DIEL BEHAVIOR PATTERNS OF PLANKTIVOROUS FISH AND THEIR PREY

A very ambitious and difficult project, but you pulled it off. An innovative, nicely designed, and well-executed study. Data should be presented in more detail. All tables should have headings. Some of the data would have more impact as histograms. Excellent discussion of your results.

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3/7/90
DISCOVERY BAY

ABSTRACT: (BMS)

In an attempt to gain a better understanding of diel patterns of both zooplankton and planktivorous fish, we observed both at Discovery Bay, Jamaica. Specifically, we observed several planktivorous fish species, including *Chromis cyaneus*, *Chromis multilineatus*, *Clepticus parrei*, *Gramma loreto*, *Myripristis jacobus*,* *Priacanthus arenatus*,* and *Apogon* sp.* (* = nocturnal), and measured zooplankton densities.

We found that zooplankton are more abundant at night than in the morning. We were then able, based on our planktivore observations, to attribute this phenomenon to a decreased risk of predation at night. Next, we established that both planktivorous fish and zooplankton are more abundant over

coral than over sand. We attributed these findings to locations of shelter (from predation) and food. Finally, we observed *Chromis cyaneus* throughout the day. We found that these fish tend to forage higher up in the water column (>1.5m above coral), in the morning, and that they descend in the evening. At this time, they stop feeding and become increasingly territorial, as they prepare to go into the coral for the night.

Introduction: (BMS)

It has been shown (Emery, 1968) that many zooplankton migrate up from coral reefs into the overlying water column at dusk, and return to their benthic caverns at dawn. While this phenomenon has been studied extensively (Sale, et al., 1976; Alldredge & King, 1977; Porter, et al., 1977, 1978; Ohlhorst, 1982), the reason behind this diel migration pattern had never been tested. Predation pressure has been proposed (Ohlhorst, 1982) as the major force selecting for this behavior. Since much research has been based on this assumption, we felt it important to test its validity.

Accordingly, we tried to determine which fish species are the most ecologically important planktivores available for observation at Discovery

Bay, Jamaica. We found (Randall, 1967) that Chromis cyaneus (Blue chromis), Chromis multilineatus (Brown Chromis), Cleptricus parrai (Creole wrasses), and Gramma loreto (Fairy Basslets) are diurnal planktivores native to Jamaica. Myripristis jacobus (Blackbar soldierfish), Priacanthus arenatus (Bigeyes), and Apogon spp. (Cardinalfish) are the only nocturnal planktivorous fish we found.

While observing these species, we discovered some interesting patterns in Blue Chromis behavior. So, we expanded our study to include observations of this species, with special regard to their foraging and territorial behaviors at different times of the day.

In all, we developed four hypotheses to test. First, we predicted, based on Ohlhorst's

(1982) study, that zooplankton densities would be higher at night than at dusk, and higher at dusk than ~~at~~ in the morning. Second, we suggest that this is due to a higher risk of predation to these plankton in the morning, as was assumed by Robertson & Howard (1978). Third, we predicted that zooplankton would exist at higher densities over coral areas than over sandy areas throughout the day and night. This prediction was based on similar findings by Alldredge & King (1977). Fourth, we hypothesized that, due to the locations of their food sources and hiding places, planktivorous fish would also be found at higher densities over coral than over sand. Our final aim was to attempt to make

some conclusions regarding Blue Chromis behavior based on our observations of their diel patterns.

Methods

We conducted our study at Discovery Bay, Jamaica, West Indies. We made sixteen dives using SCUBA at mooring 1 on the West Fore-Reef between 25 February 1990 and 5 March 1990.

At M1 we set out four 30 m long transects of cotton string with buoys 1.5 m off the bottom marking each end. All transects were in 40-50 ft of water. Three transects were laid over coral, while one was in a sand channel. We traversed each transect four times both in the morning shortly after 0900h and at dusk shortly after 1730h, and three times at night at 2100h.

Why the asymmetry?

To count fish, two divers swam abreast down the length of the transect counting the planktivorous

fish within 1.5 m of each side of the string. We analyzed these two pieces of data as seperate transects. In the morning, we counted only Blue Chromis and we noted whether they occurred above or below 1.5 m off the substrate. At night, we counted Blackber Soldierfish, Cardinal Fish, and Big Eyes, making no distinction between species, and ignoring height off the substrate.

We obtained our data on planktivore foraging by watching a focal fish for 1 minute and counting the number of times that fish opened its mouth to lunge at a zooplankton. Randal (1967) attests to the validity of this method. In taking these data, we distinguished between Blue Chromis above and below 1.5 m off the substrate, and kept seperate data sets for

morning and dusk. Further, we noted the number of aggressive interactions each Blue Chromis was involved in during the observation period. Aggressive interactions are defined here as an attack where one fish nipped at or chased another fish.

Finally, we assessed zooplankton density by towing a plankton net of 25 cm diameter along each of the transects. The net was built so that collection vials could be easily interchanged underwater. The total volume of water strained per tow was 1.42 m^3. We took plankton samples at each of the three time periods on two different days. We killed and preserved the zooplankton with ethyl alcohol and counted the total number of plankton per sample using dissecting microscopes.

We did not record species densities, nor did we measure planktan size.

Results: (compiled in table 1) (BMS)

For the most part, our results support our hypotheses, and show significant trends in Blue Chromis behavior. First, we found that zooplankton are found at high densities (81.0 ± 13.75 zooplankton/tow, n=3) at night, at intermediate densities (46.0 ± 9.06 zoopl./tow, n=4) at dusk, and at low densities (8.2 ± 2.28 zoopl./tow, n=5) in the morning. These densities are all significantly different from one another (ANOVA, $p<.001$, LSD = 16.91).

To assess predation risk to plankton, we multiplied the number of planktivores found at each time of day by the mean feeding rate of the primary planktivore of that time. Here, attack rate was assumed to reflect success rate, which is most relevant to predation risk. We used the foraging rate of Blue Chromis for

the morning (13.4 ± 3.32 attacks/min, n = 25) and dusk (0.2 ± 0.42 attacks/min, n = 10), and that of the Blackbar soldierfish (42.2 ± 10.4 attacks/min, n = 10) was used for the night computations. Feeding rates of all species are in Table 1. We then found the density of planktivorous fish in the morning (91.08 ± 57.46 fish/transect, n = 24) to be significantly greater than that at night (4.94 ± 4.36 fish/trans., n = 18) (t-test, $p < .001$). Predation risk was determined to be significantly higher in the morning (1095.25 ± 738.37 zoopl./min, n = 24) than at either dusk (7.85 ± 3.23 zoopl/min. n = 24) or night (208.61 ± 183.91 zoopl/min, n = 18) (ANOVA, $p < .001$). No significant difference was found between predation risk at dusk and night (LSD = 332.25).

Significantly more zooplankton were found

over coral (81.0 ± 13.15 zoopl./tow, n=3) than sand (21.0 ± 8.5 zoopl./tow, n=2) at night (t-test, $p < .02$). This trend (t-test, $p < .01$) was also found at dusk, when 46.0 ± 9.06 zoopl./tow (n=4) were found over coral, and 14.5 ± 3.5 zoopl./tow (n=2) were found over sand. No significant difference (t-test, $p > .05$) was found between the density of zooplankton found over coral (8.2 ± 2.28 zoopl/tow, n=5) and that found over sand (4.5 ± 4.95 zoopl./tow, n=2) during the morning.

Regarding our fourth hypothesis, we found significantly more planktivorous fish over coral substrates than over sandy ones (t-tests: $p < .001$ AM & dusk; $p < .02$ night). Specifically, in the morning 91.08 ± 57.46 fish/transect (n=24) were found over coral, and 0.3 ± 0.67 fish/transect (n=8) were found over sand; at dusk, 52.96 ± 19.54 fish/transect

(n=24) were found over coral, and only 1.38 ± 1.30 fish/transect (n=8) were found over sand; at night, 4.94 ± 4.36 fish/transect (n=18) were found over coral, while a mere 0.33 ± 0.52 fish/transect (n=6) were found over sand.

Finally, we have made several observations of Blue Chromis. Regarding location, we found that in the morning, there were 91.08 ± 57.46 fish/transect (n=24), significantly more (t-test, $p < .01$) than we found at dusk (52.96 ± 19.54 fish/transect, n=8). No Blue Chromis were ever seen at night. Within the morning samples, significantly more (t-test, $p < .001$) Blue Chromis were found above the 1.5 m transect line (73.38 ± 53.46 fish/transect, n=24) than below it (17.71 ± 11.22 fish/transect, n=24). This trend reversed at dusk, when we found significantly more (t-test, $p < .001$) Blue Chromis

below the 1.5 m line (39.25 ± 16.61 fish/transect, n=24) than above it (13.71 ± 10.18 fish/trans., n = 24).

Just as their locations varied with time, so did the nature of their behaviors. Feeding was significantly higher (t-test, $p<.001$) in the morning (13.4 ± 3.32 attacks/min, n=25) than it was at dusk (0 ± 0 attacks/min, n=10) above the 1.5 m. line; this was also true below the line, where morning feeding was 6.33 ± 1.63 attacks/min (n=15), and dusk feeding was 0.2 ± 0.42 attacks/min (n=10). Lastly, territorial behavior increased at dusk -- we saw significantly more (t-test, $p<.001$) conspecific attacks/min at dusk (2.8 ± 1.23, n=10) than we did in the morning (0.8 ± 0.77, n=15).

TABLE 1. (BMS)

I. Zoops: (in zoops/tow) Night (81.0 ± 13.75, n = 3) > Dusk (46.0 ± 9.06, n=4) > Morning (8.2 ± 2.28, n = 5)

ANOVA $p < 0.001$, LSD = 16.91, $F_3 = 71.40$

II. Predation Risk: (# plank.* F. Rate) (B. Chromis, BBSoldierfish) (units = zoops./min)

Morning (1095.25 ± 738.37, n=24) > Night (208.61 ± 183.91, n=18) ≅ Dusk (7.85 ± 3.23, n=24)

ANOVA $p < 0.001$, LSD = 332.25, $F_3 = 95.39$

Foraging Rates: (zoopl/min)

AM	Farry Basslet	6.7 ± 3.16, n=6	
	Creole wrasse	12.77 ± 3.52, n=13	
	B. Chromis >1.5m	13.4 ± 3.32, n=25	
	B. Chromis <1.5m	6.3 ± 1.63, n=15	
	Brown Chromis	≅ -same- (n=4)	
Dusk	Bl. Chromis >1.5m	0 ± 0, n=10	
	Bl. Chromis <1.5m	0.2 ± 0.42, n=10	
Night	Blackbar Soldierfish	42.2 ± 10.4, n=10	

t-test: BBS_{PM} vs. $BC_{>1.5AM}$ $p < .001$ ($t = 12.36$, $df = 33$)

Density (planktivores) (fish/transect)

Morning (91.08 ± 57.46, n=24) > Night (4.94 ± 4.36, n=18)

t-test: $p < 0.001$, $t = 6.35$, $df = 40$

III. Zoops: Coral > Sand (zoopl/tow)

AM: C (8.2 ± 2.28, n=5) ≅ S (4.5 ± 4.95, n=2) $p > .05$ ($t = 1.35$, $df = 5$)

Dusk: C (46.0 ± 9.06, n=4) > S (14.5 ± 3.5, n=2) $p < .01$ ($t = 4.74$, $df = 4$)

Night: C (81.0 ± 13.15, n=3) > S (21.0 ± 8.5, n=2) $p < .02$ ($t = 5.51$, $df = 3$)

IV. Fish: Coral > sand (fish/transect)

AM: C (91.08 ± 57.46, n=24) > S (0.3 ± 0.67, n=8) $p < .001$ ($t = 4.48$, $df = 30$)

Dusk: C (52.96 ± 19.54, n=24) > S (1.38 ± 1.30, n=8) $p < .001$ ($t = 7.46$, 30)

Night: C (4.94 ± 4.36, n=18) > S (0.33 ± 0.52, n=6) $p < .02$ ($t = 2.58$, 24 df)

V. Blue Chromis Observations:

(fish/trans.) AM (91.08 ± 57.46, n=24) > Dusk (52.96 ± 19.54, n=24) ($t = 3.08$, $df = 46$) → $p < 0.01$

(fish/trans) AM: below 1.5m (17.71 ± 11.22, n=24) < above (73.38 ± 53.46, n=24) → $p < 0.001$ ($t = 4.99$, $df = 46$)

(fish/trans) Dusk: below 1.5m (39.25 ± 16.61, n=24) > above (13.71 ± 10.18, n=24) → $p < 0.001$ ($t = 6.42$, $df = 46$)

(att/min) Feeding: Above AM (13.4 ± 3.32, n=25 > Dusk (0 ± 0, n=10) ($t = 7.71$, $df = 33$) $p < 0.001$

(att/min) Below AM (6.33 ± 1.63, n=15) > Dusk (0.2 ± 0.42, n=10) ($t = 11.62$, $df = 23$) $p < 0.001$

Attacks (<1.5m) (attack/min): Dusk (2.8 ± 1.23, n=10) > AM (0.8 ± 0.77, n=15) ($t = 5.19$, $df = 23$) $p < 0.001$

Discussion

Our data support both our first hypothesis and findings of previous studies which show that zooplankton density in the water column increases at night. In our study, zooplankton density was significantly higher at dusk than in the morning, and significantly higher still at night. As has been documented by Olhorst (1982) in Discovery Bay, ~~demonstrates~~ this increase in density is caused by demersal zooplankton migration into the water column at night.

It has been proposed that zooplankton hide in crevices in the coral by day to escape from predation. This hypothesis is based on the casual observation that there are fewer active planktivorous fish at night than at day (Olhorst, 1982)

Our second hypothesis follows from Olhurst's idea. With a formidable threat to the zooplankton as they pass twice per night through the layer of live feeding corals, and the higher abundance of basket stars (pers. obs.) at night, plankton must experience a dramatically decreased predation risk from nocturnal fish once in the water column ~~in order to~~ for this migration through the perilous coral layer to have evolved.

Our data show that the risk of predation is significantly lower (≈ 80% less) at night than in the early morning. Further, since we used only Blue Chromis foraging in assessing risk in the morning, the number should be far greater to account for foraging of Fairy Basslets, Brown Chromis and Creole Wrasses. The implication

of our finding is that the decreased risk of predation to zooplankton at night by fish could be of sufficient magnitude to select for demersal plankton migration. A literature summary could be performed to assess the combined effects of all types of plankton predation on coral reefs. With the results of the present studies, such a survey could accurately assess overall risk to zooplankton.

Several observations stemming from these data are worthy of note. Blue Chromis foraging rates were significantly lower for fish below 1.5 m ($\bar{x} = 6.38$) than fish foraging above 1.5 m ($\bar{x} = 13.4$). At first we believed that this trend was due to the fact that fish lower than 1.5 m were there to escape some danger (hence not to feed). This notion is supported by

At same time of day?

the fact that Blue Chromis close to the coral change their color to a dark purple to minimize their conspicuousness against the coral.

The foraging data for Fairy Basslets ($\bar{x} = 6.77$) and Creole Wrasse ($\bar{x} = 12.77$) suggest that the effects of height are more global. The Fairy Basslet, which was always found less than 1.5 m from the substrate foraged at the same rate as Blue Chromis at that level did.

Similarly, Creole wrasses, which were always observed higher than 1.5 m above the reef fed at a rate very similar to Blue Chromis found at that height. Further studies could look at density of zooplankton at the two heights as a possible cause for the foraging rate discrepancy between the two zones.

(It should be noted that the similarity of foraging rates for dissimilar fish in identical situations spatially and temporally prompted our use of Bluebber Soldierfish foraging data as representative of all nocturnal planktivores).

Given that predation risk is lower at night, our data make it possible to look more closely at the reasons for decreased nocturnal planktivory. The major factor is the largescale decrease in the number of planktivores from ~~day~~ morning to night (93% less). Even if we factor in a correction for the possibility of ~~[illegible]~~ fish not seen at night, the discrepancy in numbers is huge. Interestingly, nocturnal planktivores capitalize on the high zooplankton density, feeding at rates three fold the highest observed daytime

foraging rate. This observation suggests another important question. Given that competition for food is low for nocturnal planktivores, why are they not more abundant? Though out of the realm of this study, factors limiting nocturnal planktivore abundance are worthy of future research.

Our third hypothesis, that zooplankton densities over coral would be higher than densities over sand at all time periods was partially supported. In the morning samples the mean densities were not significantly different. Both at dusk and at night, however, significantly more zooplankton were found over coral than over sand. An explanation of these results could be that plankton found in the morning are

not demersal. Because they do not rest in a specific area, ~~we would expect~~ their distribution is relatively random. At dusk and night, however, most of our collected zooplankton probably were demersal, having come out of the coral. Because of this, they were found in greater numbers over coral than sand.

Our final hypothesis was that planktivorous fish would occur in higher densities over coral than over sand. Our study confirmed this with significant data for all sampling times. In fact, the only fish ever found over sand were near one of two small coral heads that fell within the transect boundaries.

Two mechanisms are likely to drive this fish abundance. First, the prey

are significantly more abundant over coral. Because of this, it would behoove the planktivores to ~~forage where their~~ remain over the coral. In addition, the fish are likely to be best protected from their predators over the darker and more heterogeneous coral than over the sand. This protection provides further impetus for the planktivorous to remain over the coral.

The final goal of our study was to characterize Blue Chromis behavior both morning and night. Analysis of our results sheds some light on behavioral trends.

Blue Chromis is a diurnal species that spends its nights in small holes in the coral substrate. Significantly higher Blue Chromis densities in the water column in the morning

probably is due to

than at dusk, ~~are consistent with~~ the fact that some proportion of the fish have settled into their night shelter by the time of our dusk dive.

You don't know this

In the morning, Blue Chromis foraging rates were significantly higher than at dusk (13.4 zoop/min vs. 0 zoop/min >1.5m). These data suggest that Blue Chromis feed actively during the day, and do not feed at dusk, even though zooplankton densities are significantly higher at dusk. It would be interesting to look at foraging rate over the course of the day. The lack of foraging at dusk could be due to a satiation effect that would be seen earlier in the afternoon. With the data presented here, however, we can only conclude that at dusk, Blue Chromis are preoccupied with finding shelter for the night.

This interpretation is consistent with the fact that significantly more Blue Chromis are above 1.5 m (75%) than below 1.5m in the morning. It is at this height that Blue Chromis forage most efficiently. At dusk, however, significantly more (75%) of the Blue Chromis are below 1.5 m. These fish are not feeding ($\bar{x}$ 0.27 P/min), but are presumably settling for the night.

The data for Blue Chromis aggression lend further support to this hypothesis. Above 1.5 m, aggression is never seen. Below 1.5 m, aggression is significantly higher at dusk ($\bar{x}$ 2.8 attacks/min) than in the morning ($\bar{x}$ = 0.8 attacks/min). We propose that Blue Chromis, which is usually a community fish, feeding in large schools, becomes territorial at dusk as it begins to guard a sleeping hole.

It has also been suggested (Gilbert, pers. comm.) that because Blue Chromis spawn at dusk at new and full moons, the agression could be a protection of spawning territories. Though the two possibilities are not mutually exclusive, and must, indeed, overlap during certain periods of the month, it is most likely given the moon phase during our study, that our observations were of territorial protection of sleeping space.

Works Cited

ALLDREDGE, A.L. & J.M. King, 1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol., Vol. 41, pp. 317-333

EMERY, A.R., 1968. Preliminary observations on coral reef zooplankton. Limnol. Oceanogr., vol 13, pp. 293-303.

OHLHORST, S.L., 1982. Diel migration patterns of demersal reef zooplankton. J. Exp. Mar. Biol. 60: 1-15

PORTER, J.W. & K.G. Porter, 1977. Quantitative sampling of demersal plankton migrating from different coral reef substrates. Limnol. Oceanogr., 22: 553-556

PORTER, K.G., J.W. PORTER, & S.L. OLHORST, 1978. Analysis of resident reef zooplankton: composition and habits. In, Coral Reefs: research methods, edited by D.R. Stoddart & R.E. Johannes, Paris, UNESCO (UNESCO monographs & Oceanographic methodology, 5), pp. 499-514.

Randall, J.E., 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. 5: 665-847

ROBERTSON, A.I. & R.K. HOWARD, 1978. Diel Trophic interactions between vertically migrating zooplankton and their fish predators in an eelgrass community. Mar. Biol. 48: 207-213

Sale, P.F., P.S. McWilliam & D.T. Anderson, 1976. Composition of the near-reef zooplankton at Heron Reef, Great Barrier Reef. Mar. Biol. 34: 59-66.