diets may be equally profitable because the species spent the same percentage of their time foraging (≈ 61.1% in both cases). If so, we would predict a lower capture rate for the high energy food type so that energy gain on different food types is equalized. Alternatively, food resources may be unlimited and dietary partitioning an artifact of learned group traditions (Chapman 1990). To test this alternative, a future study might evaluate whether the amount of available food resources (fruits, insects and leaves) exceeds, or barely meets, the energetic and nutritional needs of the local monkey populations

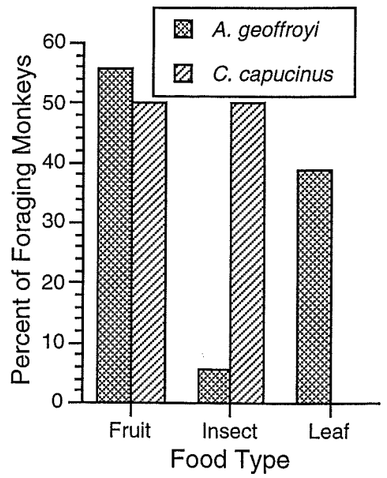


Fig. 1. Percent of *A. geoffroyi* and *C. capucinus* observed foraging on three different food types in Corcovado National Park, Costa Rica (n = 18 *A. geoffroyi* and n = 8 *C. capucinus*).

Interestingly, *A. geoffroyi* monkeys spend more time in each tree while foraging. Because the time spent foraging in each tree did not change with food type, this difference is probably a result of the different ways the species forage instead of their food preferences. *A. geoffroyi* appear more agile and use their prehensile tails more often, which gives them access to a larger proportion of the tree (pers. obs.). The greater time spent within each tree may be a result of this increase in foraging area. A study analyzing the proportion of total tree area in which the two species forage could test this hypothesis. Alternatively, movement costs might be lower for *C. capucinus* so they shift trees sooner when resources become depleted. If so, we would predict *C. capucinus* 's foraging success rate to diminish less than *A. geoffroyi*'s before they switched trees.

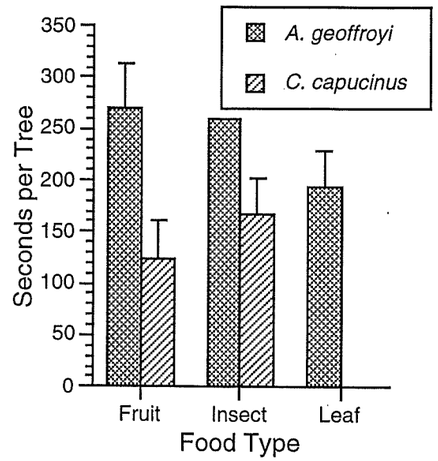


Fig. 2. Average time *A. geoffroyi* and *C. capucinus* spent per tree while foraging on different food types in Corcovado National Park, Costa Rica

.LITERATURE CITED

Chapman, Colin A. 1987. Flexibility in diets of three species of Costa Rican primates. Folia primatola **49**: 90-105.

FACTORS DETERMINING FISH DISTRIBUTION AND ABUNDANCE IN TIDE POOL COMMUNITIES

P. PARKER C. SHELBY, E. HANK TALIAFERRO, AND FRITZ GERHARDT

Abstract. Both biotic and abiotic factors control the distinct patterns in fish distribution and abundance in coastal tide pool communities. Large fish were only found in large pools, probably because physiological factors limit their ability to survive in small pools. Small fish were most apparent in small pools where they face fewer predation risks but more extreme physical conditions. Species diversity was greater in large, deep pools found low in the intertidal zone, perhaps because of more stable abiotic conditions. Within individual pools, we observed daily fluctuations in fish abundance but not species composition. Results suggest that tide pool communities are structured by both physical conditions and predation risks, but that there is also random sorting of fish during tide cycles.

Key words: fish community, physical environment, predation, tide pool

INTRODUCTION

Both biotic and abiotic factors influence patterns of distribution and abundance in organisms. Coastal tide pool communities abound with fish, aquatic plants, and hundreds of other marine and littoral organisms. These complex communities continually reform during tide cycles. The tidepools themselves are characterized by fluctuating salinity, temperature, and dissolved oxygen concentrations. The magnitudes of these physical changes depend on total water volume and the duration of time a pool is separated from the more constant marine conditions. These fluctuations in physical conditions, in conjunction with predation by large fish and birds, can affect the distribution and abundance of tide pool inhabitants.

We hypothesized that fish communities in tide pools are not random assemblages of organisms trapped by wave action and receding tides, but have predictable properties influenced by physical conditions and predation risks within these pools. Specifically, we predicted that to balance suitable physical conditions while minimizing predation risks, small fish occur predominantly in small pools, medium-sized fish occur in greatest numbers in medium-sized pools, and large fish are most abundant in large pools. Additionally, we predicted that species richness and diversity would be greater in the lower intertidal zone because of increased habitat heterogeneity and more constant environmental conditions characteristic of large, deep pools separated from the ocean for short periods of time.

METHODS

We sampled 66 tide pools on 1-4 February 1996 along the Pacific coast of Corcovado National Park, Costa Rica. For each pool, we measured depth at the deepest point, surface area to $\pm$ 0.5 m^2, temperature, substrate type (sand, sand over clay, or clay), and location (low, medium and high) in the intertidal zone. We were unable to measure water volume per tidepool, because depth was highly variable within tidepools. Because of the broad range in surface area (0.5 - 300.0 m2), we converted surface are to an ordinal rank of 1 - 5 (5 being the largest). Analyses using actual areas, as opposed to ordinal classes, were qualitatively similar but more difficult to interpret graphically. Individuals of each species of fish were counted and their sizes were estimated. For analyses, we divided all fish into three size classes: small (1 - 2 cm), medium (3 - 8 cm) and large (15 - 35 cm). Species richness and Shannon-Weiner diversity were calculated for all species, and results were standardized by area for analysis. Fish in six haphazardly-chosen pools were censused consecutively on all four days late in the tide cycle to examine day-to-day variation within pools.

We observed large fish and bird foraging behaviors in tide pools to assess predation pressures on pool residents. To evaluate the effects of bird predation, we recorded behavioral responses (no response, hide, flee) of small- and medium-sized fish to the encroaching shadow of an investigator (PPCS). To simulate large fish predation, we chased small- and medium-sized fish with our hands and feet for 15 seconds, and recorded their behavioral responses. The responses were anlayzed using G-tests.

The effects of physical environment on fish distribution and abundance were analyzed by linear regressions. Depth, location in the intertidal zone, and area did not significantly covary. We tested for day-to-day variation in the relative abundance of fish species occupying 6 pools over 4 days with a G-test.

RESULTS

Seven fish species were found in the 64 pools sampled. Small fish density decreased with increasing tide pool area (Figure 1; r = -0.35, P = 0.05). The density of medium-sized fish was unrelated to pool size (Figure 2; r = 0.02, P = 0.32). Large fish occurred at highest densities in the largest pools (Figure 3; r = 0.56, P < 0.0001). Small fish density also tended to be higher in the shallow pools (Figure 4; r = -0.22, P = 0.07), and medium-sized fish occurred in higher densities in deeper pools (Figure 5; r = 0.46, P = 0.0001). There were no obvious trends between large fish and depth. Larger pools were characterized by both greater species richness and greater species diversity (Figure 6; r = 0.35, P = 0.008 and r = 0.33, P = 0.05, respectively). Individual species, when analyzed separately, showed more significant relationships with surface area than with depth or location in the intertidal zone (Table 1). Substrate type showed did not correlate to any fish abundance.

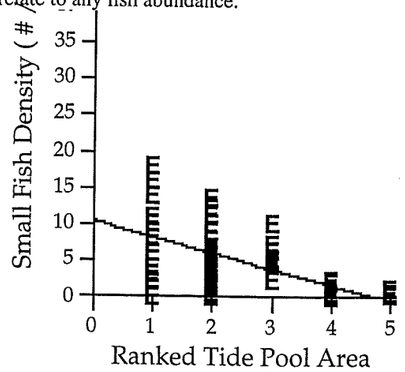
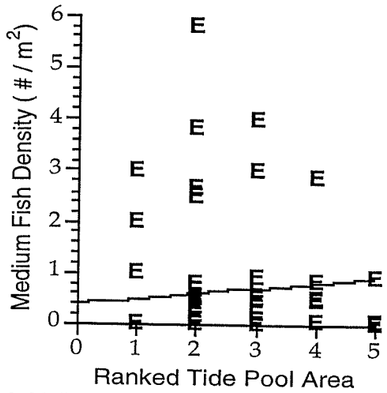


Fig. 1. Small fish density as a function of tide pool area in the intertidal zone at Sirena, Corcovado National Park, Costa Rica.

Species composition within pools remained relatively constant between days, but the relative abundances of individual species varied significantly (Table 2). In all 6 pools, differences in composition am among days resulted from the presence or absence of a single species (species 3).



.Fig. 2. Medium-sized fish density as a function of tide pool area in the intertidal zone at Sirena, Corcovado National Park, Costa Rica.

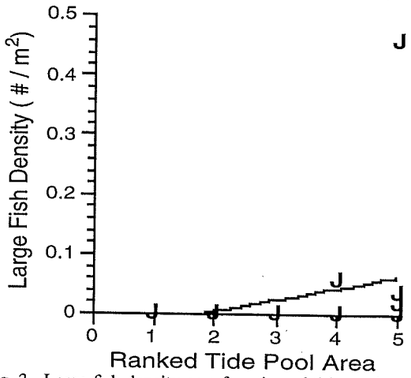


Fig. 3. Large fish density as a function of tide pool area in the intertidal zone at Sirena, Corcovado National Park, Costa Rica.

Large fish were occasionally observed preying on small fish: during 25.8 minutes of observation, we recorded an average of 0.15 attacks per minute. We observed little blue heron, great blue heron, snowy egret, brown pelican, sandwich tern, and royal tern foraging in or around the tide pools. During 11 minutes of observation, 3 snowy egrets and 1 great blue heron (Egretta caerulea and Nyctanassa violacea, respectively) captured 10 medium-sized fish in small pools < 8 cm deep and < 10 m^2 in area (average = 0.91 captures per minute). In response to the presence of a shadow, 4 of 20 small fish hid, while 16 did not respond, and 10 of 10 medium-sized fish darted away (G = 38.19, df = 2, P < 0.025). In response to mechanical movement of the water, 20 of 20 small

fish hid, but 18 of 42 medium-sized fish fled from the tide pool within 15 seconds while the other medium-sized fish turned and darted within the pool (G = 89.97, df = 2, P < 0.005).

Temperature increases and salinity decreases were greatest in a small, shallow pool located high in the intertidal zone (Table 3).

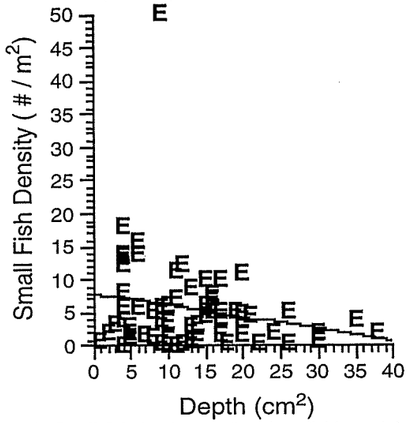


Figure 4. Small fish density as a function of tide pool depth in the intertidal zone at Sirena, Corcovado National Park, Costa Rica.

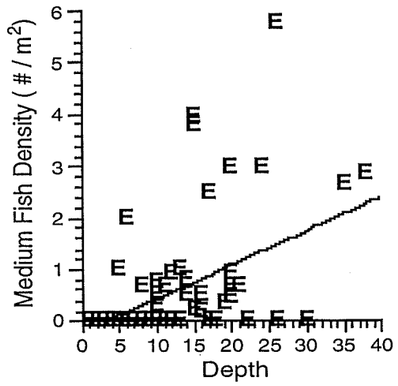


Figure 5. Medium-sized fish density as a function of tide pool depth in the intertidal zone at Sirena, Corcovado National Park, Costa Rica.

DISCUSSION

Results indicate that fish community composition in tide pools is partly determined by predictable physical conditions and predation risks, but that there is also random sorting of species. Although we did not find many small fish in the large pools, we think they were present but hiding to avoid predation. In contrast, medium-sized fish removed themselves from the large pools by swimming through channels to smaller pools. Small fish, which are less subject to predation by herons and other wading birds, may retreat to small pools where they avoid larger fish predators. At least some small fish (species 1 - 3) may be well adapted to tolerate the extremes in physical conditions found there. In particular, their high surface-to-volume ratios may increase their oxygen uptake in low oxygen situation.

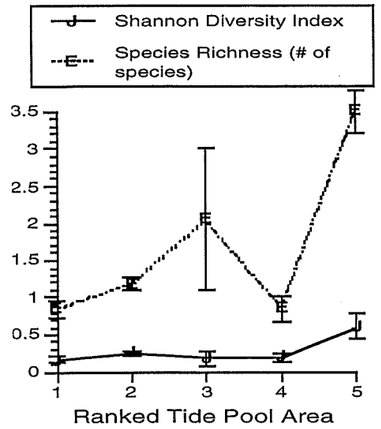


Figure 6. Shannon diversity and species richness as a function of tide pool area in the intertidal zone at Sirena, Corcovado National Park, Costa Rica.

The absence of medium-sized and large fish in the shallow pools may be explained by the lack of physical space and food resources, the inability to tolerate the more extreme physical conditions, and removal by and/or avoidance of bird predation. Medium-sized and large fish may not tolerate the higher temperatures, lower dissolved oxygen concentrations, and lower salinities found in small pools, especially those high in the intertidal zone which are isolated from the ocean for the longest time. Small and shallow pools also may have insufficient space and food resources to support medium-sized fish, which tended to school, and large fish.

Higher species richness and diversity in the large pools low in the intertidal zone may reflect increased habitat heterogeneity and more constant and tolerable physical conditions. These pools often contain a variety of substrates (sand, hard clay, pebbles and boulders), which provide a variety of habitats in which fish find food and shelter, are exposed for less time than other pools, and are more buffered from outside environmental forces (insolation, freshwater runoff). Consequently physical conditions there remain more similar to those of the open ocean.

Table 1. Regression coefficients (r) associated with environmental variables that best predict fish distribution in tide pools at Corcovado National Park, Costa Rica.

	Individual Fish Species							Shannon Diversity Index	Species Richness
Variable	1	2	3	4	5	6	7		
Depth	0.34**	- 0.08	0.18	0.46**	0.14	- 0.18	- 0.15	0.14	- 0.23
Area	0.25*	0.50**	0.28	0.36**	0.30*	0.31*	0.44**	0.27*	0.35**
Zone	0.00	- 0.25*	0.24*	- 0.17	- 0.23	- 0.23	- 0.23	0.00	- 0.21

* $p < 0.05$; ** $p < 0.01$

Table 2. Day-to-day variation in fish compostition in tide pools at Corcovado National Park, Costa Rica.

Pool Number	Area (m^2)	# of Days	# of Spp.	# of Individuals (range)	G	df	P
5	7.5	4	2 - 3	31 - 109	63.73	6	< 0.05
6	4.5	4	1 - 2	8 - 71	19.07	3	< 0.05
7	3.0	4	3	28 - 54	54.27	6	< 0.05
8	2.0	4	1	4 - 35	15.91	3	< 0.05
9	9.5	3	1 - 2	17 - 34	12.09	2	< 0.05
10	19.5	4	1 - 2	7 - 114	66.35	3	< 0.05

Table 3. Temperature and salinity variation at low tide in tide pools at Corcovado National Park, Costa Rica.

	Temperature (°C)				Saliniry (bricks)	
Time	Smal Pool [a]	Medium Pool[b]	Large Pool[c]	Ocean	Small Pool[a]	Medium Pool[b]
0730	27.6	27.0	--	27.4	2.75	3.50
0830	30.3	28.3	--	27.4	2.50	3.50
0930	32.9	30.8	27.8	27.4	--	--
1030	35.6	32.3	--	27.4	2.00	3.50
1100	37.3	34.0	--	27.4	--	--

[a]High Zone; [b] Mid Zone; [c] Low Zone

Day-to-day variation in fish communities primarily reflects changes in the number of individuals of each species present, not which species are present. This variation in abundance indicates that individual fish may not choose or defend specific territories in the intertidal zone. However, different species and sizes of fish select tide pool environments that provide a suitable balance between tolerable physical conditions, favorable foraging opportunities, and acceptable predation risks.