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Mollusks of Manuel Antonio National Park, Pacific Costa Rica

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Abstract: The mollusks in Manuel Antonio National Park on the central section of the Pacific coast of Costa Rica were studied along thirty-six transects done perpendicular to the shore, and by random sampling of subtidal environments, beaches and mangrove forest. Seventy-four species of mollusks belonging to three classes and 40 families were found: 63 gastropods, 9 bivalves and 2 chitons, during this study in 1995. Of these, 16 species were found only as empty shells (11) or inhabited by hermit crabs (5). Forty-eight species were found at only one locality. Half the species were found at one site, Puerto Escondido. The most diverse habitat was the low rocky intertidal zone. *Nodilittorina modesta* was present in 34 transects and *Nerita scabricosta* in 30. *Nodilittorina aspera* had the highest density of mollusks in the transects. Only four transects did not clustered into the four main groups. The species composition of one cluster of transects is associated with a boulder substrate, while another cluster of transects associates with site. Two clusters were not associated to any of the factors recorded. Some species were present in previous studies but absent in 1995, while others were absent in the previous studies but found in 1995. For example, *Siphonaria gigas* was present in 1995 in many transects with a relatively high density, but absent in 1962, probably due to human predation before the establishment of the park. Including this study, a total of 97 species of mollusks in three classes and 45 families have been reported from Manuel Antonio National Park. Sixty-nine species are new reports for the area: 53 gastropods, 14 bivalves and 2 chitons. There are probably more species of mollusks at Manuel Antonio National Park, than the 97 reported here, because some areas have not been adequately sampled (e.g., deep environments) and many micro-mollusks could not be identified.

Key words: Mollusks, intertidal zone, Costa Rica, Pacific, biodiversity.

Manuel Antonio National Park is a Protected Area with marine environments on the central Pacific coast of Costa Rica. The park was established 15 November, 1972 (Boza 1992), and it is located about 7 km southeast of Quepos on the central Pacific coast of Costa Rica (Fig. 1). The 682 hectares of terrestrial park border the ocean along 5 km of coastline. The park also includes 55 000 hectares of marine area and 12 small islands located a short distance from the shore. The area experiences a dry season from December to April with a rainy season from May to November. Tides are semidiurnal, with a tidal range of around 3.5 m.

Three papers have been published with information on the mollusks of Manuel Antonio and nearby areas. Bakus (1968)

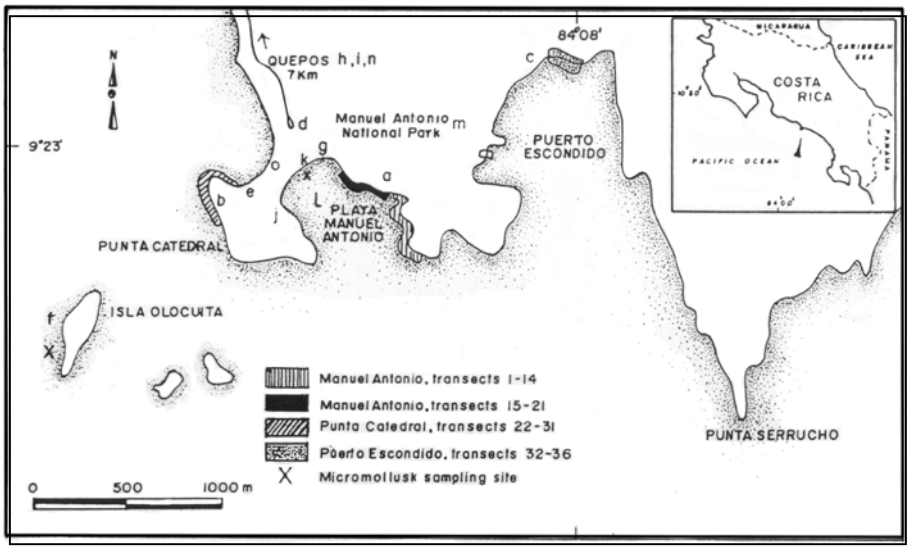

Fig. 1. Location of Manuel Antonio National Park central Pacific coast of Costa Rica. Transects and other sampling sites (see Tables 1 and 2) are indicated.

reported the presence of ten species, nine gastropods and one bivalve, consisting mainly of collections of shells from the beach. Cate (1969) reported three species of cowries. Finally, Dexter (1974), in her study of the beach fauna, reported the presence of four species of mollusks, one bivalve and three gastropods.

In this paper we present data on distribution and density of mollusks at Manuel Antonio National Park and compare it with the previous studies. We also include a list of mollusks from Manuel Antonio present in the collection of the Museo de Zoología, Escuela de Biolo-gía, Universidad de Costa Rica.

MATERIALS AND METHODS

Mollusks were qualitatively sampled in April and May 1995 from different habitats within Manuel Antonio National Park, and quantitatively along 36 transects, perpendicular to the shoreline, of variable length. The transects were separated 25 m. Sand (approximately 100 g) was collected from the beach (3 samples), and from 3 and 10 m depth, one sample from each depth (Fig. 1), and sieved to separate the micro-mollusks. The mangrove forests, the beaches and the rocky subtidal zone were visited several times to collect shells and the mollusks themselves. Specimens larger than 10 cm were not collected and notes were used to identify them. Identification of the mollusks was based on Keen (1971) and Dance (1976), following the names proposed by Skoglund (1991, 1992). Some voucher specimens were deposited at the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica. The information collected was compared with the previous studies in the area done by Bakus (1968), Cate (1969) and Dexter (1974). Finally, the mollusks of Manuel Antonio at the Museo de Zoología, Universidad de Costa Rica are included to complete the list.

The mollusks of the park were also studied along 36 transects placed throughout the rocky shores, where possible (Fig. 1). Transects were perpendicular to the shoreline extending from the lower intertidal to the upper tidal zone. Along each transect contiguous 0.25 m^2 quadrats were placed. Within each quadrat the mollusk species present were recorded along with their densities. Other data collected was

TABLE 1

Mollusks found at Manuel Antonio National Park

	Site	Habitat	Other
Class POLYPLACOPHORA			
Family CHITONIDAE			
Chiton virgulatus Sowerby, 1840	a, b, c	A	
Family ISCHNOCHITONIDAE			
Lepidozona flavida (Thiele, 1910)	a, b, c	A	
Class BIVALVIA			
Family ARCIDAE			
Anadara tuberculosa (Sowerby, 1833)	d	D	
Family MYTILIDAE			
Brachidontes adamsianus (Dunker, 1857)	a, b, c	A, B, C	
Family PTERIIDAE			
Pinctada mazatlanica (Hanley, 1856)	c		@
Family CARDITIDAE			
Cardites laticostata (Sowerby, 1833)	a		@
Carditamera affinis Sowerby, 1833	a, c	A, B	
Family LUCINIDAE			
Ctena (Ctena) galapagana (Dall, 1901)	a	E (3 m)	
Family CHAMIDAE			
Chama (Chama) echinata Broderip, 1835	a, b, c	A, B	
Chama (Chama) corallina Olsson, 1971	f (10 m)		
Family CARDIIDAE			
Acrosterigma pristipleura (Dall, 1901)	f (10 m)	F	
Class GASTROPODA			
Family LOTTIIDAE			
Lottia mesoleuca (Menke, 1851)	a, b, c	A, B	
Lottia stipulata (Reeve, 1855)	a		@
Family FISSURELLIDAE			
Diodora inaequalis (Sowerby, 1835)	c		@
Fissurella virescens Sowerby, 1835	a, b, c	A	
Fissurella longifissa Sowerby, 1863	a, b, c	A	
Fissurella rugosa Sowerby, 1835	c		@
Family TURBINIDAE			
Arene (Arena) stellata McLean, 1970	g	G	§
Arene sp.	g	G	§
Otollonia fricki (Crosse, 1865)	g	G	§
Family TROCHIDAE			
Tegula pelliserpentis (Wood, 1828)	a, b	A	
Tegula verrucosa McLean, 1970	c		*f*
Tegula panamensis (Philippi, 1849)	b	A	R
Family NERITIDAE			
Nerita scabricosta Lamarck, 1822	a, b, c	A	
Nerita funiculata Menke, 1851	b, c	A, B	
Theodoxus luteofasciatus (Miller, 1879)	d	D	
Family LITTORINIDAE			
Nodilittorina aspera (Philippi, 1846)	a, b, c	B, C	
Nodilittorina modesta (Philippi, 1846)	a, b, c	A, B	
Family RISSOIDAE			
Rissoina allemani Bartsch, 1915	g	G	§
Family VITRINELLIDAE			
Vitrinella sp.	g	G	§
Family TURRITELLIDAE			
Turritella leucostoma Valenciennes, 1832	e		@

Cont. TABLE 1

	Site	Habitat	Other
Family MODULIDAE			
Modulus disculus (Philippi, 1846)	g	G	§
Family CERITHIIDAE			
Cerithium adustum Kiener, 1841	c		*f*
Family PLANAXIDAE			
Planaxis planicostatus Sowerby, 1825	a, b, c	A, B	
Family CERITHIDEIDAE			
Cerithidea montagnei (d'Orbigny, 1839)	d	D	
Cerithidea californica Haldeman, 1840	a		@
Family HIPPONICIDAE			
Pilosabia pilosa (Deshayes, 1832)	a	E (3 m)	
Family NATICIDAE			
Polinices caprae (Philippi, 1852)	f (10 m)		
Family CYPRAEIDAE			
Zonaria arabicula (Lamarck, 1811)	a		@
Family OVULIDAE			
Jenneria pustulata (Lightfoot, 1786)	c		@
Family TONNIDAE			
Malea ringens (Swainson, 1822)	a	E (3 m)	
Family RANELLIDAE			
Linatella wiegmanni (Anton, 1839)	c		*f*
Family BURSIDAE			
Bursa corrugata corrugata (Perry, 1811)	b	A	
Family CERITHIOPSIDAE			
Cerithiopsis sp. 1	g	G	§
Cerithiopsis sp. 2	g	G	§
Family TRIPHORIDAE			
Triphora sp. 1	g	G	§
Triphora sp. 2	g	G	§
Triphora sp. 3	g	G	§
Family MURICIDAE			
Hexaplex princeps (Broderip, 1833)	c	E (1 m)	
Stronomita haemastoma (Linnaeus, 1758)	b	B	R
Thais melones (Duclos, 1832)	a, b, c	A, B	
Thais muricata (Broderip, 1833)	b	A	R
Acanthais brevidentata (Wood, 1828)	a, b, c	A, B	
Cymia tecta (Wood, 1828)	c	B	
Plicopurpura patula pansa (Gould, 1853)	a, b, c	A	
Family BUCCINIDAE			
Cantharus sanguinolentus (Duclos, 1833)	c	A	
Family FASCIOLARIDAE			
Leucozonia cerata (Wood, 1828)	c	A	
Opeatostoma pseudodon (Burrow, 1815)	a, c	E (1 m)	
Family COLLUMBELLIDAE			
Columbella labiosa Sowerby, 1822	c	A	
Columbella major Sowerby, 1832	c	A	
Costoanachis boivini (Kiener, 1841)	c	A	
Costoanachis lentiginosa (Hinds, 1844)	a	B	
Family TURBINELLIDAE			
Vasum caestus (Broderip, 1833)	a, f (3, 10 m)	F, G	
Family TEREBRIDAE			
Hastula cinerea (Born, 1778)	c		*f*
Family TURRIDAE			
Pilsbryspira melchersi (Menke, 1851)	c	B	R
Family CONIDAE			
Conus princeps Linnaeus, 1758	c	E (1m)	

Cont. TABLE 1

	Site	Habitat	Other
Conus gladiator Broderip, 1833	c		@
Conus purpurascens Sowerby, 1833	c		@
Conus fergusoni Sowerby, 1873	f (10 m)	F	
Conus patricius Hinds, 1843	f (3 m)	F	
Conus nux Broderip, 1833	c	A	
Family BULLIDAE			
Bulla punctulata Sowerby, 1850	a		*f*
Family SIPHONARIIDAE			
Siphonaria gigas Sowerby, 1825	a, b, c	A	
Siphonaria palmata Carpenter, 1857	a, b, c	A	

Sites (Fig. 1): a = Rocky zone between Playa Manuel Antonio and Playitas Gemelas; b = Punta Catedral; c = Puerto Escondido; d = Mangrove; e = Playa Espadilla; f = Isla Olocuita (depth of collection); g = playa Manuel Antonio. Habitat: A = Low rocky intertidal zone; B = Mid rocky tidal zone; C = High rocky intertidal zone; D = Mudflat; E = Rocky subtidal (depth of collection); F = Rock and sand bottom; G = Sandy substrate. Other: § = micro-mollusk; @ = Shell only; *f* = Hermit crab inhabited; R = rarely encountered.

length, overall vertical change of the transect, and whether the transect was laid across one continuous rock or a series of boulders. Ward's hierarchical clustering technique (JMP 3.0) was used to associate transects through similar species composition. The species were categorized by a number: 0) indicates that the species is absent from the transect, 1) species present with 1 to 10 individuals, 2) species with 11 to 50, 3) 51 to 250, 4) 251 to 500, and 5) species with more than 501 individuals.

RESULTS

Species lists: Three classes, 40 families and 74 species of mollusks were encountered in Manuel Antonio National Park in 1995 (Table 1). Sixty-three species were gastropods, nine were bivalves and two species were chitons. Forty-eight species were found at only one site, one at two sites and the rest at three sites. Thirty-eight species were counted at site 3 (Puerto Escondido), 29 from site 1 (between Playa Manuel Antonio and Playitas Gemelas), and 21 from site 2 (Punta Catedral). The most diverse habitat was the lower rocky intertidal zone (Table 1).

Three species were found in the mangrove forest. Of the five species found inhabited by hermit crabs, four were found exclusively at site 3, and the fifth was found only at site 1. Eleven species were found only as shells. Although 11 species of micro-mollusks are recorded here, more were found but could not be identified, thus were excluded from Table 1.

Bakus (1968) collected only ten species from the park in 1962, nine gastropods and one bivalve, mostly as cast up shells on the beach. Two families, Strombidae and Olividae were present before but not during this study (Table 2). Cate (1969) reported three species of Cypraeidae, all as *Cypraea*, two of which were not encountered in 1995 (Table 2). Dexter (1974) collected four species in her beach samples in 1971, one bivalve and three gastropods, none of them found in this study (Table 2). The list of specimens from Manuel Antonio at the Museo de Zoología contains 12 species that were not seen during the 1995 study (Table 3).

Transect data: Species distribution and categorized densities along the transects are presented in Table 4. *Nodilittorina modesta* was present in 34 of the 36 transects, followed by *Nerita scabricosta* present in 30 transects. Other species present in 24 to 26 transects are: *Nodilittorina aspera, Siphonaria gigas, Brachidontes adamsianus,* and *Thais melones*. Five species were present in only one or two transects, and with very low densities:

TABLE 2

Mollusks reported in previous studies

	Site	Ref.
Class BIVALVIA		
Family DONACIDAE		
***Donax assimilis* Hanley, 1845**	**h, i**	**D**
Family CARDIIDAE		
***Trigoniocardia guanacastensis* (Hertlein & Strong, 1947)**	**k**	**B**
Class GASTROPODA		
Family FISSURELLIDAE		
Fissurella virescens Sowerby, 1835	j, k	B
Family TROCHIDAE		
Tegula pelliserpentis (Wood, 1828)	h, i	B
Tegula panamensis (Philippi, 1849)	i	B
Family NERITIDAE		
Nerita scabricosta Lamarck, 1822	h	B
Family LITTORINIDAE		
Nodilittorina aspera (Philippi, 1846)	h	B
Nodilittorina modesta (Philippi, 1846)	h	B
Family PLANAXIDAE		
Planaxis planicostatus Sowerby, 1825	h	B
Family STROMBIDAE		
***Strombus peruvianus* Swainson, 1823**	**j**	**B**
Family NATICIDAE		
***Natica chemnitzi* Pfeiffer, 1840**	**o**	**D**
Family CYPRAEIDAE		
***Zonaria robertsi* (Hidalgo, 1906)**	**k**	**B**
***Luria isabellamexicana* (Stearns, 1893)**	**m**	**C**
***Macrocypraea cervinetta* (Kiener, 1843)**	**k, m**	**B, C**
Zonaria arabicula (Lamarck, 1811)	k, m	B, C
Family OVULIDAE		
***Neosimnia* sp.**	**l**	**B**
Family MURICIDAE		
Thais melones (Duclos, 1832)	h	B
Thais brevidentata (Wood, 1828)	k	B
***Plicopurpura columellaris* (Lamarck, 1822)**	**h**	**B**
Plicopurpura patula pansa (Gould, 1853)	h, i	B
Family FASCIOLARIIDAE		
Opeatostoma pseudodon (Burrow, 1815)	h, i	B
Family COLUMBELLIDAE		
Columbella labiosa Sowerby, 1822	i	B
Family OLIVIDAE		
***Oliva spicata* (Röding,1798)**	**k**	**B**
***Olivella semistriata* (Gray 1839)**	**n, o**	**D**
Family TEREBRIDAE		
***Hastula luctuosa* (Hinds, 1844)**	**n**	**D**
Family CONIDAE		
Conus purpurascens Sowerby, 1833	k	B
Conus nux Broderip, 1833	j	B
Family SIPHONARIIDAE		
Siphonaria gigas Sowerby, 1825	h, i	B

Sites (Fig. 1): h = Quepos: live mollusks, litoral zone, collected 20 July, 1962; i = Quepos: shells cast up on the beach, collected 20 July, 1962; j = Punta Catedral: live mollusks, litoral zone, collected 21 July, 1962; k = Playa Manuel Antonio: shells cast up on the beach, collected 21 July, 1962; l = On pink gorgonian at Manuel Antonio, collected 21 July, 1962; m = Manuel Antonio, no specific site reported; n = Playa Cocal, Quepos (9°26'N; 84°10'W): volcanic sand; o = Playa Espadilla, Manuel Antonio (9°24'N; 84°10'W): calcareous, volcanic, and quartz/feldspar sand. (Ref.): B = Bakus (1968), C = Cate (1969) and D = Dexter (1974). Species and families in **bold type** were not encountered in 1995.

TABLE 3

Mollusks collected in Manuel Antonio and deposited at the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica

Class BIVALVIA	
Family ARCIDAE	
UCR-1354	***Arca mutabilis* (Sowerby, 1833)**
Family MYTILIDAE	
UCR-3559	***Brachidontes semilaevis* (Menke, 1849)**
Family ISOGNOMONIDAE	
UCR-3558	***Isognomon (Melina) janus* Carpenter, 1857**
Family CARDITIDAE	
UCR-1272	***Carditamera radiata* (Sowerby, 1833)**
Family CHAMIDAE	
UCR-1282	***Chama (Chama) squamuligera* Pilsbry & Lowe, 1932**
Class GASTROPODA	
Family FISSURELLIDAE	
UCR-3556	***Fissurella (Cremides) microtrema* Sowerby, 1835**
UCR-3743	*Fissurella (Cremides) longifissa* Sowerby, 1863
Family TURBINIDAE	
UCR-3950	***Turbo (Callopoma) saxosus* Wood, 1828**
Family TROCHIDAE	
UCR-3567, 3572	*Tegula (Tegula) pellisserpentis* (Wood, 1828)
Family NERITIDAE	
UCR-3557, 3562	*Nerita (Theliostyla) funiculata* Menke, 1851
UCR-3570	*Nerita (Ritena) scabricosta* Lamarck, 1822
Family LITTORINIDAE	
UCR-3555	*Nodilittorina (Nodilittorina) aspera* (Philippi, 1846)
UCR-3563	*Nodilittorina (?Fossarilittorina) modesta* (Philippi, 1846)
Family CERITHIIDAE	
UCR-3552	***Cerithium (Thericium) stercusmuscarum* Valenciennes, 1833**
UCR-3955	*Cerithium (Thericium) adustum* Kiener, 1841
Family PLANAXIDAE	
UCR-3554, 3564	*Planaxis planicostatus* Sowerby, 1825
Family CALYPTRAEIDAE	
UCR-3970	***Crucibulum (Dispotaea) serratum* (Broderip, 1834)**
Family NATICIDAE	
UCR-1284	***Polinices (Polinices) otis* (Broderip & Sowerby, 1829)**
Family BURSIDAE	
UCR-3571	*Bursa (Colubrellina) corrugata corrugata* (Perry, 1811)
Family MURICIDAE	
UCR-3700	*Hexaplex princeps* (Broderip, 1833)
UCR-1509	*Thais (Vasula) melones* (Duclos, 1832)
UCR-3550	*Thais brevidentata* (Wood, 1828)
UCR-3569	*Plicopurpura patula pansa* (Gould, 1853)
Family FASCIOLARIIDAE	
UCR-1541	*Opeatostoma pseudodon* (Burrow, 1815)
Family COLLUMBELLIDAE	
UCR-1530	***Columbella fuscata* Sowerby, 1832**
UCR-3560	*Costoanachis lentiginosa* (Hinds, 1844)
UCR-3566	*Costoanachis boivini* (Kiener, 1841)
Family TURBINELLIDAE	
UCR-3699	*Vasum caestus* (Broderip, 1833)
Family OLIVIDAE	
UCR-1550	***Agaronia griseoalba* (von Martens, 1897)**
Family CONIDAE	
UCR-1273	*Conus (Stephanoconus) nux* Broderip, 1833
UCR-3565	*Conus (Conus) gladiator* Broderip, 1833
UCR-3701	*Conus (Conus) princeps* Linnaeus, 1758
Family SIPHONARIIDAE	
UCR-3551	*Siphonaria (Heterosiphonaria) palmata* Carpenter, 1857
UCR-3568	*Siphonaria (Heterosiphonaria) gigas* Sowerby, 1825

UCR-number = Mollusk collection catalogue number, Museo de Zoología, Universidad de Costa Rica. Species and families in **bold type** were not encountered in 1995.

TABLE 4

Distribution and density (individuals per m^2) of mollusks along transects

Transect	**1**	2	9	10	24	29	**3**	**4**	**5**	**6**	**7**	**8**	**23**	**22**	**25**	**11**
Chiton virgulatus	**0**	0	0	0	0	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**2**
Brachidontes adamsianus	**2**	2	3	2	2	3	**0**	**0**	**1**	**0**	**0**	**1**	**2**	**3**	**3**	**0**
Chama echinata	**0**	2	1	1	3	2	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**
Lottia mesoleuca	**1**	0	0	0	0	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Fissurella virescens	**1**	1	1	1	1	1	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**
Tegula pelliserpentis	**0**	0	0	0	0	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Nerita scabricosta	**0**	0	1	0	0	3	**3**	**4**	**3**	**3**	**2**	**2**	**0**	**1**	**4**	**1**
Nerita funiculata	**0**	0	0	0	0	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Nodilittorina aspera	**0**	4	5	5	5	1	**3**	**4**	**1**	**2**	**1**	**3**	**4**	**5**	**4**	**4**
Nodilittorina modesta	**5**	3	2	2	2	3	**3**	**1**	**3**	**2**	**2**	**2**	**2**	**3**	**3**	**3**
Planaxis planicostatus	**0**	0	0	0	0	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Thais melones	**1**	2	1	1	1	2	**0**	**0**	**1**	**1**	**1**	**0**	**1**	**0**	**0**	**1**
Thais brevidentata	**0**	2	2	1	1	2	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**2**
Plicopurpura patula pansa	**0**	0	0	1	3	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Neorapana muricata	**0**	0	0	0	0	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Opeatostoma pseudodon	**0**	0	0	0	0	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Costoanachis lentiginosa	**0**	0	0	0	0	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Conus nux	**0**	0	0	0	0	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Siphonaria gigas	**1**	2	1	1	3	2	**3**	**2**	**1**	**2**	**0**	**0**	**0**	**2**	**3**	**0**

Transect	12	15	14	13	17	16	18	**19**	21	30	27	28	36	31	35	32	34	**26**	33
Chiton virgulatus	1	1	0	0	2	0	0	**2**	1	1	2	1	1	0	1	1	0	**1**	1
Brachidontes adamsianus	2	1	1	1	1	1	1	**3**	2	2	0	1	1	0	0	0	0	**2**	0
Chama echinata	0	0	0	1	0	1	0	**1**	0	0	0	1	1	0	0	0	0	**0**	1
Lottia mesoleuca	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	**0**	0
Fissurella virescens	1	1	2	1	2	1	0	**2**	1	1	2	2	1	1	0	0	0	**2**	1
Tegula pelliserpentis	1	0	0	0	0	0	1	**1**	2	0	0	0	0	0	0	0	0	**1**	0
Nerita scabricosta	3	3	1	4	4	1	4	**4**	3	3	3	3	4	3	3	1	1	**3**	0
Nerita funiculata	0	0	0	0	0	0	0	**0**	0	2	1	1	2	0	0	1	1	**2**	1
Nodilittorina aspera	0	0	0	0	3	4	4	**2**	2	0	0	2	1	0	1	2	0	**2**	0
Nodilittorina modesta	2	2	1	3	4	2	3	**3**	1	1	1	1	1	0	1	2	1	**2**	0
Planaxis planicostatus	0	0	0	0	0	1	0	**1**	1	3	1	1	2	3	2	3	1	**1**	0
Thais melones	1	0	1	1	1	0	0	**1**	0	0	1	1	1	1	1	0	0	**1**	2
Thais brevidentata	2	1	2	1	1	1	0	**3**	0	2	3	2	0	1	0	2	1	**2**	3
Plicopurpura patula pansa	2	0	0	3	2	2	2	**2**	0	0	0	0	0	0	0	2	1	**3**	0
Neorapana muricata	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	**1**	0
Opeatostoma pseudodon	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	**0**	0
Costoanachis lentiginosa	0	0	0	0	0	0	0	**1**	1	0	0	0	0	0	0	0	0	**0**	0
Conus nux	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	**0**	1
Siphonaria gigas	2	2	3	4	3	3	0	**3**	2	0	2	2	1	0	0	2	3	**0**	0

Transects are ordered by clustering groups (Fig. 2). **Bold type** offsets every other clustered group. Abundance of each species was categorized by a number: 0) indicates that the species is absent from the transect, 1) species present with 1 to 10 individuals, 2) species with 11 to 50, 3) 51 to 250, 4) 251 to 500, and 5) species with more than 501 individuals.

mesoleuca, and *lentiginosa*. *Nodilittorina aspera* had the highest density of mollusks in the transects, more than 500 individuals/m^2. *Siphonaria gigas* was present in 25 transects, and with a relatively high density, between 10 and 250 ind/m^2.

The transect with the most species was number 19 (Bahía de Manuel Antonio, Fig. 1), with 15 species, followed by transect 26 (Punta Catedral), with 13 species. A large number of transects had between 9 and 10 species. Transects 3 and 8 (Bahía de Manuel

Antonio, area A), and transect 23 (Punta Catedral) had the least amount of species (4).

Transects clustered into four main groups leaving four transects, that remained dissimilar enough (transects 1, 19, 26, 33), not to cluster into these groups (Fig. 2). The cluster analysis associated transects through similar species composition. Clusters I and II show no relationship between species composition within clusters and orientation, relative wave action, shade of the substrate, topographic variation, transect length, overall vertical change of the transect, or whether the transect was laid across one continuous rock or a series of boulders. Cluster III had transects with similar species composition due to site, clustered transects are from the same area. Finally, transects in Cluster IV are associated according to a substrate of boulders.

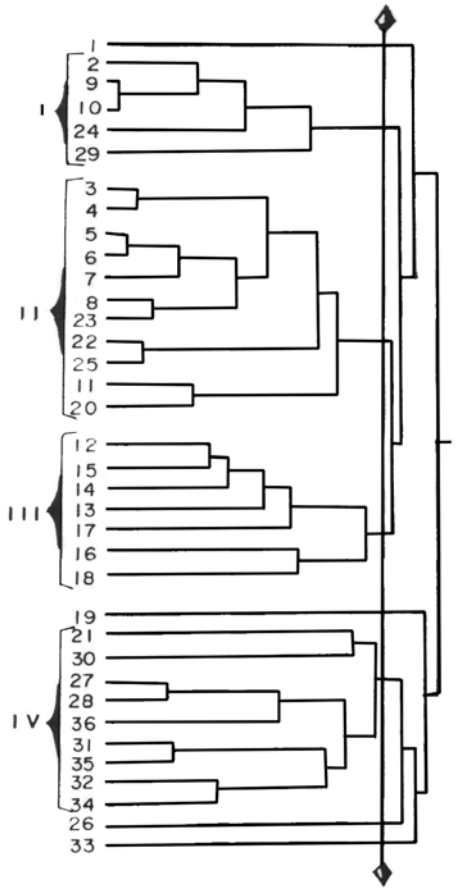

Fig. 2. Clustering of transects by species diversity of each transect using Ward's hierarchical clustering technique. Each horizontal line refers to one transect. Transects are numbered according to map (Fig. 1). The vertical line connecting the two diamonds shows how many groups are formed by clustering at this level of similarity. Every horizontal line intersecting this vertical line represents a cluster.

DISCUSSION

Species lists: Seventy-four species of mollusks were found within the boundaries of Manuel Antonio National Park, and more than half were found at only one site and most in very low densities (Table 1). This agrees with Paine's (1966) findings that tropical rocky intertidal areas do not exhibit high diversities, but a few species are present in high densities.

Connell (1972) suggests that the lower limit of a species range in the tidal zone is determined by biological factors such as competition and predation; while the upper limit is determined by abiotic factors, such as desiccation and higher temperatures. Of the 32 species found on the rocky intertidal, only two were found in the upper zone, but in very high densities, *Nodilittorina modesta* and *N. aspera*. These species are resistant to desiccation, and are free from competition in the upper intertidal zone. The mid-tidal zone was occupied exclusively by only three species, and all of them were rare. This could be explained by the fact that species in this zone do not fully escape the biological interactions of the lower intertidal, and must tolerate the abiotic factors of the upper zone. Only one species, *Brachidontes adamsianus*, inhabits all three tidal zones. This may be because there are so few bivalves in the intertidal zone, that competition for habitable substrate is negligible. Also, bivalves are particularly well adapted to dry conditions as they can seal up their shells tightly and avoid desiccation.

Mangrove forests can have a rich mollusk fauna (Cruz and Jiménez 1994), but at Manuel Antonio, only three species were found. This may be due to the fact that the mangrove at the park is small, and may also be related to

pollution from the town of Manuel Antonio. Eleven species of micro-mollusks are reported here, seven of them only as genera, because of the difficulties in identifying them. Additionally, around 20 morpho-species of micro-mollusks (some may be juveniles of larger mollusks) were found in the park, but could not be identified.

Transects: The cluster analysis suggests that there are four groups of intertidal mollusks at Manuel Antonio National Park. One of these was associated with a substrate made up of boulders (Cluster IV, Fig. 2). Disturbance by rolling boulders could be a factor determining species composition in this area than other factors. Another cluster (III, Fig. 2) showed a relationship between site and species composition, all transects are from the same area. This can be explained by the similar predation and species interaction experienced in spatially closed areas, homogenizing the species pool. There were two clusters (I and II) of widely distributed transects with all combinations of factors (substrate type and shade, topography, and wave action). There may be other factors not observed that determine the species com-position of these areas.

Comparison with the previous studies: Bakus (1968) collected in Quepos and Manuel Antonio on two days in 1962, and most specimens were present as cast up shells on the beach. Even so, some observations can be marshaled: a species that is now abundant in the park was not found in 1962, and several species that were found in 1962 were absent in 1995. The presence of some species in 1962, but not in 1995, may be explained by Spight's (1977) hypothesis that tropical species are patchily distributed throughout their range, so they can be present at one time at some locality but absent in another time. The possibility of short-term population variations accounting for the differences is refuted by two studies (Lubchenco *et al.* 1984, Ortega 1987a).

Siphonaria gigas is an edible species found in relatively high abundance in the park in 1995. Bakus (1968) did not report its presence. This may be due to human predation before the establishment of the park, as proposed by Ortega (1987b) for other areas along the Pacific coast of Costa Rica. Bakus (1968) collected at Manuel Antonio, ten years before it was declared a protected area, when fishing and shelling were permitted. These activities may have altered the species composition of the intertidal zone through any number of direct or indirect interactions (Menge 1995).

Some of the species observed by Bakus (1968) are probably present in the park but by chance not found during this study. For example, seven species were collected in two SCUBA immersions during this study; however none of the species associated with cnidarians were found in this study despite that Bakus (1968) reports the genera, *Neosimnia*, living on a pink gorgonian (probably *Leptogorgia alba*) (Table 2). Two of the three cowries reported by Cate (1969) were not found in the present study (Table 2). This probably reflects the limited surveys done in subtidal environments. Only one species, *Turritella leucostoma* was collected from the beach. Beaches have very low diversity (Rakocinski *et al.* 1991). Bakus (1968) collected a beach gastropod, *Oliva spicata* (Table 2), that has only been reported from Cocos Island, and might be an erroneous identification. Dexter (1974), in her beach fauna study, reported only 4 species of mollusks from Manuel Antonio, none of which were found during the present study (Table 2).

Twelve more species present in the Museo de Zoología collection, but not found in 1995 (Table 3), are added to the list, for a total of 97 species of mollusks from Manuel Antonio National Park. These may have been overlooked in 1995 or they may have disappeared from the area.

These 97 species that have been reported is an underestimation of the mollusk biodiversity of Manuel Antonio National Park, because most micro-mollusks have not been identified, and because subtidal environments have not been studied in detail.

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RESUMEN

La malacofauna del Parque Nacional Manuel Antonio, Pacífico central de Costa Rica, fue estudiada mediante 36 transectos perpendiculares a la costa y recolectas al azar en el sublitoral, playas y en el manglar. Se encontraron 74 especies de moluscos pertenecientes a tres clases y 40 familias: 63 gastrópodos, 9 bivalvos y 2 quitones, durante este estudio en 1995. De esas, 48 especies se encontraron solamente en un sitio. La mitad de las especies se encontraron en Puerto Escondido. *Nodilittorina modesta* estaba presente en 34 transectos y *Nerita scabricosta* en 30. *Nodilittorina aspera* tenía las densidades más altas. Treinta y dos transectos se agruparon en 4 grupos principales, quedando 4 transectos tan disimilares al resto que no figuraron en ningún grupo. La composición de especies de un grupo estaba asociada a un sustrato de cantos grandes, mientras que otro agrupa todos los transectos de un sitio. Dos grupos no estaban asociados a ninguno de los parámetros registrados. Algunas especies estaban presentes en estudios previos pero ausentes de este en 1995, mientras que otras no se encontraron antes pero si en 1995. Por ejemplo, *Siphonaria gigas* estaba presente en 1995 en muchos transecto, con densidades relativamente altas, pero ausente en 1962, probablemente debido a extracción antes de la creación del parque. Incluyendo el presente estudio, un total de 97 especies de moluscos en 3 clases y 45 familias son informadas para el Parque Nacional Manuel Antonio. Sesenta y nueve especies son nuevos informes para el área: 53 gastrópodos, 14 bivalvos y 2 quitones. Probablemente hay más especies de moluscos en el Parque Nacional Manuel Antonio que las 97 informadas aquí, debido a que hay sitios poco recolectados (e.g., aguas profundas) y no se han identificado todos los micromoluscos.

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