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Sicyases sanguineus: a Unique Trophic Generalist from the Chilean Intertidal Zone

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Stomach analyses of *Sicyases*, an amphibious marine clingfish, collected at Iquique and the Montemar region, Chile, indicate an extremely broad diet. Individual fish usually had been eating one prey type immediately prior to capture. However, there was wide within-sample variation: major prey categories include 3 plant and 3 animal phyla. Analyses indicate that the prey are obtained throughout the intertidal zone. Intertidal and shallow-subtidal prey are digested in middle to upper intertidal areas. The fish is characteristic of vertical rock walls in areas of great surf action. Its niche is unique, with no known parallel development in other rocky intertidal communities.

ALTHOUGH fish are significant functional elements in many tropical or sub-tropical shallow water systems (Bakus, 1969; Randall, 1961), it appears unprecedented for them to exert a potentially important influence on temperate zone intertidal communities. The evidence for this seems clear. Paine (1966), Paine and Vadas (1969), Connell (1970), Dayton (1971) and Estes and Palmisano (1974) have examined communities along the northeastern Pacific rim and found no evidence for fish effects. Rather, starfish, snails, sea urchins or sea otters seem to be the major determinants of the distribution and abundance of the associated species. General literature descriptions or reviews of temperate zone intertidal communities also fail to reveal fish as major components, if they are mentioned at all (Ricketts, Calvin and Hedgpeth, 1968; Morton and Miller, 1968; Lewis, 1964; Dakin, 1953; Stephenson and Stephenson, 1972).

We report here a series of observations on an amphibious clingfish, *Sicyases sanguineus*, known locally as the "pejesapo" (literally, frog-fish). It is a characteristic and apparently dominant organism of the middle and upper rocky intertidal community along the exposed coasts of western South America, ranging from southern Peru to southern Chile (Buen, 1960). Its niche, even in the Eltonian sense, seems unique, for we can find no evidence of ecological or morphological convergence towards it in geographically distinct communities. Because it is one of the larger amphibious fish, there have been examinations of its submerged and emerged oxygen metabolism and other physiological traits associated with its tolerance of aerial exposure (Vargas et al., 1957; Gordon et al., 1970; Ebeling et al., 1970). However, except for rudimentary or anecdotal observations, little is known of its ecology and behavior.

We have observed the pejesapo at a number of Chilean localities: *Iquique (20°15.5′S, 70°08′ W), *Pozo Toyo (20°25′S, 70°10′W), Punta

Fig. 1. Frontal view of *Sicyases sanguineus* illustrating the elongate, rodentiform teeth used in substrate scraping.

Patache (20°48′S, 70°12′W), Antofagasta (23°42′ S, 70°27′W), Los Molles (32°14′S, 71°32′W), *Islote Concon (32°52′S, 71°33′W), *Montemar (32°57′S, 71°32′W) and Guabun (41°50′S, 74°02′ W). Although the latitude is low at some of our stations, the annual water temperatures are comparable to more temperate zone environments. For example, at Antofogasta they range from 14.9 to 20.7 C (Guiler, 1959). Observation intervals were: Aug.–Sept. 1974; Oct.–Nov. 1975; and June–July 1976. Stomach analyses of freshly netted or pole-hooked individuals were performed at the asterixed areas.

General Observations

The pejesapo is characteristic of exposed rocky shorelines and is commonly encountered where ocean swells break against vertical rock walls. We did not find it in either the protected waters around Punta Arenas, the south end of the island of Chiloe, or any of the islands between Chiloe and continental Chile. The missing factor is predictable wave action and the associated surge. The other two most likely local determinants of *Sicyases* distribution, vertical walls and ample benthic prey (mainly barnacles, mussels and certain ubiquitous algae), were present and even abundant.

The fish are gregarious and often congregate on walls which they seem to prefer to other possible rock habitats, though we did observe them occasionally in boulderfields (Pozo Toyo, Antofagasta Bay). When exposed they are alert, and can detect moving objects over distances from 10–15 m. Their capture with long-handled nets requires careful and persistent stalking. Ebeling et al. (1970) and Viviani (1975) provide further observations on their overall responses to desiccating habitats.

Diet

There are few data on the feeding and diet of *Sicyases.* Viviani (1975) gives a brief prey species list, accompanied by the comment that they prefer barnacles. They have a typical buck tooth appearance, with a series of 4 long, incisor-like teeth protruding beyond the "lips" of the upper jaw, complemented by four shorter chisel-like teeth on the lower jaw (Fig. 1, Ebeling et al., 1970). These are used in at least two ways. The most common feeding mode is for an exposed fish to anchor itself with its ventral sucker on a flat, usually smooth vertical surface, and then to swing its head in a small arc (perhaps 30° in total), repeatedly raking its teeth downward in 2–4 cm strokes along the way. Minor repositioning may be necessary during the process. The resultant impression left on an algal covered surface is of a fan-shaped series of parallel strokes.

In Fig. 2, we present an enlarged view of presumed pejesapo scrapings (2A) compared with those generated by an invertebrate grazer, most likely a limpet (2B). The patterns are readily distinguished in the field. Also note that the pattern in 2A appears to be sub-divided into series of scrapes of about the same width, composed of either 2 or sometimes 4 distinct but narrower, bands. The mean width of pairs of scrapes is about 2 mm; the width across the 2 central front teeth of a 15 cm (standard length) pejesapo is about 3 mm. Hence, though not observed directly, the size and peculiar shape of these marks, and the unlikelihood that this particular pattern (2A) could be attributed to an herbivorous mollusc, all provide strong circumstantial evidence suggesting they were caused by *Sicyases* grazing.

A second mode, which we infer from shells of the gastropod *Fissurella* taken from pejesapo stomachs, is for the fish to insert its teeth under the limpet's shell and then twist. The action produces a characteristic break in the shell's

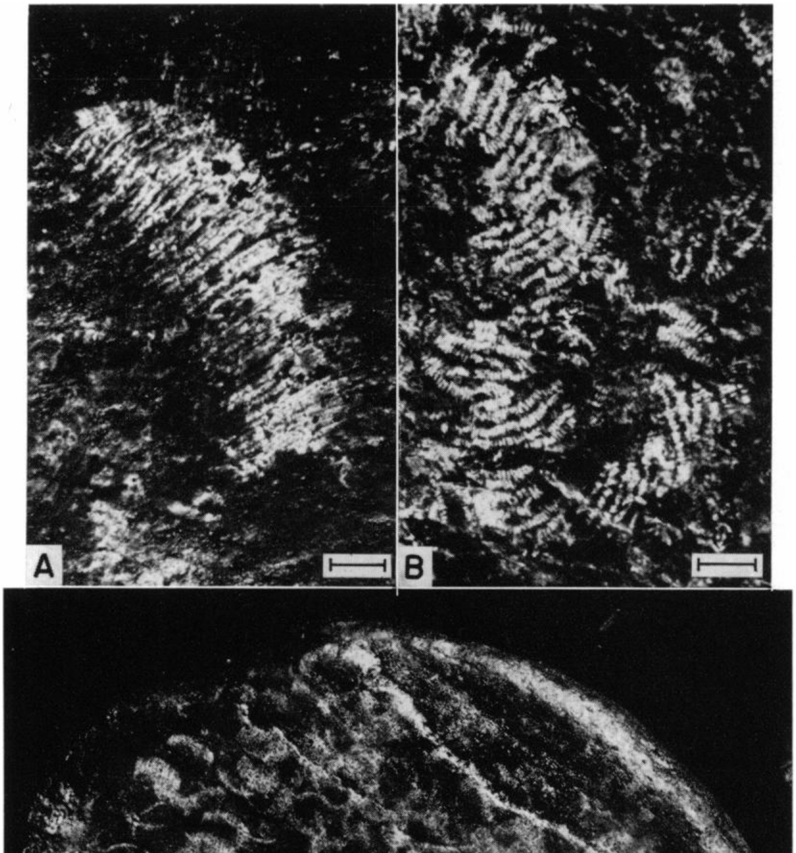

Fig. 2. A. Presumed *Sicyases* grazing marks in a thin layer of encrusting algae. B. Radular marks of an herbivorous gastropod in the same encrusting algae. C. A heavily grazed rock surface, presumably by pejesapo. Scale Bars: A and B, 0.5 cm, C, 5.0 cm.

anterior or posterior end. These prey are unlikely to be taken by generalized scraping and are probably attacked individually. Shells of *Fissurella* spp. showing these characteristic breaks can be found abundantly in windrows along the strand line. Their ubiquity implicate the pejesapo as a major mortality factor. In contrast, hundreds of observations of invertebrate predators, especially the starfish *Heliaster helianthus*, reveal both a pronounced and effective *Fissurella* escape response and a very low incidence of capture.

Table 1 is a tabulation of pejesapo stomach contents classified by species and location. The phyletic breadth is enormous. In Table 2 we summarize these data, and provide an indication

TABLE 1. SPECIFIC CONTENTS OF PEJASAPO STOMACHS, TABULATED BY AREA. Total numbers of animal prey consumed are given. Plant prey are ranked as abundant (++), present (+), or uncommon (–).

	Prey species	Islote Concon 1975	Islote Concon 1976	Montemar Marine Lab	North Montemar	Iquique
brown algae	*Petalonia* sp.	+	+			
	Colpomenia sp.					–
green algae	*Enteromorpha intestinalis*	–				
	Ulva lactuca	++	++	++		++
red algae	*Porphyra columbina*	+	–	–		–
	Chaetangium sp.	–				
	Gelidium pusillum		–			
	Corallina chilensis			++		++
	Lithophyllum sp.				++	–
	Iridaea laminariodes		++			
	Gymnogrongus sp.	–				
	Filamentous red algae	++		–	+	
chitons	*Chiton cumingsi*	1				
bivalves	*Brachidontes granulata*					1
	Perumytilus purpuratus		10	9		
	Semimytilus algosus	371	31	78	7	17
gastropods	*Siphonaria lessoni*	1	4	11		
	Fissurella cumingi	2				
	F. crassa	1				2
	F. latimarginata	3				
	Fissurella sp.				1	
	Collisella ceciliana			4		12
	C. araucana	1				
	Collisella sp.	43				
	Scurria parasitica	1				
	S. viridula					1
	Prisogaster niger		61			
	Littorina araucana					15
	Concholepas concholepas				egg mass	
barnacles	*Chthamalus cirratus*			2		9
	C. scabrosus		30	50		16
	Balanus flosculus	32	35	77	121	89
	B. laevis	12	6	3	10	3
	Megabalanus psittacus	2	20		3	1
	barnacles	23				9
crabs	*Acanthocyclas gayi*	2				
	crab					1
other arthropods	isopod	2				
	amphipod			4		1
	insect larvae					1
sea urchin	*Tetrapigus niger*	5				

of the degree to which individual fish, though tending to be characterized by some particular prey taxon, vary dramatically. Consider, for instance, the stomach contents of fish collected on the Montemar Marine lab property. We examined only 9 fish there; two were essentially empty, but in the remaining 7, 5 different prey categories predominated, and these belong

TABLE 2. SUMMARY OF THE PHYLETIC COMPOSITION OF *Sicyases'* DIET, AND AN INDICATION OF THE CONCENTRATION ON SPECIFIC PREY SPECIES BY INDIVIDUAL FISH.

	Number of fish with particular food types forming >50% of stomach volume										
Place	Sample Size	No. of Phyla represented	*Corallina*	Barnacles	*Ulva*	*Semimytilus*	Filamentous red alga	*Perumytilus*	*Iridaea*	*Siphonaria*	*Lithophyllum*
Iquique	11	6	2	5	2						
Islote Concon 1975	11	6			3	5	1				
Islote Concon 1976	8	5		1	1	1		1	3		
N. Montemar	9	3		3							3
Montemar Marine Lab	9	4	1	2	2	1				1	

to 4 phyla. The same extensive variation is apparent throughout our data even though the fish were taken from the same limited area, usually fairly high in the intertidal, and at roughly the same time. The trophic breadth is unusual, and can be expressed in other ways. At each of the 5 sample localities, spanning 12.3° of latitude, the major food types of individual fish are about equally divided between plant and animal matter. When all areas are pooled, animal matter predominated 18 times, plant matter 20. If we examine the 48 stomachs individually irrespective of area or date, 31 were found to contain both plant and animal material, 3 were empty, 10 contained solely animal and 4 solely plant matter. The evidence indicates that *Sicyases* is a trophic generalist with major fractions of its diet composed of both plant and animal moieties.

Although we have not presented a tabulation, by fish, of the individual items, certain conclusions regarding the foraging behavior of *Sicyases* can be inferred. The fish are clearly feeding when in the upper intertidal: of the 38 full stomachs in which a single prey species predominated, 12 were filled with such characteristic upper intertidal species as *Iridaea laminariodes, Ulva lactuca* and *Perumytilus purpuratus.* Oddly enough, 21 stomachs were dominated by low intertidal or shallow subtidal prey despite the fish's capture higher up. *Lithophyllum* sp., *Semimytilus algosus, Balanus flosculus, Megabalanus psittacus,* the urchin *Tetrapigus atra* and *Collisella* new sp. are all predominantly lower zone organisms. The implication is that the pejesapo, when full, may leave the water and digest its meal while exposed.

DISCUSSION

The pejesapo is unusual on at least two ecological grounds: it is unique both in terms of its high-intertidal foraging habits and in terms of the breadth of its diet. We know of no other organism, vertebrate or invertebrate, exhibiting convergent ecological traits. For instance, on many high latitude rocky shores, shorebirds prey extensively on mussels and limpets; they are not known to eat either barnacles or algae. A similar case could be made for carnivorous gastropods which may also consume barnacles, but not algae. On the other hand, the algae are eaten by a variety of herbivorous gastropods; these do not actively prey on animals, but may dislodge them accidentally while feeding. Although the absence of specific convergence is not unexpected, it stands in contrast to the patterns drawn by Cody (1974) and Fuentes (1976) for Chilean and Californian birds and lizards, respectively.

The significance of dietary breadth of *Sicyases,* which appears characteristic of the species throughout its broad geographic range, is not entirely clear. The fish appears to be a true generalist; of the major prey types available, it avoids only the encrusting green alga *Codium dimorphum* and sea anemones (both abundant in coastal Chile). It also seems incapable of preying on larger members of most prey species. We have photographed it coexisting with large chitons, limpets, (especially *Scurria viridula*) and *Fissurellas,* all of which it eats when they are small. The lower intertidal algal community of Chile is characterized by a strongly bimodal size distribution: the species are either very large (*Durvillea antarctica* or *Lessonia nig-*

rescens) or crustose coralline species (probably *Lithophyllum* sp.). The conspicuous bimodality could be generated by effective grazing by pejesapo on most community members below some size threshold. Other grazers may contribute to this bimodality as well.

The community influence of *Sicyases* is tantalizing to contemplate. The fish is abundant and, although we possess no data, it is exploited heavily from shore throughout its range and can be purchased readily in public markets. It seems voracious, the majority of stomachs examined being full regardless of season or location of capture. It preys on most species throughout the intertidal zone showing little evidence for selectivity. Is it, then, a keystone predator (Paine, 1969) in the sense that its removal would produce major community alterations? Such strong roles have been demonstrated in other temperate zone systems for starfish (Paine, 1966), sea otters (Estes and Palmisano, 1974) and lobsters (Mann and Breen, 1972). We answer this question in the negative for two reasons. First, *Sicyases* can not control the distribution and abundance of prey species capable of monopolizing the spatial requisite, because these prey can become too large to be consumed. Second, many less generalized invertebrate consumers, some of which have also escaped in size from *Sicyases*, coexist with it in the middle and lower zones. One experiment (Viviani, 1975) indicates that their combined foraging pressure would compensate for *Sicyases*' absence.

Probably the most interesting question generated by our observations is why the ecological role successfully occupied by *Sicyases* on Chilean shores has not been assumed by other clingfish species elsewhere. Comparable habitats can be found along most temperate zone shores, with other clingfish species present, and with comparable resource spectra available. Further, there has been no apparent convergence towards the *Sicyases* "niche," even from distantly related taxa. The question remains unanswered, and may perhaps be unanswerable if *Sicyases*' success derives from historical accident or evolutionary caprice.

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The Ecology and Burrowing Behavior of the Chihuahuan Fringe-footed Lizard, *Uma exsul*

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The Chihuahuan Desert lizards *Uma e. exsul* and *U. e. paraphygas* are morphologically and ecologically less specialized for life on loose aeolian sand than are the other species of the genus. They do not occur in large areas of vegetationless sand, and are probably limited to areas in which rodents can maintain open burrows year-round. *Uma exsul* use these burrows to escape from predators and for nocturnal retreat. Only in an area with very dense, low-growing vegetation did we see them bury in loose sand at night. Unlike other species in the genus, *U. exsul* occurs on dunes in which a large amount of silt is mixed with the sand, and it also lives on hardened silt substrates side by side with *Holbrookia maculata*.

Body temperatures of active *U. exsul* averaged 38.7 C (S.E. = 0.4, n = 45), the same as other species in the genus, but *U. exsul* begin activity later in the morning than do the specialized forms. In this respect the behavior of *U. exsul* is like *Callisaurus*. Like the other species in the genus, *U. exsul* shows no physiological adaptations for sand-swimming; heart rates of buried lizards are lower than those of lizards on the surface, but the difference reflects inactivity, not a submergence bradycardia.

THE contemporary dune systems of interior North America, though geographically extensive, appear to have geological histories going back no farther than the middle Pliocene Epoch (Norris, 1958). This geological youthfulness coupled with Pleistocene climatic changes probably explains the paucity of psammophilous lizards in North American dunes in comparison to the extensive lizard faunas of older dunes in Africa, Asia and Australia. The contrast is increased by the fact that many niches for sand-swimming reptiles that are filled by specialized lizards in Old World dunes are occupied by snakes in North America. Only some of the horned lizards (*Phrynosoma*), the sand lizards (*Callisaurus, Holbrookia, Uma*) and the California legless lizards (*Anniella*) are specialized for life in loose aeolian sand. *Uma* is the only genus entirely restricted to these deposits (Mosauer, 1935; Norris, 1958).

The three species of *Uma* living west of the Continental Divide have been studied in some detail (Mosauer, 1932, 1935; Stebbins, 1944; Pough, 1969a,b,c, 1970). Little is known of the Mexican forms *exsul* and *paraphygas* which occur in the Chihuahuan Desert beyond the comments in the original descriptions (Schmidt and Bogert, 1947; Williams et al., 1959; Carpenter, 1967; Commins and Savitsky, 1973). [The Chihuahuan Desert forms have been recognized as species; however, we are presenting evidence elsewhere that *paraphygas* is best treated as an allopatric subspecies of *U. exsul* (Morafka and Pough, ms.).]

Uma e. exsul is restricted to extreme southeastern Coahuila and *U. e. paraphygas* occurs in southeastern Chihuahua and the Laguna del Rey of adjacent Coahuila. The range of the species is limited to the Mapimian subprovince of the Chihuahuan Desert Biotic Province (in the sense of Morafka, 1976). This region is poorly differentiated desert and short-grass prairie refugium.