fish (e.g. Fishelson et al. 1987) and the food quality of the algae (e.g. Horn and Neighbors 1984, Neighbors and Horn 1991). However, apart from the work of Horn and coworkers on the temperate stichaeid *Cebidichthys violaceus* (e.g. Horn et al. 1982, Horn and Neighbors 1984), there are few studies of marine herbivorous fish in which the role of both seasonal and ontogenetic factors in diet composition have been examined in detail.

Odax pullus is a good species for such a dietary study. It is a common inhabitant of subtidal reefs in New Zealand, and is more abundant and reaches a larger size at the southern end of its range (Ayling and Cox 1982). *O. pullus* feeds on fucoid and laminarian macroalgae, and shows evidence of feeding selectively on different plant tissues (Choat and Clements 1993a). As a temperate species, it is exposed to considerable seasonal variation, which has been shown to influence the availability and nutrient content of food plants (e.g. Horn and Neighbors 1984).

Previous work suggests that many herbivorous fishes undergo an initial carnivorous phase before switching to herbivory as adults (Montgomery 1977, Horn et al. 1982, Rimmer 1986, Bellwood 1988). Frequently, the shift to herbivorous feeding is accompanied by an elongation of the gut (Montgomery 1977, Rimmer 1986). *Odax pullus* is known to undergo considerable changes in body shape with growth (Ritchie 1976), although little is known about ontogenetic changes in the alimentary morphology and diet of this species.

The present study seeks to describe factors influencing the diet composition of the herbivorous odacid *Odax pullus*. A focus of this study is the way in which its diet varies as a function of the seasonal occurrence of algal structures such as reproductive receptacles (Delf 1939, Dawson 1940). The present study also describes the influence of ontogeny on diet and gut length in *O. pullus*.

Materials and methods

Sampling of *Odax pullus* was mainly carried out just outside the Cape Rodney to Okakari Point Marine Reserve, near Leigh, 100 km north of Auckland (146°46′ to 49′E; 36°16′S). In addition, some fish were collected at Taranga (Hen) Island, about 27 km due north of the marine reserve. Subtidal habitats, algal diversity and biota did not differ greatly between the sampling areas visited during the study. General information on the physical environment of the Marine Reserve can be found in Gordon and Ballantine (1976), and Choat and Schiel (1982) provide details of subtidal habitats and biota.

Odax pullus were collected by spear, either using snorkel or SCUBA equipment, at approximately monthly intervals from February 1983 to September 1984. Since *O. pullus* lacks a gastric stomach, the gut was divided into anterior intestinal swelling and posterior intestine for gut analysis [see Clements and Bellwood (1988) for a description of the gut anatomy in this species]. Within 2 h of capture, the standard length of each fish was measured to 1 mm, and weight to 1 g. The entire gut was then removed, and the intestinal swelling and intestine separated. Gut contents were removed from the intestinal swelling and intestine and spread over absorbent paper to remove excess fluid. The contents were then added to a measured amount of 10% formalin in a measuring cylinder and the volume of contents were calculated by displacement. The total volume of the gut contents was calculated by combining the intestinal swelling and intestine results for each fish. Only fish collected between 10.00 hrs and dusk were used for volume analysis, to avoid confounding the daily cycle of gut filling (Choat and Clements 1993b) with possible seasonal changes in volume of gut contents. In addition, specimens in which the gut was holed by the spear during collection were not used for volume analysis. As a consequence, the sample sizes for volume analysis were usually less than those for the dietary analysis. For the purposes of analysis of variance, the gut-content volume data were standardised by fish weight to remove the effect of size. The following formula was used:

$$\frac{\ln(\text{gut content vol} + 1)}{\ln \text{fish wt}}.$$

Gonads were removed following capture and fixed in Bouin's fixative for 48 h. They were then cleaned, weighed to 0.01 g, and then stored in 70% isopropyl alcohol. Gonad material from every specimen of *Odax pullus* was sectioned and examined under a microscope at low power to verify sex.

Fish were categorised on the basis of size, tide and season. Individuals <180 mm standard length (SL) were classed as juveniles, individuals 180 to 280 mm SL were classed as subadults, and individuals >280 mm SL were classed as adults. These size classes approximate stages of sexual maturity based on examination of gonad material. Juveniles have immature gonads, subadults show sympathetic seasonal changes in gonad development but do not develop ripe eggs, and adults are reproductively mature. The size of 280 mm SL was also a convenient demarcation point between subadults and adults to create balanced samples for analysis of variance. Seasons in this study were defined as follows: September to November: spring; December to February: summer; March to May: autumn; June to August: winter. Fish collected between mid-flow and mid-ebb tides were classed as high tide, while fish collected between mid-ebb and mid-flow tides were classed as low tide. Sample sizes based on the above categories are presented in Table 1.

Gut measurements were made after fixation in 10% formalin. Since pre-fixation hardens the gut, this prevented bias caused by uneven stretching of fresh gut between specimens, although it may have resulted in some shrinkage. The intestinal swelling was measured as the distance between the termination of the oesophagus and the first point of flexion in the gut, while the intestine was measured as the distance from the distal end of the intestinal swelling to the anus. Intestinal swelling length and intestine length were combined to give total gut length.

The choice of categories of dietary items for this study largely follows the results of Choat and Clements (1993a), who reported the following nine food types as present in two summer samples of adult *Odax pullus* collected in the same study area: (a) thallus tissue of the laminarian alga *Ecklonia radiata*; (b) thallus tissue of the fucoid algae *Carpophyllum* spp.; (c) receptacles of *Carpophyllum* spp.; (d) thallus tissue of the fucoid alga *Xiphophora chondrophylla*; (e) Rhodophyceae; (f) bryozoans; (g) hydroids; (h) gastropods; (i) crustaceans.

Table 1. *Odax pullus*. Sample sizes used for diet analysis in present study. Sample sizes of fish used for gut-content volume analysis are given in parentheses where they differ from dietary samples

Season	Tide	Adults	Subadults	Juveniles	Totals
Spring	high	11 (10)	16 (15)	12 (7)	39 (32)
	low	1	1	–	2
Summer	high	25 (24)	7 (6)	18 (14)	50 (44)
	low	5	3 (2)	1	9 (8)
Autumn	high	21 (9)	19 (14)	16 (14)	56 (37)
	low	41	13 (12)	5	59 (58)
Winter	high	3	6	11 (9)	20 (18)
	low	8	13 (11)	18 (17)	39 (36)
Totals		115 (101)	78 (67)	81 (67)	274 (235)

The growing germinal tips and bladder vesicles (which are not gas-filled as in the fucoid genus *Sargassum*) of *Carpophyllum* spp. were abundant in some of the fish examined in the present study, and were easily distinguished from the characteristic reproductive receptacles of this genus (Delf 1939, Dawson 1940). These structures, referred to henceforth as *Carpophyllum* vesicles, were therefore incorporated as a separate dietary category. In addition, the bryozoan category of Choat and Clements (1993a) was expanded to include other sessile organisms including ascidians, *Turbellaria* sp. and sponges. In the present study, this category is referred to as "sessile organisms". Specimens of the algal dietary categories were collected in the field, and used as reference material to identify material in the gut.

The method used for quantitative analysis of the dietary components follows that described in Choat and Clements (1993a). This transect technique is a modification of a line-intercept method developed for estimating coverage and particle density (Lucas and Seber 1977), and has particular application to analyses of plant material from rumen and faecal samples (Seber and Pemberton 1978). The contents of the intestinal swelling were agitated and spread evenly over a perspex tray. One of two different-sized trays were used for each fish, depending on the amount of gut contents present. The base of the largest tray was divided into a 100 × 100 mm grid, with ten transects spaced at 10 mm intervals across the tray. The base of the smaller tray was also divided into ten equidistant 100 mm transects which, in this case, were 5 mm apart.

Four randomly selected transects were counted per tray (i.e., per individual fish). This number was determined by error estimates in a pilot study. The tray was placed under a binocular microscope, and the extent of each transect covered by particles of a particular food category was recorded. These values were then summed to give the proportions of each food category per transect. These proportional data were transformed into percentages to remove the effect of varying gut volume (and hence the amount of material in each tray). A mean of the four transects was then calculated, giving an estimate of the relative proportion of the ten dietary categories ingested by each individual fish.

The dietary analysis data for all 274 fish were then subjected to principal-component analysis using the covariance matrix. Principal-component analysis identifies new axes that best summarise the multivariate information in the data set (Dunn and Everitt 1982). These new axes, termed principal components, are combinations of the old variables, and are independent of each other. Each axis summarises as much of the total variation as possible, subject to the constraint of being independent of the preceding axes. The amount of variation explained by each axis is measured by its eigenvalue. The first few of these new synthetic variables that summarise large amounts of the variation of the original variables can then be used in univariate analyses as summaries of the variables (B. McArdle personal communication). Thus, in the present study, vector scores from the principal-component analysis were used in analyses of variance to test the importance of factors such as fish size and season in explaining the most important trends in the data set.

The unbalanced nature of the data necessitated that analysis of variance be performed on randomly selected subsamples of the principal-component scores, so that cell sizes were balanced throughout. Due to limited sample sizes at low tide in both spring and summer (Table 1), it was not possible to test the effects of size, season and tide simultaneously for all samples. Therefore, the effects of season and tide were tested separately on subsamples of the data. A two-factor design (3 size classes × 4 seasons) was used to test the effect of size and season on the diet composition of fish collected at high tide. A three-factor design (3 size classes × 2 seasons × 2 tides) was used to test the effect of tide on fish collected in autumn and winter. Analyses of variance using these two designs were performed on the standardised gut-content volume data and the vector scores from the first three principal components (i.e., eight analyses). In each case, the total degrees of freedom was 35. In all cases, the assumption of homogeneity of variance was tested prior to analysis using Cochran's test (Guenther 1964). All statistical analyses were performed using SYSTAT Version 5.2, Evanston, Illinois.

Results

The eigenvalues and variances of the first three principal components (PCs) extracted from the covariance matrix of the ten dietary variables of *Odax pullus* are presented in Table 2. These first three PCs explained 94.4% of the total variance in the data set. The other PCs were therefore of minor importance, and were not considered further.

The first PC accounted for 55.7% of the variance in the proportions of the ten diet categories, and reflected a trend in the relative amounts of *Ecklonia radiata* and red algae in the diet. Principal Component 1 in fish collected at high tide differed significantly with fish size and season (Table 3). Principal Component 1 did not differ significantly with tide in autumn and winter samples (Table 3).

The second PC explained 26.9% of the variation in the data set. It was a trend in the relative proportions of *Carpophyllum* spp. thallus and red algae in the diet. Principal Component 2 differed significantly with size in fish collected at high tide (Table 4). Principal Component 2 did not significantly differ with season and tide in high tide and autumn and winter samples, respectively (Table 4).

The third PC explained 12.8% of the variance in the dietary data. It reflected a trend in the relative proportions of *Carpophyllum* spp. thallus and *Carpophyllum* spp. reproductives, and to a lesser extent the proportion of red algae. This trend did not differ between fish size classes or tides, but did differ significantly with season in fish collected at high tide (Table 5). In summary, the principal-component analysis suggested that most of the variation in the diet of *Odax pullus* can be explained by

Table 2. *Odax pullus*. First three principal components obtained from dietary variables ($n = 274$)

Character	Principal components		
	1	2	3
Ecklonia radiata	−35.72	−10.13	−1.43
Carpophyllum spp. thallus	0.28	21.62	−10.91
Carpophyllum spp. reproductives	7.08	6.02	15.88
Carpophyllum spp. vesicles	2.32	0.33	2.95
Xiphophora chondrophylla	−0.01	0.21	−0.17
Red algae	23.45	−17.48	−7.15
Sessile organisms	−0.23	0.23	0.00
Hydroids	0.04	0.08	0.40
Gastropods	1.04	−0.39	0.42
Crustaceans	1.75	−0.49	0.01
Eigenvalue	1885.64	912.08	433.13
% of total variance explained	55.70	26.94	12.79
Cumulative variance explained	55.70	82.64	94.43

Table 3. *Odax pullus*. ANOVAs of Principal Component 1 by size and season for fish collected at high tide, and by size and tide for fish collected in autumn and winter. PC: Principal Component; SS: sum of squares; MS: mean square

Source	SS	*df*	MS	*F* ratio	*P*
PC1 by size and season for fish collected at high tide					
size	15745.688	2	7872.844	10.091	0.001
season	10102.838	3	3367.613	4.316	0.014
size × season	11201.745	6	1866.957	2.393	0.059
error	18725.243	24	780.218		
Total	55775.514	35			
PC1 by size and tide for fish collected in autumn and winter					
size	36266.328	2	18133.164	13.986	<0.001
season	4518.528	1	4518.528	3.485	0.074
tide	1440.962	1	1440.962	1.111	0.302
size × season	1112.085	2	556.043	0.429	0.656
tide × season	1471.490	1	1471.490	1.135	0.297
size × tide	164.077	2	82.039	0.063	0.939
size × season × tide	958.228	2	479.114	0.370	0.695
error	31117.274	24	1296.553		
Total	77048.972	35			

Table 4. *Odax pullus*. ANOVAs of Principal Component 2. Further details as in legend to Table 3

Source	SS	*df*	MS	*F* ratio	*P*
PC2 by size and season for fish collected at high tide					
size	11267.629	2	5633.814	8.893	0.001
season	2536.018	3	845.339	1.334	0.287
size × season	2399.277	6	399.879	0.631	0.704
error	15204.840	24	633.535		
Total	31407.764	35			
PC2 by size and tide for fish collected in autumn and winter					
size	8318.655	2	4159.327	7.056	0.004
season	88.799	1	88.799	0.151	0.701
tide	3.547	1	3.547	0.006	0.939
size × season	486.262	2	243.131	0.412	0.667
tide × season	285.723	1	285.723	0.485	0.493
size × tide	1263.937	2	631.968	1.072	0.358
size × season × tide	2386.268	2	1193.134	2.024	0.154
error	14146.756	24	589.448		
Total	26979.947	35			

Table 5. *Odax pullus*. ANOVAs of Principal Component 3. Further details as in legend to Table 3

Source	SS	*df*	MS	*F* ratio	*P*
PC3 by size and season for fish collected at high tide					
size	323.788	2	161.894	0.540	0.590
season	9483.834	3	3161.278	10.546	<0.001
size × season	2884.446	6	480.741	1.604	0.189
error	7194.223	24	299.759		
Total	19886.291	35			
PC3 by size and tide for fish collected in autumn and winter					
size	452.921	2	226.460	0.929	0.409
season	1.232	1	1.232	0.005	0.944
tide	451.988	1	451.988	1.853	0.186
size × season	845.617	2	422.808	1.734	0.198
tide × season	1.832	1	1.832	0.008	0.932
size × tide	75.248	2	37.624	0.154	0.858
size × season × tide	707.325	2	353.662	1.450	0.254
error	5852.869	24	243.870		
Total	8389.032	35			

Table 6. *Odax pullus*. ANOVAs of ln gut-content volume +1/ln weight. Further details as in legend to Table 3

Source	SS	*df*	MS	*F* ratio	*P*
ln gut-content vol +1/ln wt by size and season for fish collected at high tide					
size	0.032	2	0.016	370.051	<0.001
season	0.001	3	0.0003	5.411	0.005
size × season	0.002	6	0.0003	6.447	<0.001
error	0.001	24	0.00004		
Total	0.036	35			
ln gut-content vol +1/ln wt by size and tide for fish collected in autumn and winter					
size	0.563	2	0.282	42.009	<0.001
season	<0.001	1	<0.001	<0.001	0.997
tide	<0.001	1	<0.001	<0.001	0.987
size × season	0.012	2	0.006	0.879	0.428
tide × season	0.004	1	0.004	0.541	0.469
size × tide	0.003	2	0.0015	0.211	0.811
size × season × tide	0.008	2	0.004	0.587	0.564
error	0.161	24	0.007		
Total	0.751	35			

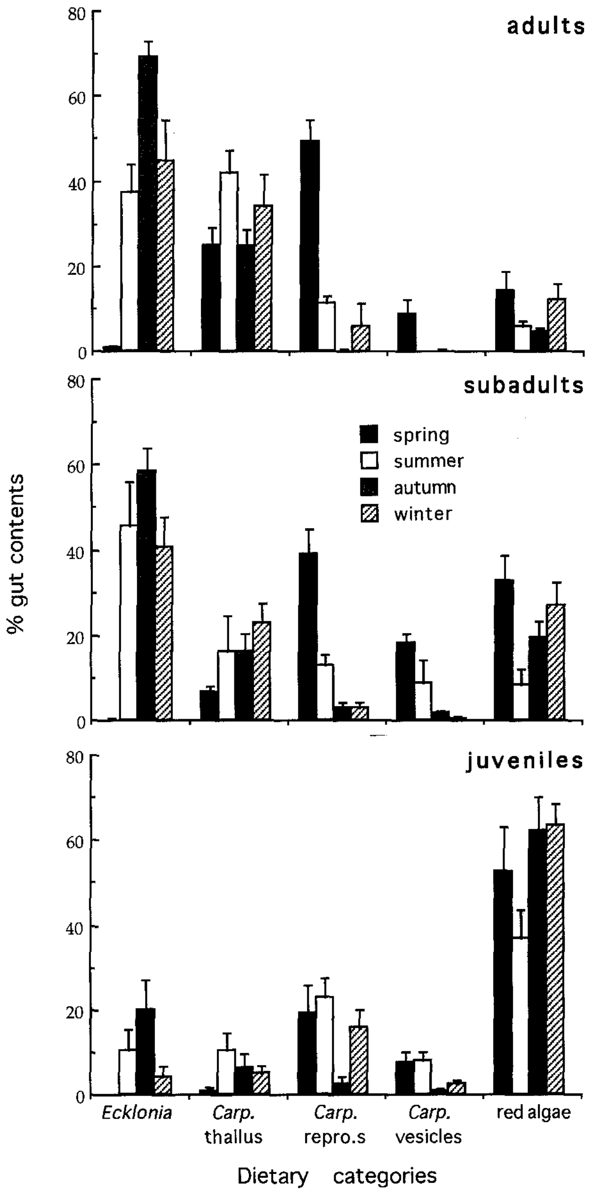

Fig. 1. *Odax pullus*. Proportions of major dietary categories. Three size classes of fish were sampled over four seasons. Data are means +1 SE. *Ecklonia*: *E. radiata*; *Carp.* thallus: *Carphophyllum* spp. thallus; *Carp.* repro.s: *Carpophyllum* spp. reproductives; *Carp.* vesicles: *Carpophyllum* spp. vesicles

fluctuations in the amounts of four of the dietary categories: *Ecklonia radiata*, *Carpophyllum* spp. thallus, *Carpophyllum* spp. reproductives and red algae. The analysis of variance results suggested that size of fish and season significantly influenced the diet composition of fish collected at high tide, but tide did not influence diet composition of fish collected in autumn and winter. In the light of these results, season and size of fish are delineated in graphical analyses, while tides are pooled.

The proportions of the ten dietary components in adult, subadult and juvenile *Odax pullus* are presented in Figs. 1 and 2, with the results delineated by season. Ontogenetic trends are apparent in several of the dietary categories. Adults and subadults fed predominantly on *Ecklonia radiata* and *Carpophyllum* spp., while juveniles fed predominantly on epiphytic red algae (Fig. 1). Juveniles also ate more gastropods and crustaceans than subadults and adults (Fig. 2). The gastropods eaten by *O. pullus* in this study were mostly rissoids, with a few topshells found in larger fish. Of the 274 *O. pullus* examined in this study, 130 contained some crustacean material. The composition of this material by decreasing order of occurrence was: unidentified crustacean fragments 44%, gammarid amphipods 33%, *Amphiroidea* sp. (an isopod) 16%, sphaeromid isopods 4%, caprellid amphipods 2% and idoteid isopods (*Euidotea* sp. and *Paridotea* sp.) 1%. All these crustacean taxa are algal-dwelling (Morton and Miller 1968). The most obvious seasonal trend in the data was the intake by adults and subadults of large amounts of *Carpophyllum* spp. reproductives in spring. Associated

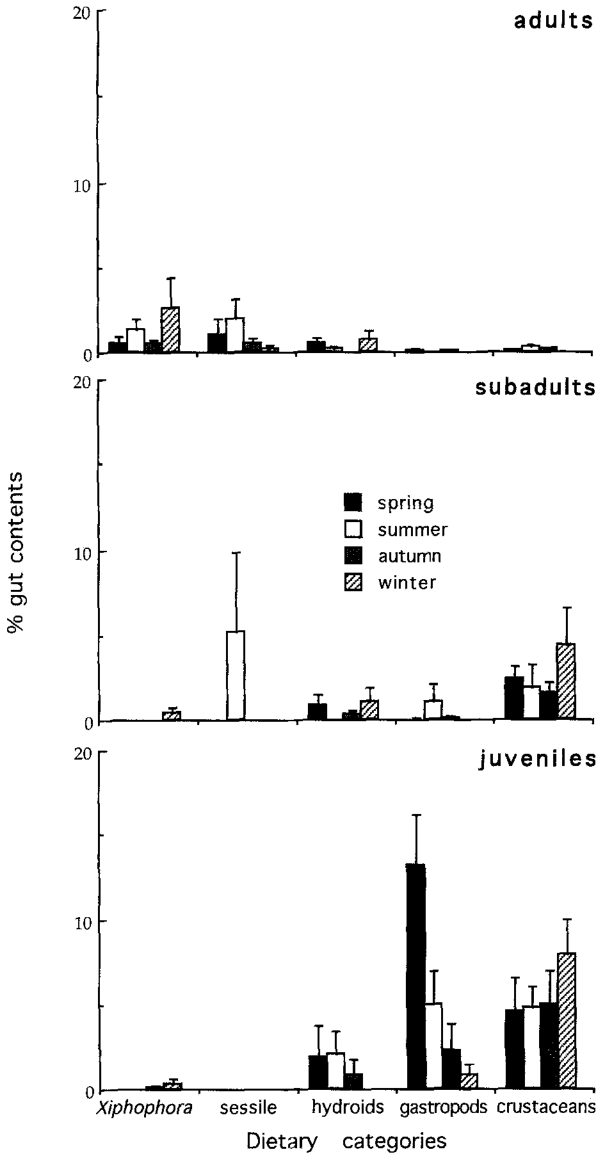

Fig. 2. *Odax pullus*. Proportions of minor dietary categories. Three size classes of fish were sampled over four seasons. Data are means +1 SE. *Xhiphophora*: *X. chondrophylla*; sessile: sessile organisms

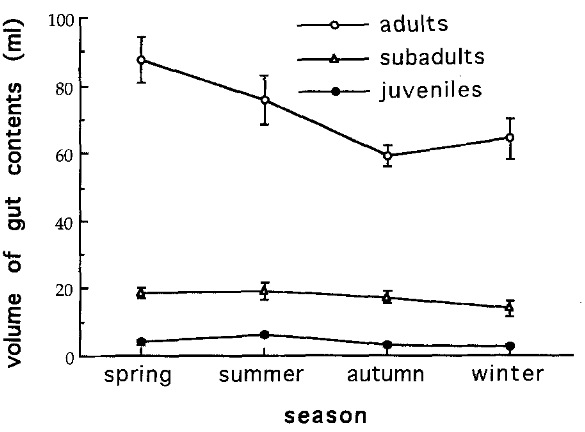

Fig. 3. *Odax pullus*. Seasonal gut-content volume variation. Three size classes of fish were sampled over four seasons. Data are mean ±1 SE

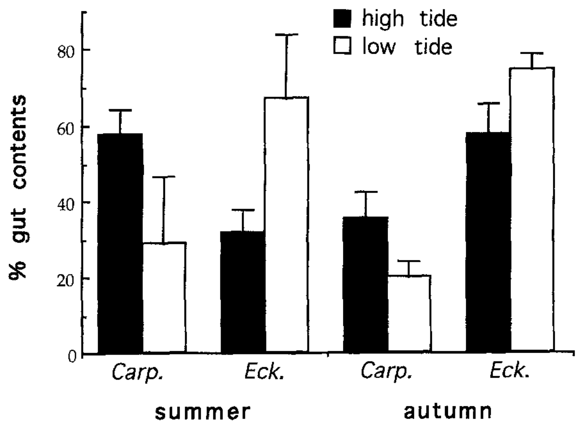

Fig. 4. *Odax pullus*. Proportions of *Ecklonia radiata* and *Carpophyllum* spp. in diet of adults at high and low tides for summer and autumn samples. Data are means +1 SE. Data for *Carpophyllum* spp. were calculated by pooling the thallus, reproductives and vesicle categories for each fish and recalculating means and errors. *Carp.*: *Carpophyllum* spp. tissue; *Eck.*: *E. radiata*

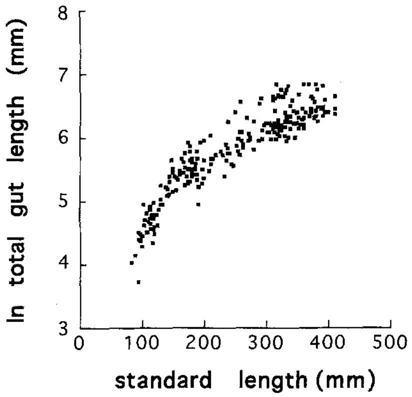

Fig. 5. *Odax pullus*. ln total gut length as function of standard length. Each data point represents an individual fish

with this was a decrease in the proportion of *E. radiata* consumed in spring.

The gut-content volume data are presented in Fig. 3. Standardised gut content volume differed significantly with size and season in fish collected at high tide, although there was a significant size × season interaction (Table 6). Standardised gut-content volume did not differ significantly with tide in autumn and winter samples (Table 6).

Although tide did not influence PCs 1 to 3 or standardised gut-content volume in autumn and winter samples (Tables 3 to 6), behavioural observations (Choat and Clements 1993b) prompted a graphical comparison of the amount of *Ecklonia radiata* and *Carpophyllum* spp. in the diet at different tidal states. Data for adults collected in summer and autumn (the two seasons with the largest sample sizes for adults) are presented in Fig. 4. The values for total *Carpophyllum* spp. were derived by summing the proportions of thallus, reproductives and vesicles for each fish and then recalculating means. Fig. 4 shows that adult fish collected in summer and autumn tended to eat more *E. radiata* at low tide, and conversely more *Carpophyllum* spp. at high tide.

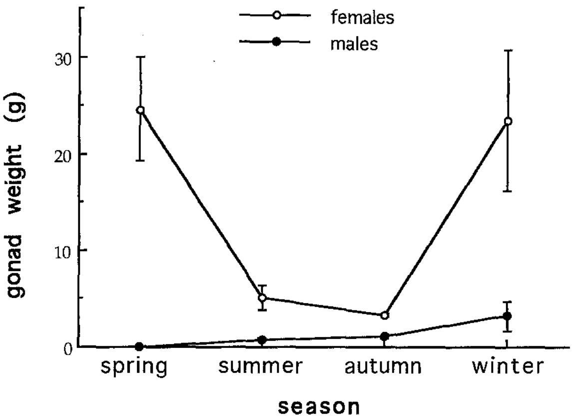

Fig. 6. *Odax pullus*. Gonad weight of adults as a function of season. Means ±1 SE

The results of the gut-length measurements are presented in Fig. 5. These data show that the rate at which gut length increased relative to standard length was greatest in juveniles (the smallest specimen collected was 85 mm SL). In adults and subadults, the rate at which the gut lengthened relative to the size of the fish slowed. The point at which this developmental change occurs appears to be ~150 mm SL. This is consistent with the changes seen in diet composition.

The gonad weight of adult *Odax pullus* collected during this study is presented in Fig. 6. Gonad weight peaked in winter and spring.

Discussion

The results of this study confirm the finding of Choat and Clements (1993a) that adult and subadult *Odax pullus* feed in a highly selective manner on a small range of algal taxa. The predominance in spring of the reproductive receptacles and vesicles of *Carpophyllum* spp. in the diet of subadult and adult *O. pullus* demonstrates that this selectivity extends to particular plant components. The reasons behind this degree of selectivity are unclear. Much of the recent literature on algal selectivity by herbivorous fishes has focussed on the influence of algal secondary metabolites (Horn 1989, Irelan and Horn 1991). The major food species of *O. pullus*, *Ecklonia radiata* and *Carpophyllum* spp., contain high concentrations of phenolics relative to sympatric algal species (Steinberg 1989). Thus, the selection of dietary taxa by *O. pullus* does not seem to be predicated by an attempt to avoid these chemicals.

It has been suggested that the reproductive receptacles of *Carpophyllum maschalocarpum*, a preferred food of adult *Odax pullus*, may be lower in phenolic content than the laminae (Steinberg 1989). Thus, it is possible that the within-plant distribution of phenolics influences food choice by the herbivore. Another explanation for the spring predominance of reproductive receptacles in the diet of *O. pullus* may be related to nutritional content. It has been suggested that the herbivorous stichaeid *Cebidichthys violaceus* may selectively take younger, distal portions of algae that are higher in protein (Horn and Neighbors 1984). The reproductive receptacles of fucoid macroalgae contain elevated levels of polysaccharides and protein (Kaur and Vijayaraghavan 1992), and would be expected to be nutritionally superior to thallus tissue.

Carpophyllum spp. reproductive receptacles may be especially important for *Odax pullus* in spring, since levels of the storage polysaccharide laminaran and the sugar alcohol mannitol in the laminae of *Ecklonia radiata* are low at this time of year (Stewart et al. 1961). It is interesting to note that at this time of year in Australia, where *Carpophyllum* spp. does not occur, the congeneric species *O. cyanomelas* consumes the entire primary lamina and meristem of *E. radiata* (Jones and Andrew 1990). Feeding by both *O. pullus* and *O. cyanomelas* is usually concentrated on the secondary laminae of *E. radiata* (Clements and Bellwood 1988, Choat and Clements 1993a). Furthermore, the annual peak in consumption of *E. radiata* by *O. pullus* in autumn coincides with the yearly peak in laminaran content of thallus tissue of this alga (Stewart et al. 1961). These correlations suggest that seasonal variation in the storage polysaccharide content of dietary algae may be an important factor in food choice by *O. pullus*.

The first principal component identified the major trend in the diet data as a shift from a red algae-dominated diet to an *Ecklonia radiata*-dominated diet. The analysis of variance and the graphs show that this trend is size-related. Ontogenetic shifts in diet composition have been reported previously in many other herbivorous and omnivorous teleosts (e.g. Montgomery 1977, Bell et al. 1980, Rimmer 1986, Bellwood 1988). Several factors may be invoked to explain this dietary shift in *Odax pullus*.

Firstly, there is some evidence that adult and juvenile *Odax pullus* have slightly different depth distributions (Ayling and Cox 1982, Meekan 1986). Choat and Schiel (1982), working in the same subtidal habitats as sampled in the present study, found that fucoid macroalgae (including the genus *Carpophyllum*) were generally more dominant in shallow water. The laminarian alga *Ecklonia radiata* gradually replaced the fucoids with depth (Choat and Schiel 1982). It is thus possible that the diet of *O. pullus* reflects ontogenetic habitat differences, with juveniles feeding upon shallow stands of *Carpophyllum* spp. and their associated epifauna and rhodophyte epiphytes.

Secondly, the ontogenetic shifts in the diet of *Odax pullus* may be related to the morphological and physiological ability of the fish to process different dietary items at different development stages. Gut length increases very rapidly relative to standard length in juvenile *O. pullus*, as it does in many herbivorous fishes which undergo an ontogenetic shift from animal to plant foods (Montgomery 1977, Rimmer 1986, Horn 1989). *O. pullus* also displays marked ontogenetic variation in head shape (Ritchie 1976). This variation is particularly reflected in the snout angle, which increases from about 30° in small juveniles to over 80° in large adults (Ritchie 1976). This trend towards a deeper head, and therefore an increased gape, in adults is largely caused by an increase in cheek depth (Clements 1985). This results in a greater surface area for the attachment of the jaw musculature, and therefore an increase in bite power (Clements and Bellwood 1988). The combination of a shorter gut with less absorptive area and a weaker jaw apparatus may therefore preclude small juveniles from feeding on the tough adult diet of phaeophyte thallae.

A third factor in the ontogenetic dietary shift observed in *Odax pullus* may involve the amount of protein necessary for the rapid growth of juveniles (Horn 1989). A carnivorous juvenile phase is characteristic of many taxa of herbivorous fishes, including stichaeids (Montgomery 1977), girellids (Bell et al. 1980), kyphosids (Rimmer 1986) and scarids (Bellwood 1988). Juvenile *O. pullus* ingest considerably more animal material than adults, mainly in the form of crustaceans and gastropods. It is likely that subadult *O. pullus* also take some crustacean material deliberately. *Amphiroidea falcifer* is a large and active isopod which inhabits the interstices of *Ecklonia radiata* laminae (Morton and Miller 1968). It is therefore very difficult to envisage how this crustacean could be ingested accidentally on such a frequent basis. It is quite possible, however, that the smaller crustaceans found infrequently in adult *O. pullus* were taken incidentally during the course of feeding on phaeophytes.

The relative proportions of *Ecklonia radiata* to *Carpophyllum* spp. in adult *Odax pullus* at high and low tide suggest that the lack of a significant result in the tidal analysis of variance may have been due to insufficient sample size. As discussed earlier on (fifth paragraph of this section), these algae differ in depth distribution in the sampling area (Choat and Schiel 1982). It is likely that the shallower *Carpophyllum* spp. stands are more accessible to feeding by *O. pullus* at high tide, particularly in turbulent conditions. The predominance of *Carpophyllum* spp. in the diet of adult *O. pullus* at high tide may therefore indicate a preference for this alga over *Ecklonia radiata*, as the latter is accessible regardless of tidal state. This suggestion of a feeding preference for *Carpophyllum* spp. is reinforced by behavioural observations presented elsewhere (Choat and Clements 1993 b). While it is possible that tidal state influences the dietary composition of *O. pullus*, there is no evidence that it affects feeding rate (gut-content volume data in the present study, feeding rate data in Choat and Clements 1993 b).

The significant interaction between season and size in the analysis of variance on the gut-content volume data appears to be the result of a difference in the annual pattern between juveniles on the one hand and adults and subadults on the other. Gut-content volume peaks in summer for juveniles and in spring for larger fish. It is very difficult to interpret seasonal trends in gut-content volume and diet for juvenile *Odax pullus* because of their rapid growth. This has the effect of confounding size with season, although this problem is ameliorated to some extent by the prolonged spawning season (and thus prolonged settlement period) of *O. pullus* (Ritchie 1969).

The annual peak in gut-content volume and thus feeding activity of adults in spring coincides both with the seasonal availability of the preferred food of *Odax pullus*, *Carpophyllum* spp. reproductive receptacles, and gonad maturity. Ritchie (1969) investigated the relationship between gut depot fat (the liver is not used for lipid storage in *O. pullus*) and gonad development. He found that depot fat was at a maximum when spawning commenced in mid-winter, and declined to a minimum at the end of summer when spawning ceased. A similar relationship between fat accumulation and spawning was described for a tropical surgeonfish by Fishelson et al. (1987). In the latter study, a changeover in diet from turfing algae in summer to nutritionally superior green algae in winter allowed the accumulation of fat reserves, which then provided a base for gonad development. The seasonal relationships between feeding activity, energy content of dietary algae (especially storage polysaccharides), diet choice and reproductive activity appear to be a fruitful subject for future research in *O. pullus*.

In conclusion, diet choice by *Odax pullus* appears to be influenced by a large number of interacting factors, including size, season, and possibly tidal state. The high degree of dietary selectively displayed by this species suggest its suitability for testing hypotheses of dietary constraint in the context of seasonal variation in the nutritional content of algae. Furthermore, the marked ontogenetic changes in the morphology of *O. pullus* makes this species an excellent model for investigating developmental factors associated with the onset of herbivory in an herbivorous fish. The relationships between gut morphology and physiology, jaw morphology, development of endosymbiotic microbiota (Clements 1991) and diet selection in *O. pullus* promise to be a rewarding area for future research.

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