Rev. Biol. Trop., 17(2): 165-185, 1970

Species diversity and ecology of tidepool fishes in three Pacific coastal areas of Costa Rica

by

Peter L. Weaver*

(Received for publication March 21, 1969)

Several Pacific coastal areas of Central America have tidepools but relatively little is known of the fish species which occupy them. Three such areas are Playas del Coco, Tamarindo and Rincón de Osa, Costa Rica (Fig. 1). At Playas del Coco and Tamarindo, rocky shorelines provide an abundance of tidepools which are isolated twice daily from the ocean. The pools are relatively stable in morphology due to the firm substrate. At Rincón de Osa, daily tidal fluctuations leave isolated brackish pools in the delta of the Rincón River. These pools have mud bottoms which vary periodically in morphology due to heavy precipitation and subsequent alterations in the substrate. The inherent differences in the physical and chemical character of the respective environments, namely, aspects of tidepool morphology and salinity, provide an excellent opportunity for comparison of species composition, species diversity and ecology in areas which represent the extremes in tidepool habitats.

This study has two primary objectives: first, to identify the tidepool fish species and determine their size and abundance, and second, to investigate the relationship between species diversity of tidepool fishes and the complexity of their habitat. To achieve the second objective, an appropriate species diversity factor was needed. Species diversity may be most easily expressed as the total number of species present in an area. Total species counts, however, have two drawbacks, namely, they fail to consider species abundance and they depend heavily on sample size (MACARTHUR, 7). To overcome this difficulty, a more refined measure of species diversity, the information theory formula,

* Biology Department, University of Puerto Rico, Río Piedras, Puerto Rico.

$$H = -\sum_{i=2}^{N} pi \log_e pi$$

was employed. "H" is the appropriate measure of the uncertainty of the diversity of the next individual in a census. "N" is the number of species in the tally and "pi" is the proportion of the total number of individuals which belong to the "ith" species. Thus the measure of "equally common species" is merely the logarithm of the number of "equally common species". The measure of "unequally common species" however must be converted to "equally common species" by raising "e" to the "H" power, the final operation giving a number which accords to the actual diversity of the area (7).

The main advantage with "H" is that it may be employed to determine species diversity from species abundance as well as habitat diversity from site components. The habitat diversity, referred to as tidepool diversity, was the summation of two habitat components, an area-depth relationship and the percentage of loose rock cover (Fig. 2). The area-depth relationship was calculated from the percentages of the total tidepool surface area which were occupied by the designated depth classes, i.e., 0-14.9 cm, 15.0-29.9 cm, and greater than 30.0 cm. The loose rock cover of the tidepool substrate was then projected to the surface, and the total percentage of loose rock to surface area determined (Fig. 2).

PROCEDURE

FIELD PROCEDURE: Tidepools were visited at times of low tide and maximum length, width and depth were recorded. The tidepool surface was then mapped to scale on graph paper. The 15 cm and 30 cm contour intervals were plotted and all exposed rocks were included in the sketch. After measurement, rotenone was applied in sufficient quantities to rapidly kill all tidepool fishes. The fishes were collected and placed immediately in 10 percent formalin. Tidepool shorelines and loose rock surfaces were carefully checked for rotenone-resistant species before departing from the site.

LABORATORY PROCEDURE: All fishes collected at the tidepools were kept in 10 percent formalin and examined at a later date. The following procedure was used for each tidepool:

1. Identification of all fishes, to species when possible;
2. Total count of all individuals by species;
3. Measurement of each fish to the nearest millimeter of standard length (length from middle of upper lip to base of caudal fin);
4. Determination of wet-weight of all preserved fish;
5. Determination of total tidepool surface area and the areas within each contour by planimeter;
6. Computation of total tidepool volume by multiplication of the planimeter contour areas by mean depth between contours (i.e., 7.5 cm, 22.5 cm and x cm midpoint (Fig. 2);

7. Computation of average depth by division of total volume by total surface area;
8. Calculation of the tidepool diversity factor in the following manner:
   a. Determine the percentage of the total surface area occupied by the 15 cm and 30 cm contour;
   b. Use the information theory formula to determine "H";
   c. Add "H" to the percentage of total surface area covered by loose rocks on the tidepool bottom. This sum is the tidepool diversity factor;
9. Determination of species diversity based on the initial sample from each tidepool.

RESULTS

The results are presented in three sections corresponding to the areas studied.

PLAYAS DEL COCO: Table 1 lists total biomass, average depth, surface area, volume, tidepool diversity factors and species diversity factors according to tidepool for Playas del Coco. No correlation was shown between species diversity and depth, biomass and depth, species diversity and surface area, biomass and surface area, species diversity and volume, biomass and volume or biomass and tidepool diversity. Only the relationship between species diversity and tidepool diversity showed significant positive correlation for the nine tidepools studied (Fig. 3). The t test value (t) was 2.539 and the correlation coefficient (r) was 0.874.

Table 2 indicates fish species and occurrence, the latter being divided into several separate categories, namely: total number of individual occurrences of each species *(A)*; presence of a species within a sampled tidepool (*B*); presence of a species within tidepools sampled during the day (*C*); total number of individual occurrences of each species within tidepools sampled during the day (*D*); presence of a species within tidepools sampled at night (*E*); total number of individual occurrences of each species within tidepools sampled at night (*F*); presence of a species within tidepools sampled for the first time (*G*); total number of individual occurrences of each species within tidepools sampled for the first time (*H*); successional presence of a species within tidepools sampled on numerous occasions (*I*); total number of individual successional occurrences of each species within tidepools sampled on numerous occasions (*J*); and, percentage of total fish collected at Playas del Coco (*K*). These categories facilitate the classification of fishes as regular, occasional or rare tidepool occupants, and, in addition, suggest whether certain species are resident or mobile with respect to the tidepool habitat and nocturnal or diurnal in occurrence within the tidepool zone. The following arbitrary classifications have been assigned after examination of the data (Table 2):

1. Regular tidepool occupants - presence of a species in six to 19 tidepool samples.

2. Occasional tidepool occupants - presence of a species in three to five tidepool samples.

3. Rare tidepool occupants - presence of a species in one or two tidepool samples.

TABLE 1

Species diversity and tidepool diversity factors at Playas del Coco.

Tidepool	Total Biomass Grams	Avg. Depth cm	Sur. Area m^2	Vol. m^3	Tidepool Diversity Factor	Species Diversity Factor*	
A	120.7	11	4.70	0.42	0.507	1.210	3.348
B	45.9	9	2.06	0.19	0.267	0.871	2.392
C	25.6	8	2.25	0.17	0.800	1.258	3.518
D	311.4	15	9.45	1.46	1.635	1.309	3.699
E	30.8	9	3.78	0.34	0.341	0.907	2.479
F	1.2	7	1.04	0.07	0.000	0.600	1.821
G	147.0	11	3.93	0.44	1.226	1.481	4.401
H	33.4	23	2.84	0.66	1.235	1.409	4.073
I	334.3	14	5.24	0.74	0.807	1.252	3.501

* The first column represents "H" and the second column the value for "equally common species".

Table 3 shows a tentative classification of the behavior of fishes with respect to occupancy of tidepools. Assignment to a category is arbitrary, based on the available data in table 2.

TABLE 2

*Fish species and occurrences at Playas del Coco**

Family, Genus-species	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*J*	*K*
Antennariidae											
Antennarius sanguineus	1	1	1	1	—	—	1	1	—	—	0.01
Blenniidae											
Ophioblennius steindachneri	10	3	1	2	2	7	2	7	1	2	0.86
Brotulidae											
Ogilbia ventralis	1	1	1	1	—	—	1	1	—	—	0.01
Chaetodontidae											
Chaetodon humeralis	1	1	1	1	—	—	1	1	—	—	0.01
Clinidae											
Malacoctenus zonifer	404	15	8	162	7	242	8	188	7	116	33.50
Mnierpes macrocephalus	14	5	4	5	1	9	5	14	—	—	1.16
Genus species	1	1	—	—	1	1	1	1	—	—	0.01
Gobiesocidae											
Gobiesox daedaleus	61	11	8	26	3	35	7	47	4	14	5.07
Tomicodon petersi	6	2	2	6	—	—	1	5	1	1	0.50
Gobiidae											
Bathygobius ramosus	330	15	10	294	5	36	8	281	7	49	27.40
Gobulus hancocki	4	1	—	—	1	4	—	—	1	4	0.33
Genus species	1	1	—	—	1	1	1	1	—	—	0.01
Holocentridae								—			
Holocentrus suborbitalis	1	1	—	—	1	1	1	1	—	—	0.01
Labridae											
Halichoeres dispilus	1	1	—	—	1	1	—	—	1	1	0.01
Pseudojulis notospilus	4	2	1	1	1	3	2	4	—	—	0.33
Halichoeres sellifer	1	1	1	1	—	—	1	1	—	—	0.01
Halichoeres sp.	1	1	—	—	1	1	1	1	—	—	0.01
Muraenidae											
Gymnothorax dovii	5	3	3	5	—	—	3	5	—	—	0.43
Muraena lentiginosa	1	1	1	1	—	—	1	1	—	—	0.01
Uropterygius necturus	1	1	1	1	—	—	1	1	—	—	0.01
Mugilidae											
Chaenomugil proboscidens	62	6	4	18	2	44	5	48	1	14	5.15
Mugil cephalis	13	3	1	2	2	11	2	7	1	6	1.09
Pomacentridae											
Abudefduf saxatilis	135	5	2	5	3	130	3	25	2	110	11.42
Nexilarius concolor	74	9	6	47	3	27	6	47	3	27	6.71
Eupomacentrus flavilatus	47	3	2	2	1	45	2	2	1	45	3.92
E. acapulcoensis	24	4	2	14	2	10	1	14	2	10	1.99
Scorpaenidae											
Scorpaenodes xyris	1	1	1	1	—	—	1	1	—	—	0.01
Serranidae											
Epinephelus labriformis	3	2	1	2	1	1	1	2	1	1	0.02
Total	1203	—	—	—	—	—	—	—	—	—	100.00

* Refer to text for meaning of letters *A* through *K*.

TABLE 3

Tentative classification of the behavior of fishes with respect to occupancy of tidepools at Playas del Coco

Occupants	Regular	Occasional	Rare
Resident	*Chaenomugil proboscidens* *Bathygobius ramosus*	*Gymnothorax dovii* *Mnierpes macrocephalus*	*Muraena lentiginosa* *Uroptergius necturus*
Nocturnal and Mobile	———	*Eupomacentrus flavilatus* *Abudefduf saxatilis* *Ophioblennius steindachneri* *Mugil cephalis*	———

Table 4 is a compilation of fish biomass, length, species composition and total number variations in successive day and night sampling. The initial total biomass of fishes collected during the day always exceeded the total biomass of successive samples collected on subsequent days. In like manner, initial total biomass of fishes collected at night always exceeded the total biomass of successive samples collected on subsequent nights. In most cases, the initial and successive total biomass of fishes collected at night exceeded those collected during the day. Average length and biomass per fish increased in successive samplings. Total number of fishes and number of species tended to decline in successive samplings.

RINCON DE OSA: Table 5 lists total biomass, average depth, surface area, volume, tidepool diversity factors and species diversity factors according to tidepool for Rincón de Osa. Statistical analyses were not conducted since the total number of tidepools sampled was limited to three.

Table 6 indicates fish species and occurrence. Occurrence was divided into the same categories that were used at Playas del Coco. The following arbitrary classifications were assigned:

1. Regular tidepool occupants - presence of a species in four or five tidepool samples.
2. Occasional tidepool occupants - presence of a species in two or three tidepool samples.
3. Rare tidepool occupants - presence of a species in only one tidepool sample.

TABLE 4

Fish biomass, length, species composition and total number variations in successive day and night samplings at Playas del Coco.

Tide-pool	Date	Time of Day*	Biomass in gms	Average Biomass/ Fish in gms	Avg. Fish Length in mm	Total No. of Fishes	Total No. of Species
A	7/ 7/67	day	120.7	1.19	30	100	8
	7/14/67	day	11.4	1.43	33	8	3
	7/15/67	night	193.8	1.69	38	114	6
	7/16/67	night	4.7	4.70	57	1	1
B	7/ 7/67	day	45.9	0.66	27	69	5
	7/14/67	day	13.6	1.24	34	11	2
	7/15/67	night	6.2	2.07	40	3	2
	7/16/67	night	0.0	0.00	00	0	0
C	7/14/67	day	25.6	0.47	27	54	6
	7/16/67	night	89.9	1.11	38	67	4
D	7/14/67	day	311.4	1.36	37	229	16
	7/15/67	night	740.7	4.50	46	165	9
	7/15/67	day	18.4	1.67	43	11	2
	7/16/67	night	78.3	3.73	48	21	3
E	7/16/67	day	30.8	0.88	35	25	3
F	7/16/67	day	1.2	0.17	16	7	2
G	7/16/67	day	147.0	3.58	41	62	9
H	7/16/67	day	33.4	1.51	38	22	6
I	7/18/67	night	334.3	1.38	36	242	13

* Day = time between sunrise and sunset.

Night = time between sunset and sunrise.

TABLE 5

Species diversity and tidepool diversity factors at Rincón de Osa.

Tidepool	Total Biomass Grams	Average Depth cm	Sur. Area m^2	Vol. m^3	Tidepool Diversity Factor	Species Diversity Factor*	
A	508.0	25	28.0	7.0	1.070	2.101	8.200
B	206.2	18	118.0	20.8	0.985	1.026	2.785
C	135.4	27	89.0	23.1	1.044	0.930	2.536

* The first column represents "H" and the second column the value for "equally common species".

TABLE 6

*Fish species and occurrence at Rincón de Osa**

Family Genus-species	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*J*	*K*
Bothidae											
Citharichthys gilberti	15	2	1	12	1	3	2	15	—	—	3.61
Cyprinodontidae											
Oxyzygonectes dovii	10	5	3	4	2	6	3	4	2	6	2.41
Eleotridae											
Eleotris picta	24	3	3	24	—	—	2	8	1	16	5.77
Gobiomorus maculatus	76	5	3	13	2	3	3	37	2	39	18.34
Gerridae											
Eucinostomus sp.	18	3	1	2	2	16	2	3	1	15	4.33
Gobiesocidae											
Gobiesox potamius	3	1	1	3	—	—	—	—	1	3	0.72
Gobiidae											
Awaous transandeanus	3	2	1	2	1	1	2	3	—	—	0.72
Bathygobius andrei	45	4	2	27	2	18	2	29	1	16	10.86
Evorthodus minutus	1	1	1	1	—	—	1	1	—	—	0.24
Gobionellus microdon	9	2	1	5	1	4	2	9	—	—	2.14
G. sagittula	8	2	1	3	1	5	2	8	—	—	1.92
Lutjanidae											
Lutjanus argentiventris	4	1	1	4	—	—	1	4	—	—	0.96
L. novemfasciatus	11	2	1	10	1	1	1	10	1	1	2.65
Poeciliidae											
Poecilia sphenops	1	1	1	1	—	—	—	—	1	1	0.24
Poeciliopsis turrubarensis	187	5	3	74	2	113	3	105	2	82	45.09
TOTAL	415	—	—	—	—	—	—	—	—	—	100.00

* Refer to text for meaning of letters *A* through *K*.

Table 7 is a compilation of fish biomass, length, species composition and total number variations in successive day and night samplings. Total biomass and average biomass per fish decreased in successive samples whereas average fish length increased only slightly. The total number of fishes and number of species also declined.

TABLE 7

Fish biomass, length, species composition and total number variations in successive day and night samplings at Rincón de Osa.

Tide-pool	Date	Time of Day*	Biomass in gms	Average Biomass/ Fish in gms	Average Fish Length in mm	Total Number of Fishes	Total Number of Species
A	7/25/67	day	508.0	8.62	56	59	11
	7/25/67	night	122.1	3.21	57	38	6
	7/28/67	day	160.0	1.25	25	141	7
B	7/25/67	night	206.2	1.56	39	132	9
C	7/29/67	day	135.4	3.01	46	45	6

* Day = time between sunrise and sunset.

Night = time between sunset and sunrise.

TAMARINDO: Table 8 lists total biomass, average depth, surface area volume, tidepool diversity factors and species diversity factors according to tidepool for Tamarindo. Biomass and species diversity showed no significant correlation with depth, surface area, volume or tidepool diversity.

Table 9 indicates fish species and occurrence. The latter was divided into the same categories that were used at Playas del Coco. Diurnal and nocturnal samplings however were not differentiated. The following arbitrary classifications were assigned on the basis of occurrence:

1. Regular tidepool occupants - presence of a species in 14 to 45 tidepool samples.
2. Occasional tidepool occupants - presence of a species in seven to 13 tidepool samples.
3. Rare tidepool occupants - presence of a species in one to six tidepool samples.

TABLE 8

Species diversity and tidepool diversity factors at Tamarindo.

Tide-pool	Total Biomass Grams	Average Depth cm	Sur. Area m^2	Vol. m^3	Tidepool Diversity Factor	Species Diversity Factor*	
A	41	8.0	0.59	0.05	0.25	0.81	2.25
B	7	18.0	0.05	0.01	1.11	0.87	2.39
C	122	7.0	1.88	0.13	0.45	1.51	4.75
D	34	11.0	1.65	0.18	0.73	0.82	2.27
E	334	9.0	7.06	0.64	0.51	1.49	4.44
F	629	7.0	14.24	1.00	1.00	1.22	3.39
G	326	7.0	5.90	0.41	0.10	1.30	3.67
H	81	10.0	2.76	0.28	1.40	1.26	3.53
I	13	31.0	0.70	0.22	0.92	1.01	2.75
J	99	8.0	3.94	0.32	1.15	1.51	4.75
K	46	8.0	1.12	0.09	0.70	1.26	3.52
L	1074	21.0	40.20	8.44	1.53	2.00	7.38
M	586	19.0	58.40	10.60	1.30	1.79	6.00
N	116	8.0	8.63	0.69	0.52	0.63	1.88
O	1910	19.0	20.63	3.92	1.51	2.21	9.10
P	995	16.0	14.11	2.26	1.45	1.52	4.57
Q	1883	18.0	27.51	4.95	1.35	1.72	5.58
R	77	8.0	15.80	1.26	0.14	1.37	3.94
S	116	10.0	17.40	1.74	0.50	1.27	3.56

* The first column represents "H" and the second column the value for "equally common species".

Table 10 shows a tentative classification of the behavior of fishes with respect to occupancy of tidepools. Assignment to a category is arbitrary based on the available data in Table 9.

Table 11 is a compilation of fish biomass, length, species composition and total number variations in successive samplings. The initial total biomass of fishes collected exceeded the total biomass of successive samples in all but two instances, tidepools B and J. Average length and biomass per fish fluctuated in succesive sampling with some tidepools showing an increase and others a decrease. The total number of fishes and number of species tended to decline in successive samplings.

TABLE 9

*Fish species and occurrence at Tamarindo**

Family, Genus-species	*A*	*B*	*G*	*H*	*I*	*J*	*K*
Blenniidae							
Hypsoblennius brevipinnis	13	3	3	13	—	—	0.52
Ophioblennius steindachneri	44	7	6	39	1	5	1.77
Brotulidae							
Ogilbia ventralis	3	2	2	3	—	—	0.12
Chaenopsidae							
Genus, species	2	2	1	1	1	1	0.08
Chaetodontidae							
Pomacanthus zonipectus	1	1	1	1	—	—	0.04
Cirrhitidae							
Cirrhitus rivulatus	1	1	1	1	—	—	0.04
Clinidae							
Malacoctenus costaricanus	19	4	4	19	—	—	0.76
M. ebisui	3	3	2	2	1	1	0.12
M. zonifer	711	29	17	576	12	135	28.62
Mnierpes macrocephalus	273	19	15	263	4	10	10.98
Paraclinus beebei	5	3	3	5	—	—	0.20
P. mexicanus	10	4	4	10	—	—	0.40
Gobiesocidae							
Arcos rhodospilus	8	5	5	8	—	—	0.32
Gobiesox daedaleus	41	10	9	40	1	1	1.65
Tomicodon petersi	18	9	6	13	3	5	0.72
Gobiidae							
Bathygobius ramosus	458	20	14	434	6	24	18.43
Gymneleotris seminudus	6	3	2	5	1	1	0.24
Genus, species	2	2	1	1	1	1	0.08
Holocentridae							
Holocentrus suborbitalis	44	7	5	41	2	3	1.77
Labridae							
Pseudojulis notospilus	32	12	10	29	2	3	1.29
Thalassoma lucasanum	1	1	1	1	—	—	0.04
Lutjanidae							
Lutjanus aratus	1	1	1	1	—	—	0.04
Microdesmidae							
Clarkichthys bilineata	1	1	1	1	—	—	0.04
Muraenidae							
Echidna nebulosa	3	2	2	3	—	—	0.12
Gymnothorax dovii	11	9	7	9	2	2	0.44
Muraena clepsydra	3	3	3	3	—	—	0.12
M. lentiginosa	28	5	4	27	1	1	1.13
Mugilidae							
Chaenomugil proboscidens	86	8	5	80	3	6	3.46
Mugil cephalis	80	12	5	42	7	38	3.22

TABLE 9 (cont.)

Family Genus-species	*A*	*B*	*G*	*H*	*I*	*J*	*K*
Orectolobidae							
Ginglymostoma cirratum	2	2	2	2	—	—	0.08
Pomacentridae							
Abudefduf saxatilis	287	12	7	107	5	180	11.55
Microspathodon dorsalis	8	1	1	8	—	—	0.32
Nexilarius concolor	198	21	15	182	6	16	7.96
Eupomacentrus flavilatus	3	3	2	2	1	1	0.12
E. acapulcoensis	63	10	9	60	1	3	2.53
Pomadasyidae							
Pomadasys leuciscus	14	1	1	14	—	—	0.56
Serranidae							
Epinephelus labriformis	1	1	1	1	—	—	0.04
Tripterygiidae							
Axoclinus lucillae	1	1	1	1	—	—	0.04
Family							
Genus species	1	1	—	—	1	1	0.04
Total	2486	—	—	—	—	—	100.00

* Refer to text for meaning of letters *A* throngh *K*.

TABLE 10

Tentative classification of the behavior of fishes with respect to occupancy of tidepools at Tamarindo.

Resident Tidepool Occupants		
Regular	*Occasional*	*Rare*
Bathygobius ramosus	*Gymnothorax dovii*	*Echidna nebulosa*
Nexilarius concolor	*Holocentrus suborbitalis*	*Muraena clepsydra*
Malacoctenus zonifer	*Ophioblennius steindachneri*	*Muraena lentiginosa*
Mnierpes macrocephalus	*Eupomacentrus acapulcoensis*	
	Pseudojulis notospilus	
	Gobiesox daedaleus	
	Chaenomugil proboscidens	

TABLE 11

Fish biomass, length, species composition and total number variations in successive day and night samplings at Tamarindo.

Tide-pool	Date	Biomass in gms	Average Biomass/ Fish in gms	Average Fish Length in mm	Total No. of Fishes	Total No. of Species
A	9/2/67	41	2.41	46	17	4
	9/2/67	1	0.50	16	2	1
B	9/2/67	7	1.16	29	6	3
	9/2/67	8	2.00	47	4	2
	9/3/67	—	—	—	—	—
C	9/2/67	122	2.35	45	52	8
	9/2/67	27	2.25	41	12	3
	9/3/67	—	—	—	—	—
D	9/2/67	34	2.12	45	16	3
	9/2/67	8	2.00	43	4	2
	9/3/67	—	—	—	—	—
E	9/2/67	334	2.37	43	141	8
	9/2/67	236	3.63	44	65	3
	9/3/67	—	—	—	—	—
F	9/2/67	629	2.38	40	264	10
	9/2/67	292	3.52	40	83	4
	9/3/67	2	1.00	37	2	1
G	9/2/67	326	3.26	43	100	7
H	9/3/67	81	3.52	56	23	5
	9/3/67	29	3.22	45	9	2
	9/4/67	7	7.00	77	1	1
I	9/3/67	13	2.00	38	6	3
	9/3/67	12	3.00	56	4	2
	9/4/67	—	—	—	—	—
J	9/3/67	99	1.68	38	59	7
	9/3/67	405	2.65	41	153	7
	9/4/67	2	1.00	16	2	1
K	9/3/67	46	2.19	44	21	6
L	9/4/67	1074	2.42	40	443	20
	9/5/67	46	2.19	42	21	6

TABLE 11 (Cont.)

Tide-pool	Date	Biomass in gms	Average Biomass/ Fish in gms	Average Fish Length in mm	Total No. of Fishes	Total No. of Species
M	9/4/67	586	3.60	42	163	13
	9/5/67	24	1.71	38	14	5
N	9/5/67	116	1.32	38	88	8
	9/6/67	11	0.78	36	14	3
O	9/5/67	1910	7.52	51	254	23
	9/6/67	442	14.26	56	31	11
P	9/6/67	995	11.44	54	87	12
	9/7/67	200	200.00	420	1	1
Q	9/6/67	1883	1.42	61	133	18
	9/7/67	311	38.80	94	8	4
R	9/6/67	77	1.30	39	59	8
	9/7/67	—	—	—	—	—
S	9/6/67	116	1.05	35	110	10
	9/7/67	12	1.50	39	8	3

DISCUSSION

The discussion considers each study area separately.

PLAYAS DEL COCO: The tidepools studied at Playas del Coco ranged from 0.07 m^3 to 1.46 m^3 in volume (Table 1). This variation in volume was the smallest of the three areas studied. In addition, the tidepools were nearly equidistant from the ocean at low tide. With these variables held within a relatively narrow range, certain aspects of tidepool morphology, namely, depth, surface area and total loose rock on the substrate, could account for species differentiation and abundance.

Species diversity showed significant positive correlation with the tidepool diversity factor, the most appropriate measure devised in this study to evaluate the complexity of the tidepool environment (Fig. 3). At the five percent level used in the statistical analysis to test the null hypothesis that regression is not significant, a more discrepant value of "t" than 2.365 is likely to occur less than five percent of the time if the null hypothesis is true. Therefore, the calculated "t" value of 2.539 at seven degrees of freedom would be highly improbable if regression were nonsignificant.

Likewise, at the same significance level and degrees of freedom, the correlation coefficient, the measure of intensity of association of variables, would exceed .666 only five percent of the time if the null hypothesis were true. The calculated value of .874 would be a very unlikely occurrence if regression were nonsignificant.

Successive day and night samplings revealed that fishes of greater average biomass and length replaced the smaller tidepool occupants. The average size and biomass continually increased in successive samples until an apparent limit was reached. This trend may indicate that the principal occupants of the undisturbed tidepools are small fishes which dominate the environment to the near exclusion of larger fishes.

Once the pool has been poisoned and the smaller occupants removed, the tidepool environment is open to colonization by larger fishes of the same species which usually reside in the littoral zone during high tide. Successive poisonings continuously induce fewer numbers of larger fishes to exploit the tidepool habitat. Finally, the fish of tidepool size indigenous to the microregion around the tidepool may be exhausted by continuous poisoning.

Successive sampling disclosed another aspect of tidepool fish ecology, namely, that total biomass, average biomass per fish and average fish length in samples taken at night were higher than those taken during the day. This may be due to the movement of larger littoral zone fishes into the tidepools during evening and early morning hours.

The primary purpose of successive tidepool sampling was to determine whether certain species were resident or mobile with respect to tidepools. Tentative classifications of fish behavior were assigned in the following manner:

1. A resident tidepool occupant was defined as a regular or occasional tidepool species which had 75 percent or greater occurrence of individual fishes in the initial samples of tidepools poisoned on numerous occasions. The Moray eels, family Muraenidae, were considered for classification on a family basis rather than a species basis because of their similarity in behavior.

2. A nocturnal mobile occupant was defined as a regular or occasional tidepool species which had 70 percent or greater occurrence of individual fishes in successive samples of tidepools poisoned on numerous occasions.

All of the classifications are included in the results (Table 3). They are arbitrary and should be verified by further research.

RINCÓN DE OSA: Only three tidepools were found in the delta of the Rincón River. Isolation of these pools from the main flow of the river depends upon two factors, low tide and the absence of local precipitation. During the research in the Rincón area, sampling was hindered by heavy precipitation and subsequent high flows in the river. Continuous contact was maintained between the main river channel and shoreline tidepools. In addition, this same heavy precipitation noticeably altered the morphology of tidepool A (Table 5).

The tidepools at Rincón de Osa ranged from 7.0 m^3 to 23. 1 m^3 in volume (Table 5). This variation in volume is substantially greater than that found in the Playas del Coco area.

No attempt was made to correlate biomass and species diversity with depth, surface area, volume or tidepool diversity because of the paucity of data. It will be noted, however, that the species diversity of tidepool A is substantially larger than that of tidepool B or C (Table 5). Since all of the tidepools were similar in that they had mud bottoms without loose rock cover, this difference in diversity might be attributed to a large log suspended in tidepool A.

Successive day and night samplings in tidepool A revealed that total biomass decreased from 508.0 to 122.1 grams and average biomass per fish from 8.62 to 3.21 grams while the average fish length increased from 56 to 57 millimeters. This apparent paradox is resolved when the size of five or six of the largest initial occupants is considered. These big fishes account for a considerable portion of total biomass as well as average biomass and average length per fish. The contribution to fish biomass, however, is more significant than that to fish length.

One final point of interest is in demonstrating the salinity variation and species diversity changes induced by the heavy precipitation in the tidepools at Rincón de Osa. According to Bussing (personal communication), *Gobiesox potamius* is a fresh water clingfish. Yet, after successive heavy rainfalls on 26 and 27 July, three individuals were encountered in tidepool A. All other individuals in the pool, however, were brackish water species.

TAMARINDO: The tidepools at Tamarindo ranged from 0.01 m^3 to 10.60 m^3 in volume (Table 8). This variation in volume is much greater than that at Playas del Coco. Furthermore, the tidepools were situated at various distances from the ocean at low tide.

Biomass and species diversity showed no correlation with depth, surface area, volume or tidepool diversity. Sampling did disclose, however, a variation of species distribution within the intertidal zone. *Bathygobius ramosus* dominated shallow rocky pools high in the intertidal zone. *Malacoctenus zonifer,* on the other hand, was abundant in pools throughout the intertidal zone. *Mnierpes macrocephalus* was more common in rocky pools low in the intertidal zone, while *Eupomacentrus acapulcoensis* was usually found in deeper pools adjacent to the ocean. The Labridae, Holocentridae and Blenniidae were both larger and more abundant in pools low in the intertidal zone.

Successive day and night samplings revealed that the initial total biomass of fishes collected exceeded the total biomass of successive samples in all instances except those of tidepools B and J (Table 11). Average length and biomass per fish fluctuated in successive sampling with some tidepools showing an increase and others a decrease. The total number of fishes and number of species tended to decline in successive samplings.

Tentative classifications of the residence or mobility of fishes have been designated (Table 10). These were subjectively assigned according to the same criteria employed for Playas del Coco.

SUSCEPTIBILITY TO ROTENONE: Numerous species and families showed distinct reactions to rotenone. *Mnierpes macrocephalus* was very susceptible, but frequently was able to escape to adjacent tidepools by "hopping". *Mugil cephalis* and *Chaenomugil proboscidens,* often present in groups of six to 15 fishes, were also very susceptible. The families Pomacentridae, Holocentridae and Blenniidae were very susceptible. *Malacoctenus zonifer* was susceptible, but often partially left the water. The Muraenidae were somewhat resistant and frequently would leave the water in search of other pools. *Bathygobius ramosus* was highly resistant and nearly always would partially leave the water and cling to the sides and bottoms of rocks. Gobiesocidae was another family very resistant and difficult to recover. Finally, the Labridae were very resistant and made their appearance at the water surface well after most species had been removed. Even at this time they were quite lively.

ACKNOWLEDGEMENTS

I am indebted to several individuals for their suggestions in project design, data collection and final presentation: Dr. Robert Werner, Department of Zoology, State University of New York, Syracuse, for suggestion of tidepool variables which might be correlated with fish species diversity; Dr. Robert L. Rudd, Department of Zoology, University of California, Davis, for suggestion of possible components of a tidepool diversity factor; Professor William Bussing, Department of Biology, University of Costa Rica, for assistance in fish collection and identification and continuous aid throughout the project; fellow O.T.S. student Don Duszynski, Department of Zoology, Colorado State University, for aid in field work and typing of the manuscript; and Dr. Mildred E. Mathias, Department of Botany, University of California, Los Angeles, for enthusiastic encouragement and support during the two months of the Organization for Tropical Studies program.

SUMMARY

Thirty-one tidepools were sampled a total of 69 times and 4,104 fishes were collected from three separate Pacific coastal areas of Costa Rica. Sixty-five species were determined, weighed and measured according to tidepool. Biomass and species diversity for each area were plotted against depth, surface area, volume and a tidepool diversity factor which was determined from the information theory formula. Only the relationship between species diversity and tidepool diversity for Playas del Coco showed significant correlation.

At Playas del Coco and Rincón de Osa, rotenone poisoning of the same tidepools during successive low tides resulted in an increase in average fish length. At Tamarindo this was not evident. Biomass changes induced by successive rotenone poisonings varied among the three sites.

RESUMEN

Existen grandes diferencias en la morfología de las pozas entre mareas de Playas del Coco, Rincón de Osa y Tamarindo, en el Océano Pacífico en Costa Rica. El ambiente en Playas del Coco y Tamarindo se puede calificar de rocoso

y estable; el de Rincón de Osa como de cieno y variable. Las características del agua también varían en las tres localidades, siendo la de Playas del Coco y Tamarindo marina y la de Rincón de Osa salobre.

Los peces de estas pozas varían en cada sitio. En Playas del Coco se encontró 14 familias y 28 especies; en Tamarindo 20 familias y 39 especies; y 8 familias y 15 especies en Rincón de Osa. Doce familias y 17 especies fueron comúnes a Playas del Coco y Tamarindo; tres familias y ninguna especie a Tamarindo y Rincón de Osa; y dos familias y ninguna especie a Playas del Coco y Rincón de Osa.

En Playas del Coco no hubo correlación entre la diversidad de especies y la profundidad de la poza, biomasa y profundidad, diversidad de especies y área de superficie, biomasa y área de superficie, diversidad de especies y volumen de agua, biomasa y volumen, ni entre biomasa y el factor de diversidad de la poza. Sí hubo una correlación significativa entre la diversidad de especies y el factor de diversidad de la poza entre mareas.

En Tamarindo no hubo correlación de biomasa y diversidad de especies con la profundidad, el área de superficie, el volumen ni la diversidad de la poza.

En Playas del Coco muestreos posteriores revelaron una reducción en la biomasa total y aumento en la longitud promedio, en la longitud y en la biomasa de los peces. En Rincón de Osa hubo reducción en la biomasa total y en la biomasa promedio, y aumento en la longitud promedio. En Tamarindo muestreos posteriores dieron como resultado la disminución de la biomasa total. No hubo relación aparente entre la longitud promedio de los peces y la biomasa. En todas las localidades el muestreo contínuo produjo disminución en el número de especies, así como en el de individuos por especie.

REFERENCES

1. ALLEE, W. C.
1934. Concerning the organization of marine coastal communities. *Ecol. Monogr.*, 4: 541-554.

2. CONNELL, J. H. & E. ORIAS
1964. The ecological regulation of species diversity. *Amer. Nat.*, 98: 399-414.

3. ELTON, C., & R. S. MILLER
1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. *J. Ecol.*, 42: 460-496.

Fig. 1. Three tidepool areas on the Pacific coast of Costa Rica.

1

4. Greenwood, P. H., D. E. Rosen, S. H. Weitzman & G. S. Myers
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Amer. Mus. Nat. Hist.,* 131: 339-456.

5. MacArthur, R. H.
1965. Patterns of species diversity. *Biol. Rev.,* 40: 510-533.

6. MacArthur, R. H. & J. MacArthur
1961. On bird species diversity. *Ecology,* 42: 594-598.

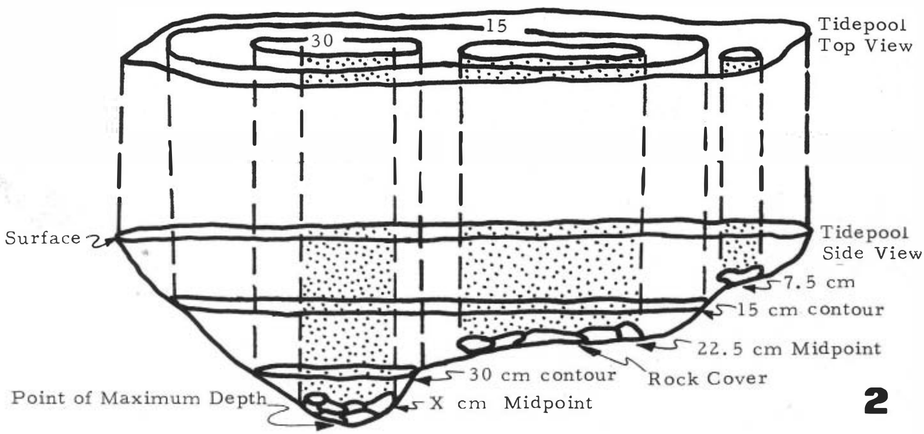
7. MacArthur, R. H., H. Rechar & M. Cody
1966. On the relation between habitat selection and species diversity. *Amer. Nat.,* 100: 319-332.

8 Meek, S. E. & S. F. Hildebrand
1925. The marine fishes of Panama. *Field Mus. Nat. Hist. Publ.* No. 226, Zool. Ser. 15: 1-1045.

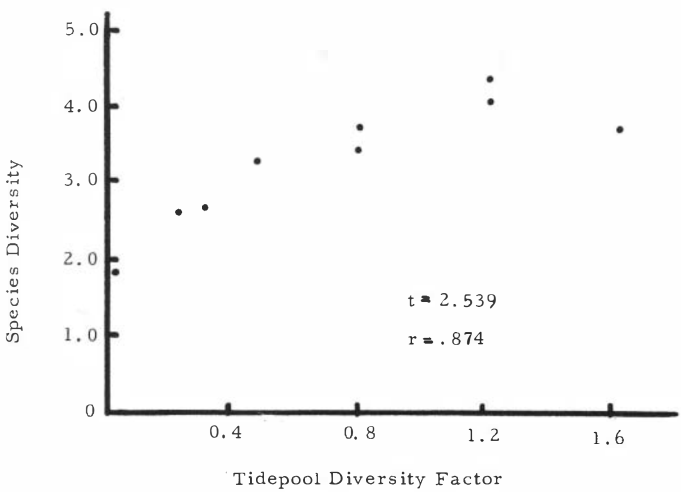
9. Schultz, L. P.
1949. A futher contribution to the ichthyology of Venezuela. *Proc. U. S. Nat. Mus.,* 99: 1-211.

Fig. 2. Imaginary tidepool illustrating the components of the tidepool diversity factor.

Fig. 3. The relationship between species diversity and tidepool diversity factor.


15
30
Tidepool
Top View
Tidepool
Side View
Surface
7.5 cm
15 cm contour
22.5 cm Midpoint
Rock Cover
30 cm contour
X cm Midpoint
Point of Maximum Depth

2


5.0
4.0
3.0
2.0
1.0
0
Species Diversity
0.4
0.8
1.2
1.6
Tidepool Diversity Factor
t = 2.539
r = .874

3