DIET OF SCARTELLA CRISTATA : AN ARTIFICIAL HABITAT-ASSOCIATED BLENNY (PISCES : BLENNIIDAE)

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DIET
BLENNIES
GUT-CONTENT
BEHAVIOR
ONTOGENETIC SHIFT
INVERTEBRATE PREY

ABSTRACT. – Ontogenetic feeding shifts, diel feeding and differential feeding between sexes in the molly miller, *Scartella cristata* (Family Blenniidae), were characterized by dietary analysis. Gut-content analysis was performed on juvenile and adult *S. cristata* (n = 62) based on 24-h collections from two rock jetties in northwestern Florida. Direct observation suggested that sexes have different activity regimes ; males were encountered more frequently during day collections while females were encountered more frequently during night collections. *S. cristata* was observed biting algal turf, and its diet consisted of algae and associated invertebrates with a lesser contribution from benthic and demersal invertebrates. An ontogenetic shift from predation on demersal and benthic invertebrates among juveniles to a fuller exploitation of the algal turf as adults was observed. ANOVA was employed to examine the influence of site, sex and time of collection on total gut-content biomass (including algae) and total invertebrate prey biomass. Although there was no site effect in total biomass comparisons, differences between sampling sites contributed significantly to variation in male and female total invertebrate biomass suggesting that local abundance of invertebrates may influence feeding by *S. cristata*. Although no differences in total gut-content biomass among females collected during the day and night were detected, females contained a significantly higher invertebrate biomass during the night than during the day due to foraging on demersal invertebrates. During the day, males and females ingested similar invertebrate prey taxa, and total gut-content biomass estimates and total invertebrate biomass did not differ in males and females. Males were observed to actively nest guard clutches of eggs and this behavior may have lead to a reduced activity regime thereby decreasing male foraging on demersal invertebrates.

RÉGIME ALIMENTAIRE
BLENNIES
CONTENU STOMACAL
COMPORTEMENT
CHANGEMENTS ONTOGÉTÉTIQUES
INVERTÉBRÉS

RÉSUMÉ. – Les changements alimentaires ontogénétiques, la nutrition de jour et de nuit et la nutrition différentielle entre les sexes chez *Scartella cristata* (Blenniidae) sont caractérisés par l'analyse du régime alimentaire. Une analyse du contenu stomacal a été effectuée sur des individus juvéniles et adultes (n = 62) à partir d'un échantillonnage sur une période de 24 h, près de deux jetées rocheuses au nord-ouest de la Floride. Nos observations suggèrent que les deux sexes ont une activité alimentaire différente ; les mâles se rencontrent plus fréquemment au cours des récoltes de jour, les femelles au cours des récoltes de nuit. *Scartella cristata* a été observé broutant sur la couche algale, et le régime alimentaire se compose d'algues et d'invertébrés associés à ce milieu, avec une légère contribution des invertébrés démersaux et benthiques. Un changement ontogénétique a aussi été observé, les juvéniles passant de la prédation sur les invertébrés démersaux et benthiques à l'exploitation de la couche algale lorsqu'ils deviennent adultes. Une ANOVA est utilisée pour étudier l'influence du site, du sexe, et de l'heure de récolte sur la biomasse totale des contenus stomacaux (incluant les algues) et la biomasse totale en invertébrés. Si aucun effet du site n'est observé à partir des comparaisons des biomasses totales, les différences entre les sites ont contribué significativement à la variation en biomasse totale en invertébrés des mâles et des femelles, suggérant que l'abondance locale d'invertébrés pourrait influencer l'alimentation opportuniste de *S. cristata*. Bien qu'aucune différence dans la biomasse totale des contenus stomacaux ne soit détectée entre les femelles recueillies le jour et la nuit, celles-ci contiennent une biomasse en invertébrés significativement plus élevée durant la nuit, liée à une nutrition sur les invertébrés démersaux. Durant le jour, les mâles et les femelles ingèrent des taxons d'inver-

tébrés similaires, et la biomasse totale estimée des contenus stomacaux et des invertébrés ne diffère pas entre mâles et femelles. Les mâles ont été observés en train de garder activement les couvées d'œufs, et ce comportement peut avoir conduit à une réduction de leur activité alimentaire, diminuant ainsi leur prédation sur les invertébrés démersaux.

INTRODUCTION

Members of the family Blenniidae (Pisces; Order Perciformes) are benthic fishes that inhabit hard substrates including breakwaters and jetties (Moyle & Cech 1988). These fishes are integral to marine littoral zone faunal assemblages in the tropics and subtropics (Greenfield & Johnson 1990, Clarke 1994). Blennies are oviparous, and their reproductive cycle is marked by complex behavior between sexes (Sabates 1994). Eggs are spawned in clumps attached to the substratum and typically are guarded by males until hatching (Peters 1981, Côte & Hunte 1989). After hatching, blennies disperse as ichthyoplankton and rapidly develop fang-like teeth, suggesting a planktivorous diet (Côte & Hunte 1989). However as late metalarvae, larval teeth are resorbed and closely-packed combteeth erupt (Peters 1981, Labelle & Nursall 1985), suggesting an algal scrapping lifestyle.

Scartella cristata, the molly miller, has a life history characteristic of the family Blenniidae, and is native to the eastern and western Atlantic where it inhabits shallow water (≤ 3 m) (Greenfield & Johnson 1981). In the northern Gulf of Mexico, *S. cristata* is an abundant species associated with anthropogenic structures such as oil platforms and rock jetties (Mobley pers obs). Although published accounts of the diet of blennies are available (Stephens *et al.* 1970, Stoner & Livingston 1980, Goldschmid *et al.* 1984; Lindquist & Dillaman 1986, Kotrschal *et al.* 1991), few have addressed the influences of feeding periodicity, sexual behavior or ontogeny on feeding ecology. We therefore sought to characterize *S. cristata*'s trophic status by investigating ontogenetic feeding shifts and diel feeding behavior between sexes. Specifically, diet was examined to compare variations in the total gut-content biomass and the biomass of invertebrate prey during ontogenetic growth, between males and females during the day and night, and between two collection sites in northwestern Florida.

METHODS

Study Area : A total of 62 specimens of *S. cristata* was collected on anthropogenic rock jetties in Destin East Jetties, Destin, Florida and St. Andrews State Recreation Area, Panama City Beach, Florida (with permission from the Florida Department of Environmental Protection). Twenty-nine individuals were collected from Destin East Jetties over 24 h on August 31-September 1, 1996. Thirty-three individuals were collected from St. Andrews State Recreation Area over a 24-h period on October 12-13, 1996. Collections were made with hand nets, snorkel equipment, and flashlights (for collection at night) at 1 m depth within the upper subtidal zone. Each fish was placed within an individual jar and fixed with 10 % formalin. A broad size range (19-78 mm standard length (SL)) of fish was obtained.

Gut Content Analysis : SL (to nearest mm) was recorded for all specimens. The gut of *S. cristata* is a relatively undifferentiated simple tube. Therefore, the entire gut from mouth to anus was analyzed. The gut was removed, measured for total gut length, and stained in a solution of 10 % formalin and rose bengal. For all 62 fish, sex was assigned as male, female or immature (i.e. lack of gonad development and differentiation) by examining the gonads and, in some instances, by anal-fin morphology (Smith 1974). The gut of each specimen was then dissected under a Wild M-8 stereo-dissecting microscope. Each gut content was assayed for prey taxonomic identity and the number of prey using whole individuals, where possible. When partial invertebrate prey were encountered, only the head parts and, in the case of barnacles, penises, were counted. Dietary items were identified to the lowest taxon possible (Barnes 1980, Heard 1982, Higgins & Thiel 1988). After first removing larger prey items, the total gut contents were

Table I. – Food categories and mean dry weights of prey used in biomass estimates for *S. cristata.*

Food item	Mean Dry Weight (mg)
organic matter	--
mysids	3.0
isopods	0.4
amphipods	0.1
tanaids	0.1
barnacles	0.04
bivalves	0.04
halacarid mites	$1 \cdot 10^{-5}$
harpacticoid copepods	$2 \cdot 10^{-6}$
ostracods	$5 \cdot 10^{-6}$
decapod zoea	$5 \cdot 10^{-6}$
nematodes	$2 \cdot 10^{-7}$

then concentrated with a vacuum pump, Buchner funnel, Erylemyer flask and 0.045 μm filter paper. Total gut contents were dried in an oven for 24 h at 80 °C and weighed with an Ohaus balance (± 1 mg). Dry weights of invertebrate prey taxa were assigned (Table I) by using average dry weight values of prey (Faubel 1982, Widbom 1984, Dauvin & Joncourt 1989, Gaston *et al.* 1996, Driscoll *et al.* 1997 ; Baltz *et al.* 1998, and Fleeger unpubl). Total gut-content dry weight (mg) was then recorded, and individual invertebrate prey dry weights were summed for each fish based on occurrences. Weight of the summed invertebrate prey was subtracted from the total gut-content weight to serve as an estimate of gut-content organic matter. Sand particles, present in low numbers in a few individuals, were removed before total gut content dry weight was assayed. Weights may have been skewed due to preservation in formalin, however the uniform use of this technique allowed the results to be consistently biased (Hyslop 1980).

Diet : All collections of *S. cristata* were pooled to examine two fundamental influences on diet. Ontogenetic preferences (< 30, 30 < 40, 40 < 50, 50 < 60 and > 60 mm SL) and the influence of gender (male and female) on night (2000-0600 h) and day (0600-2000 h) foraging on dietary composition were examined. Mean biomass, mean percent of biomass of individual food categories (%T), and frequency of occurrence (FO) of individual food groups were then used to characterize each pooled data set.

Mean numerical frequency of food categories, per individual of a pooled data group, was first calculated and frequency of occurrence (FO) of individual food categories was then tabulated by following recommendations by Berg (1979) for fishes with a diet comprised principally of vegetative material. The gut-content dry weight for each prey item was first summed for each fish and was standardized with respect to SL for each individual following the recommendations for gravimetric analysis by Hyslop (1980) and was used as a functional unit of total gut-content biomass :

$$\text{total gut-content biomass} = \frac{\text{total gut} - \text{content dry weight (mg)}}{\text{SL (mm)}}$$

Dry weights for all invertebrate prey were also summed for each fish and divided by SL for a total invertebrate-prey biomass estimate within each pooled data set.

The percentage of prey biomass (%T) was also calculated for each individual prey taxon. The sum of individual prey weights within each prey category was divided by the sum of the total biomass using the following formula :

$$\text{Percentage of prey biomass (\%T)} = \frac{\text{sum of all prey dry weight} \times 100}{\text{total gut} - \text{content biomass}}$$

The percent gut-content biomass of the remaining amorphous organic material present in the gut was estimated by subtracting the total of all invertebrate prey dry weight biomass from the total biomass for each individual. Percentage of prey total biomass (%T) of individual prey groups was used as a relative comparison between different pooled data sets as a measure of dietary significance.

Sixty-two juveniles and adults were pooled from both St. Andrews and Destin collections into five size classes (< 30, 30 < 40, 40 < 50, 50 < 60, > 60 mm SL), and were analyzed for influences of body size on dietary composition. Biomass and the total invertebrate prey biomass were tested for normality and homoscedasticity before analysis among night and day collections of adult *S. cristata* (n = 59). Males collected at night were not included in analyses due to small sample sizes (Destin : n = 2 ; St. Andrews : n = 1). Therefore, an adequate comparison between male and female biomass and total invertebrate prey biomass during nighttime collections could not be assessed. Instead, several two-way, Model II Analysis of Variances (ANOVA's) were employed to elucidate the dietary preferences of *S. cristata* with JMP statistical software (SAS Institute Inc.). Comparisons were made between (1) males and females during the day at the two sites and (2) night and day samples for females at the two different sites for both total gut-content and total invertebrate-prey biomass estimates.

RESULTS

In the field, feeding behavior of *S. cristata* was observed during all sampling times and consisted of swallowing bites and nips of the algal turf associated with anthropogenic rock jetties of the study sites. Amorphous material, non-differentiated or non-quantifiable material, was classified as organic matter and consisted of macroalgae, microalgae (benthic diatoms), sessile organisms (bryozoans, sponges, tunicates), and detritus, and comprised most of the total gut-content biomass (Tables II and III). Quantifiable prey included sessile animals (barnacles and bivalves), benthic mobile prey (harpacticoid copepods, isopods, amphipods, tanaids, ostracods, nematodes and halacarid mites) and demersal crustaceans (mysid shrimp and decapod zoea).

Harpacticoid copepods were the most frequently encountered prey item. They were present in approximately 90 % of all gut contents, and this proportion was similar when compared among ontogenetic size classes and sexes during all times of day. However, harpacticoid copepods always comprised a very small portion, < 0.1 % of the total gut-content biomass (Tables II and III).

The contribution of algae and invertebrates to the total gut-content biomass varied among the five size classes of *S. cristata* (Table II). The smallest size class of *S. cristata* (< 30 mm SL) displayed the smallest total gut-content biomass (0.1 mg SL^{-1} ± 0.06) but the highest percentage of invertebrate biomass (34.9 %T) with the bulk of the prey consisting of larger invertebrates (i.e., mysids, isopods, barnacles, tanaids and bivalves). The largest size class (> 60 mm SL) contained the highest total gut-content biomass (0.5 SL^{-1} ± 0.3) which consisted of algae and organic matter

Table II. – Mean total gut-content biomass, mean SL, prey biomass (%T) and frequency (FO) of food categories pooled between Destin and Panama City collections for five ontogenetic size classes of *S. cristata*.

Size Class (mmSL)	< 30 (n = 8)		30 < 40 (n = 17)		40 < 50 (n = 16)		50 < 60 (n = 16)		> 60 (n = 5)	
Mean mmSL ± SD	26.25 ± 3.11		36.29 ± 2.77		45.44 ± 2.58		54.06 ± 2.89		65.02 ± 7.02	
Mean biomass (mg/SL) ± SD	0.10 ± 0.06		0.25 ± 0.13		0.46 ± 0.23		0.47 ± 0.29		0.52 ± 0.38	
	%T	FO	%T	FO	%T	FO	%T	FO	%T	FO
organic matter	65.2	100	90.6	100	89.1	100	90.2	100	96.2	100
mysids	18.5	12.5	0	0	2.6	12.5	6.0	6.3	1.9	20
isopods	5.9	37.5	4.9	23.5	4.5	50	2.1	37.5	0	0
amphipods	0.9	25	1.7	35.3	2.6	56.3	1.0	81.3	0.8	40
tanaids	4.7	37.5	1.5	35.3	0.2	18.8	0.1	18.3	0.3	40
barnacles	3.2	75	1.1	47	0.8	56.3	0.3	31.3	0.4	40
bivalves	1.7	25	0.2	17.6	0.2	17.6	0.2	12.5	0.5	40
halacarid mites	0	0	< 0.1	23.5	< 0.1	6.3	0	0	< 0.1	20
harpacticoid copepods	< 0.1	87.5	< 0.1	82.4	< 0.1	87.5	< 0.1	93.8	< 0.1	100
ostracods	< 0.1	37.5	< 0.1	41.2	< 0.1	37.5	< 0.1	18.3	< 0.1	60
decapod zoea	< 0.1	12.5	< 0.1	11.8	< 0.1	6.3	< 0.1	12.5	0	0
nematodes	0	0	< 0.1	5.9	< 0.1	17.6	< 0.1	12.5	0	0
total invertebrate prey	34.9	100	9.4	94.0	10.9	94.0	9.8	94.0	3.8	100

(96.2 % of the total) and invertebrates (3.8 % of the total). In the intermediate size classes, the total gut-content biomass increased with increasing size but the percentage of invertebrates contributing to the total was nearly constant at about 10 %.

Adult male and female *S. cristata* had contrasting activity regimes during the 24-h feeding cycle. Eighty-eight percent of all males (n = 26) were encountered during the daylight samples whereas 54 % of all females (n = 33) were encountered during the night. ANOVA revealed no significant difference in total gut-content biomass between males and females collected during the day ($F_{1,34} = 0.11$; P = 0.74) and no significant effect of sampling between sites was observed ($F_{1,34} = 0.83$; P = 0.37). However, a significant interaction effect was noted between site and male and female daytime collections ($F_{1,34} = 4.16$; P = 0.05). No significant difference in total gut-content biomass between females sampled during the night and females sampled during the day was observed ($F_{1,29} = 0.79$; P = 0.38) although a trend was observed for females (females contained, on average, 0.44 mg SL^{-1} during the day but 0.34 mg SL^{-1} at night). No significant differences between collection sites was observed ($F_{1,29} =$ 3.34; P = 0.08) and no interaction between female collections and site was found ($F_{1,29} = 0.156$; P = 0.22).

No significant difference was detected between male and female total invertebrate prey biomass during the day collections ($F_{1,34} = 1.88$; P = 0.18). However, a significant site difference was observed in total invertebrate prey biomass estimates between the Destin and St. Andrews collection sites ($F_{1,34} = 10.14$; P < 0.01). No significant interaction between gender and site was observed ($F_{1,34} = 2.19$; P = 0.15). A comparison between night and day samples revealed a significant difference in total invertebrate prey biomass among females ($F_{1,29} = 5.87$; P = 0.02). During the night, invertebrate prey were much more common (Table III) (22 % invertebrate prey at night, mostly comprised of isopods and mysids, opposed to 7.9 % total invertebrate prey biomass during the day). A significant site affect was again encountered when comparing female night and day total invertebrate biomass estimates between the Destin and St. Andrews collection sites ($F_{1,29} = 10.88$; P > 0.01) and no significant interaction between site and time was observed ($F_{1,29} = 0.88$; P = 0.36).

Table III. – Mean total gut-content biomass, mean SL, prey biomass (%T) and frequency (FO) of food categories pooled between Destin and Panama City of male and female, night and day collections of *S. cristata*.

Sex/time of collection	Males / Night (n = 3)		Females / Night (n = 18)		Males / Day (n = 23)		Females / Day (n = 15)	
Mean mmSL ± SD	54.00 ± 9.16		43.27 ± 8.99		45.83 ± 12.63		45.13 ± 10.46	
Mean biomass (mg/SL) ± SD	0.30 ± 0.13		0.34 ± 0.22		0.37 ± 0.26		0.44 ± 0.32	
	%T	FO	%T	FO	%T	FO	%T	FO
organic matter	90.5	100	78.0	100	98.1	100	92.1	100
mysids	6.0	33.3	9.4	16.7	0	0	1.0	6.7
isopods	1.1	33.3	10.4	72.2	0.5	17.4	0.6	26.7
amphipods	2.3	100	0.71	50	0.4	34.8	4.0	34.8
tanaids	0.1	33.3	< 0.1	5.6	0.6	26.1	1.0	60
barnacles	0	0	1.2	77.7	0.1	30.4	0.9	53.3
bivalves	0	0	0.2	16.7	0.1	13.0	0.4	26.7
halacarid mites	0	0	< 0.1	5.6	< 0.1	13.0	< 0.1	20
harpacticoid copepods	< 0.1	100	< 0.1	77.8	< 0.1	91.3	< 0.1	93.3
ostracods	< 0.1	100	< 0.1	11.1	< 0.1	34.8	< 0.1	46.7
decapod zoea	0	0	< 0.1	27.8	< 0.1	4.3	< 0.1	6.7
nematodes	0	0	< 0.1	11.1	< 0.1	17.4	< 0.1	13.3
total invertebrate prey	9.5	100	22.0	95.7	1.9	94.4	7.9	93.3

DISCUSSION

Members of the family Blenniidae are known to have a wide array of dietary preferences, ranging from generalized with differing degrees of opportunism (Kotrschal *et al.* 1991) to highly specialized herbivory or carnivory (Stoner & Livingston 1980, Moyle & Cech 1996). Omnivory in fishes has generally been interpreted as a compromise strategy supplementing energy from primary food sources with protein from scarce animal prey (Bowen *et al.* 1995). Invertebrates have been shown to be high in food quality, both protein and energy content, compared to algae, macrophytes, and detritus (Benavides *et al.* 1994; Bowen *et al.* 1995). Dietary protein has also been shown to be directly proportional to energy required for growth, development, and sexual reproduction in fishes (Benavides *et al.* 1994). Our data suggest that *S. cristata* feeds primarily on algae and sessile invertebrates but is inclined to feed on demersal and benthic vagile invertebrates, perhaps to supplement protein requirements.

Harpacticoid copepods have been cited as an essential food source of many juvenile fishes, as well as an important component of benthic food chains (Alheit & Scheibel 1982, Gee *et al.* 1985).

In this study, harpacticoid copepods were the most frequently encountered invertebrate in *S. cristata* gut contents, with the highest numerical frequency of all invertebrates. Harpacticoid copepods contribute to the baseline dietary protein requirement of many fishes and can provide superior nutritional quality (Volk *et al.* 1984). In *S. cristata,* however, the contributions of harpacticoid copepods to the total gut-content biomass was very low (< 0.01 % of the total for all samples) due to their small individual dry weight. Harpacticoid copepods were likely ingested with the consumption of large pieces of the algal turf, where phytal harpacticoid copepods are presumably abundant (Hicks & Coull 1983, Hicks 1985). Ontogenetic feeding shifts in fishes are common but have not been well documented (Toepfer & Fleeger 1995). They appear to function as adaptations for the maximization of energy intake during growth and with changes in resource availability (Villiers 1980, Swenson & McCray, 1996). In *S. cristata,* numbers of invertebrate prey decreased and the utilization of algae increased during growth, a trend opposite of the life history of many fishes (Villiers 1980, Grossman 1980, Toepfer & Fleeger 1995, Aarnio *et al.* 1996). There was no obvious relationship between the SL of fish and the size of invertebrate prey; juveniles more frequently

ingested a higher percentage of biomass of the largest prey, mysid shrimp. The adult reliance on algal food resources may be associated with morphological constraints associated with a dietary specialization to herbivory or to adult behaviors that require large investments in time (i.e., territorial defense in males and females and nest guarding in males are common in blennies), minimizing available time for other foraging strategies.

An effect of collection site on total invertebrate gut-content biomass estimates was observed between the two study sites. Although St. Andrews and Destin jetties are situated ~ 100 km apart from each other, they both support similar algal and faunal communities (Mobley pers obs). Because comparisons were made between the two jetties six weeks apart from each other, time of year might explain the differences observed in invertebrate total gut-content biomass estimates. Demersal invertebrates are known to vary in space and time (Metaxas & Scheibling 1994) and it is possible that prey availability was different at the two jetties studied due to a variety of environmental factors (tidal regime, season, etc). No site effect was observed for total gut-content biomass which suggests that *S. cristata* may compensate for differences in prey availability by consuming a greater amount of alternative food sources.

Total gut-content biomass estimates were similar in collections of males during the day and females during the day and night, although the relative proportion of invertebrates and organic matter (mostly algae) significantly differed. There was no significant difference between the total invertebrate biomass of male and female *S. cristata* during the day, which suggests that adults of both sexes ingest the same total amount of food. During the night, however, invertebrate prey became more common in the gut contents of female *S. cristata*. The high proportions of demersal invertebrates with known nocturnal foraging behavior (Ohlhorst 1982, Youngbluth 1982, Armonies 1989, Oishi & Saigusa 1999) suggest that nighttime foraging on invertebrates increases in female *S. cristata*. Short-term dietary shifts among fish predators have been correlated with vertical movements of planktonic crustaceans (Robertson & Howard 1978) and may explain this dietary shift. Grossman *et al.* (1980) hypothesized benefits in nighttime feeding include avoidance of visually-oriented predators and an increase in the availability of major prey.

Male *S. cristata* were frequently observed defending nest sites in barnacle and oyster shells at the time of collection, and multiple egg clutches in different stages of development (denoted by color) within a single nest were common (Mobley pers obs). Furthermore, Smith (1974) noted an increase in fidelity of *S. cristata* males to their

burrows during periods of sexual activity. These observations suggest that male *S. cristata* were rare in night collections in the present study (only three were collected at night thus rendering gut-content analysis inconclusive) because of a high incidence of nest guarding of egg clutches. Males of many blennies contribute a large portion of their time to the care of eggs and their defense from predators, and as a result, experience a decrease in feeding during the breeding season (Nursall 1981, Marrano & Nursall 1983, Côte & Hunte 1989). Although total gut-content biomass of male *S. cristata* in this study was not reduced in day collections compared to that in females, nest guarding may preclude males from taking advantage of demersal invertebrates during the nighttime. If so, food quality in male *S. cristata* may well be reduced by its nest-guarding behavior.

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