

Molluscan assemblage from a tropical intertidal estuarine sand-mud flat, Gulf of Nicoya, Pacific, Costa Rica (1984-1987)

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Abstract: The availability of data sets covering more than a year is scarce for tropical environments. Advances in hardware and software speed-up the re-analysis of old data sets and facilitates the identification of hidden data patterns. From February 1984 to April 1987 (49 sampling dates), core samples (17.7cm², 15cm deep) were collected at low tide at a sand-mud flat in the mid upper Gulf of Nicoya estuary, Pacific, Costa Rica. Predator exclusion experiments (cages 0.5x0.5x0.2m, galvanized wire, mesh size 5mm), were conducted at the site in 1985 (dry and rainy seasons sets). Samples were preserved with 5% buffered formalin in sea water stained with Rose Bengal, and washed after 24 hours on a 500 micron mesh sieve. The 1120 cores yielded a total of 112 morphological species of which the mollusks were represented by 23 species, and included the bivalves *Tellina rubescens*, *Tagelus bourgeoisae*, *Dosinia dunkeri* and *Leukoma asperrima*, and the gastropods, *Natica unifasciata*, *Nassarius luteostomus*, *Costoanachis rugosa* and *Turbonilla* sp. The 23 species are indicative of a relatively rich sedimentary molluscan fauna. *T. bourgeoisae* had a seasonal oscillation, with higher abundances during the rainy seasons. *T. rubescens* was not seasonal, but presented an oscillation with peaks at about 1.5 year intervals. Many empty shells of *Cosmioconcha modesta*, lower number of *N. luteostomus* and a few of *T. rubescens* were found with boreholes by the predatory snail *N. unifasciata*. *T. rubescens* was not significantly more abundant inside or outside cages. *T. bourgeoisae* showed a significant increase within the caged areas. The numerical fluctuations of the mollusks became more important during the rainy season of 1985. Red tide outbreaks in the Gulf of Nicoya in 1985 may have had an impact on the molluscan populations. Rev. Biol. Trop. 59 (3): 1135-1148. Epub 2011 September 01.

Key words: *Natica*, *Nassarius*, *Costoanachis*, *Turbonilla*, *Tagelus*, *Tellina*, *Dosinia*, *Leukoma*, benthos, estuary, tidal flat, cages, boreholes, Gulf of Nicoya, Costa Rica.

From 1980 to 1983, an ecological survey was conducted in the Gulf of Nicoya estuary to provide baseline information on the Gulf in support of management policies. Many papers covering the fields of physical, chemical and biological oceanography were published (see references in Vargas & Mata 2004) making this embayment one of the better known tropical estuaries worldwide (Vargas & Solano 2011). These studies were followed by a three year survey of an intertidal 400m² plot in the mid upper estuary (Vargas 1989).

The intertidal survey methods were not specifically designed for the detection of the abundance pattern of any particular species (Vargas & Solano 2011). However, the gastropods *Natica unifasciata*, *Nassarius luteostomus*, *Turbonilla* sp., and *Costoanachis rugosa*, and the bivalves, *Tellina rubescens*, *Tagelus bourgeoisae*, *Leukoma asperrima* and *Dosinia dunkeri*, appeared regularly in the samples over the study period. Information to date on most of these species consists of entries in malacological collections, with scarce data on their abundance

fluctuations and ecology. The early work by Gonor (1965) on the predator-prey relationships of *N. unifasciata* on *N. luteostomus* at Golfito Bay (Pacific, Costa Rica), and the report by Palacios *et al.* (1986) on the reproduction of the commercially important, *Protothaca asperrima* (now *Leukoma asperrima*) from the Gulf of Nicoya, are notable exceptions.

Caging experiments were conducted by Vargas (1988, 1996) at the site to test for the impact of crab, fish and bird predation on the benthic community. There were changes in the abundances of several of the numerically dominant species, and in the composition of the community, as revealed by multivariate statistics. However, the relatively lower abundance mollusks were not analyzed further. The advances in hardware and software during the last decades speed-up the re-analysis of old data sets and facilitates the identification of hidden data patterns.

The objective of this paper is to make accessible complementary data on the abundance fluctuations and ecology of this molluscan assemblage (an artificial group of interacting species).

MATERIALS AND METHODS

From February 1984 to April 1987 (total: 49 sampling dates) core samples (17.7cm², 15cm deep) were collected by Vargas (1987, 1988) in lower intertidal at the Punta Morales (mean tidal range: 3m) sand-mud flat in the mid upper Gulf of Nicoya (10°N, 85°W), Pacific coast of Costa Rica. The study was conducted on a 20x20m area of the flat, about 20m from the edge of a white sand beach (see map in Vargas 1987). In 1984 and 1985, 28 cores (0.05m²) were collected (12 to 18 days intervals, 25 dates). A monthly sampling scheme was followed (14 cores, 0.02m²) from 1985 to 1987 (24 dates).

Macropredator (birds, fish and crabs) exclusion experiments (cages 0.5x0.5x0.2m, galvanized wire, mesh size 5mm), were conducted by Vargas (1988,1996) at the site in 1985 (dry and rainy seasons sets, eight cages each). He deployed sixteen cages that were

pushed 0.1m into the sediment and left for periods of one (8 cages), two (4 cages) and three (4 cages) months after which they were lifted and 14 cores taken from inside and 14 outside (84 cores each) the caged areas.

Samples were preserved with 5% buffered Rose Bengal stained formalin in sea water, and washed with freshwater on a 500 micron mesh sieve. Sorted (30X dissecting scope) specimens were stored in 70% ethanol. A collection of morphological species was assembled and a code assigned to each one. Molluscan species identification was based on Keen (1971), and later updated with Skoglund (1992), Cruz-Soto & Jiménez-Ramón (1994), Valdés & Camacho-García (2004), Rodríguez-Sevilla *et al.* (2009), Magaña & Espinosa (2009), and www.marinespecies.org (March 2011).

Seasonality and temporal trends for the 49 dates were analyzed with the Generalized Additive Model (GAM) of the free mgcv package in *The R Project for Statistical Computing* (Wood 2006), with abundance data $\log_{10}(x+1)$ transformed to homogenize variances. The GAM was carried out with the family *quasi* (Chaloupka *et al.* 2008). Species abundances inside and outside cages were compared with a paired Student's t test on the log transformed monthly totals (Normality and equality of variances were tested previously). Chi-square tests were used to determine significant season (dry vs rainy) differences. A SIMPER analysis (Clarke & Warwick 1994, Hammer *et al.* 2001) was applied to the data for each condition (caged vs uncaged). The percentage of change attributable to mollusks and other assemblages was obtained using PAST (Hammer *et al.* 2001).

RESULTS

A total of 1 120 sediment cores were processed, representing an area of 1.98m². On average, the sediments at the flat were 65% sand and about 35% mud. Other information on environmental data is included in Vargas (1987,1988,1989) and Vargas & Solano (2011).

The 1 120 cores yielded a total of 112 species. The polychaete worms were represented

by 45 species and the crustaceans by 29. A group of 15 species included flatworms, nemerteans, two sipunculans, oligochaetes, two brachiopods, two echinoderms, hemichordates, a lancelet and a gobiid fish (Vargas 1989).

The mollusks were represented by 23 species and their abundances are included in Table 1. The deposit feeding pink bivalve, *Tellina rubescens* was most abundant and ranged in length from 5mm to 40mm. Many small bivalves of various shapes and less than 5mm were pooled as unidentified juveniles (Table 1). Among the gastropods, *Natica unifasciata* was observed frequently crawling on the sediment surface and leaving behind a mucous

lined track. A group of the scavenger snail, *Nassarius luteostomus* was observed (Dec. 26th, 1984) feeding on a dead *Callinectes arcuatus* crab, and a few gaping *T. rubescens* were found (Aug. 19th, 1985) lying on the sediment surface. The abundances of the bivalves, *T. rubescens*, *T. bourgeoisae*, *L. asperrima* and *D. dunkeri*, are included in Figs. 1 and 2, for 1984-1985 and 1984-1987, respectively. The abundances of the gastropods, *N. unifasciata*, *Turbonilla* sp., *N. luteostomus* and *C. rugosa* collected from 1984 to 1987 are included in Fig. 3. *C. rugosa* was found only from August 1985 to March 1986 (Fig. 3B). Only the GAModels applied to the abundances of,

TABLE 1

List of mollusks collected by coring at a 400m² plot at the Punta Morales intertidal sand-mud flat. Gulf of Nicoya estuary, Pacific coast of Costa Rica (1984-1987). Code numbers as in Vargas (1987, 1988, 1989). G=Gastropoda, B=Bivalvia. General feeding modes for each family: DF (Deposit feeder), SF (Suspension feeder), CA (Carnivores), PA (Parasitic), SC (Scavenger). N=total number of individuals collected

Code	Class	Family	Species	Feeding modes	N
50	B	Tellinidae	<i>Tellina rubescens</i> Hanley, 1844.	DF	522
71	B		Bivalvia, unidentified juveniles.	FF	426
55	B	Solecurtidae	<i>Tagelus bourgeoisae</i> Hertlein, 1951.	FF	208
45	G	Naticidae	<i>Natica unifasciata</i> Lamarck, 1822.	CA	55
72	B	Pyramidellidae	<i>Turbonilla</i> sp.	PA	54
75	G	Calyptraeidae	<i>Calyptraea mammilaris</i> (Broderip, 1834).	FF	49
46	G	Nassariidae	<i>Nassarius luteostomus</i> (Broderip & Sowerby, 1829).	SC	47
52	G	Vitrinellidae	<i>Solariorbis</i> (?) sp.	DF	40
83	B	Veneridae	<i>Leukoma asperrima</i> (Broderip & Sowerby, 1835).	FF	38
49	B	Veneridae	<i>Dosinia dunkeri</i> (Philippi, 1844).	FF	33
51	G	Cylichnidae	<i>Acteocina</i> sp.	CA	25
104	B	Carditidae	<i>Carditamera radiata</i> (Sowerby, 1833).	FF	22
99	G	Columbellidae	<i>Costoanachis rugosa</i> (Sowerby, 1832).	CA	21
54	B	Tellinidae	<i>Tellidora burneti</i> (Broderip & Sowerby, 1829).	DF	19
47	B	Columbellidae	<i>Cosmioconcha modesta</i> (Powys, 1835).	CA	13
48	B	Corbulidae	<i>Corbula nasuta</i> Sowerby, 1833.	DF	9
53	G	Nassariidae	<i>Nassarius complanatus</i> (Powys, 1835).	SC	9
100	G	Cerithiidae	<i>Ceritium stercusmuscarum</i> Valenciennes, 1833.	SF	7
91	G	Cyrenoididae	<i>Cyrenoida panamensis</i> Pilsbry & Zetek, 1931.	DF	6
101	B	Veneridae	<i>Anomalocardia subrugosa</i> (Wood, 1828).	FF	5
119	B	Mactridae	<i>Mactra fonsecana</i> Hertlein & Strong, 1950.	FF	3
70	G	Batillariidae	<i>Rhinocoryne humboldti</i> (Valenciennes, 1832).	DF	1
90	G	Nassariidae	<i>Nassarius wilsoni</i> (C.B. Adams, 1852).	SC	1
115	G	Naticidae	<i>Natica chemnitzii</i> (Pfeiffer, 1848).	CA	1

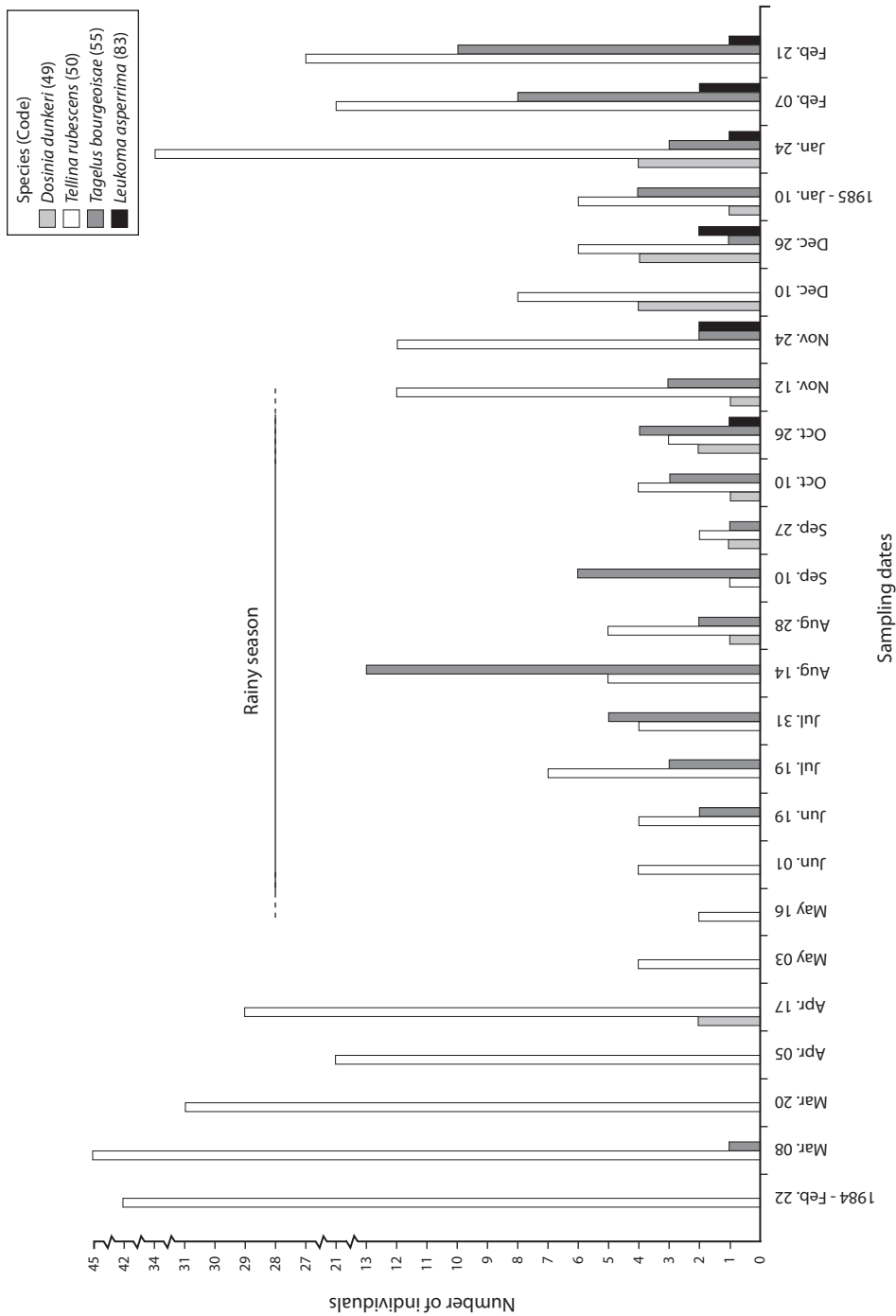


Fig. 1. Number of individuals of the bivalves *Dosinia dunkeri*, *Tellina rubescens*, *Tagelus bourgeoiseae* and *Leukoma asperrima* collected by coring (28 cores/date) at a 400m² plot at the Punta Morales sand-mud flat (10°04'N - 84°58'W), Gulf of Nicoya estuary, Pacific coast of Costa Rica, February 1984 to February 1985 (25 sampling dates).

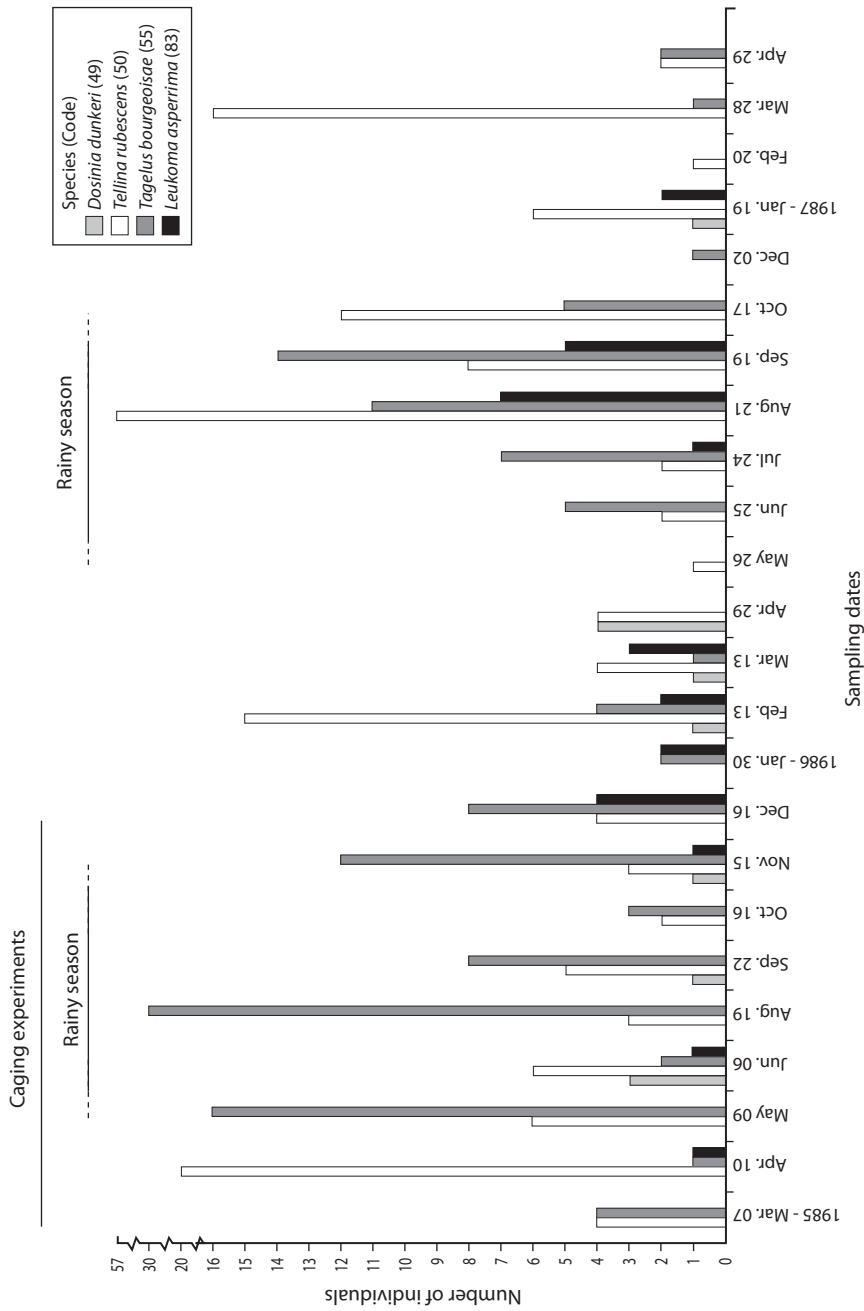


Fig. 2. Number of individuals of the bivalves *Dosinia dunkeri*, *Tellina rubescens*, *Tagelus bourgeoiseae* and *Leukoma asperrima* collected by coring (14 cores/date) at a 400m² plot at the Punta Morales sand-mud flat (10°04'N - 84°58'W), Gulf of Nicoya estuary, Pacific coast of Costa Rica. March 1985 to April 1987 (24 sampling dates).

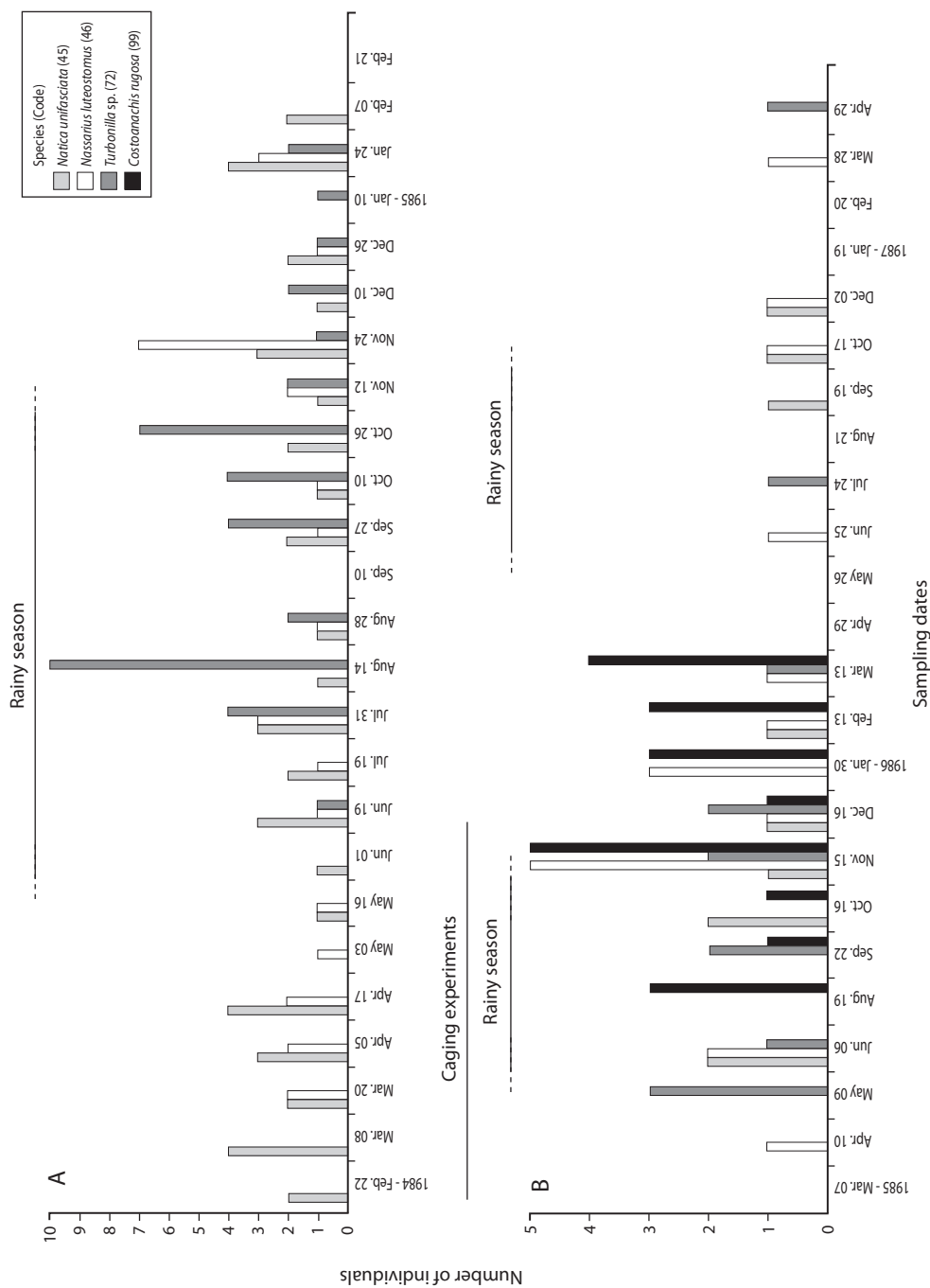


Fig. 3. Number of individuals of the gastropods *Natica unifasciata*, *Nassarius luteostomus*, *Turbonilla* sp. and *Costoanachis rugosa* collected by coring (A: 28 cores/date, February 1984 to February 1985. B: 14 cores/date, March 1985 to April 1987) at a 400m² plot at the Punta Morales sand-mud flat (10°04'N - 84°58'W), Gulf of Nicoya estuary, Pacific coast of Costa Rica.

T. bourgeosai, *T. rubescens* and *Turbonilla* sp., accounted for greater than 40% of the explained deviance (Fig. 4). For the 49 dates, a significant seasonal oscillation was detected for *T. bourgeosiae* ($t=3.1$, $p=0.003$), with higher abundances during the rainy seasons. Moreover a temporal trend (Fig. 4) was detected with a peak during mid 1985 ($F=6.2$, $p=0.002$). The GAM applied to *T. rubescens* data did not identify a seasonal peak ($t=-1.63$, $p=0.111$), but rather an oscillation (Fig. 4) with peaks at about 1.5 years intervals ($F=2.9$, $p=0.02$).

Caging experiments (8 dates) indicated that abundances of *T. rubescens* were not significantly affected by predator exclusion ($t=0.5$, $g.l.=7$, $p=0.642$). Both within and outside the cages *T. rubescens* exhibited significant seasonal abundance ($\chi^2=25.8$, $p<0.001$ and $\chi^2=9.6$, $p=0.002$, respectively) with greatest numbers found during the dry season (Fig. 5A,B). On

the other hand, *T. bourgeosiae* showed no significant seasonal differences in abundances inside or outside the cages (χ^2 , $p>0.05$), but a significant increase ($t=2.49$, $g.l.=7$, $p=0.042$) inside the caged areas (Fig. 5C, D).

The relative contribution to changes in molluscan abundances relative to total benthic abundances inside and outside caged areas is included in Table 2. The mollusks were a numerically more important component of the benthos during the rainy season inside (38.2%) and outside (56.3%) the cages than during the dry season (17.7 and 11.2 %, respectively). The community presented high values of change during the rainy season than during the dry season for both treatments, inside and outside cages (Table 3). *T. bourgeosiae* increased its percentage share during the dry season (Table 3), with a peak of 10% in both treatments in the first months of the rainy season (Table 3).

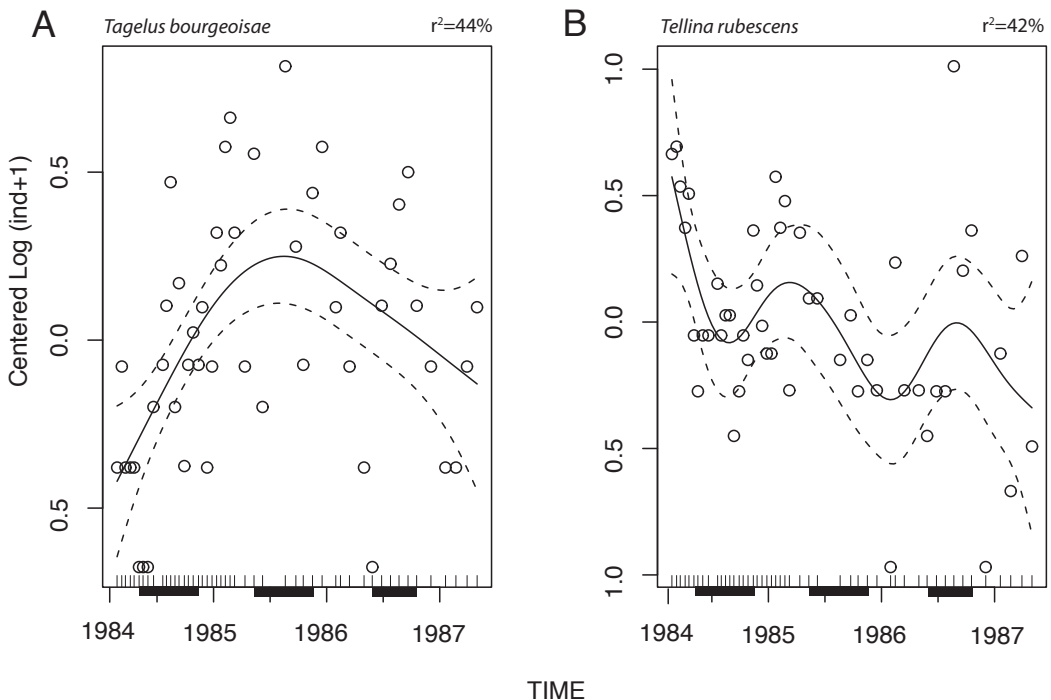


Fig. 4. Generalized Additive Models (GAM) for the abundances of A: *Tagelus bourgeosiae* and B: *Tellina rubescens*, February 1984 to April 1987. Solid line is the fitted value for the model. Broken lines are the 95% confidence limits. Deviances explained were 44 and 42%, respectively. Dark bars at the bottom = rainy seasons.

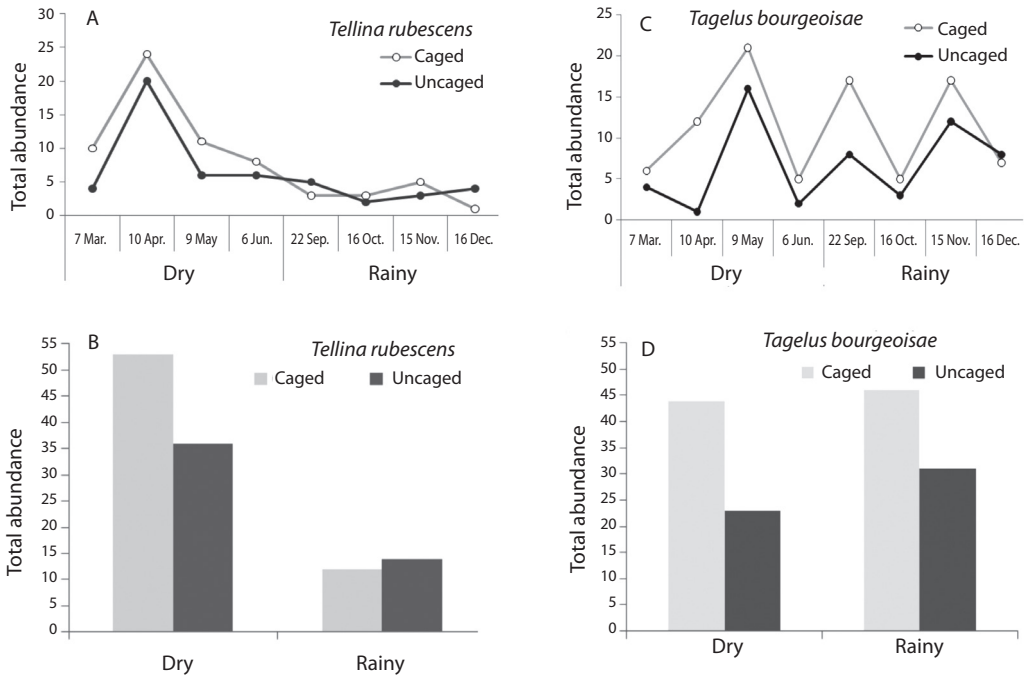


Fig. 5. Total abundances of A: *Tellina rubescens*, C: *Tagelus bourgeoisae* in cores taken inside (caged) and outside (uncaged) cages during the dry and rainy season sets of experiments. Cages were sampled after 1 (Mar. 7, Jun. 6), 2 (Apr. 10), and 3 (May. 9) months during the dry season. Cages were also sampled after 1 (Sep. 22, Dec. 16), 2 (Oct. 16) and 3 (Nov. 15) months during the rainy season. B, D: Total abundances inside and outside cages during the dry and rainy seasons. Punta Morales sand-mud flat (10°04' N-84°58' W), Gulf of Nicoya estuary, Pacific, Costa Rica. 1985.

T. rubescens made up a greater percentage of the benthos in the first months of the dry season in both treatments (~4 to 5%), Table 3. The importance of the molluscan assemblage to community change was relatively low compared to the annelids and crustaceans, with a maximum value of ~17% in both seasons inside or outside cages (Tables 2 and 3).

DISCUSSION

The 23 molluscan species in this study were collected from an area of 400m² and represent only a fraction of the diversity of the Punta Morales sand-mud flat. This intertidal area changes gradually to more sandy conditions to the East and is sharply bounded by a white sand beach to the North and by rocky

outcrops to the West (see map in Vargas 1987), and each of these biotopes would be expected to have its own assemblage of species. In a grab survey at 41 stations (2 to 46m deep, 500 micron sieve) in the Gulf of Nicoya, the benthic macrofauna was represented by 205 species, of which 120 (58.6%) were polychaete worms, 46 (22.4%) crustaceans, 22 (10.7%) mollusks and 17 were represented by other groups (Maurer & Vargas 1984). Therefore the 23 species found at the small site in Punta Morales (Table 3), indicate a relatively rich molluscan fauna. The mollusks of Punta Morales are likely to be even more diverse as additional species of shelled gastropods and unidentified juvenile bivalves were not adequately included in this study. Moreover, Hoisæter (1998) listed 252 species of shelled gastropods hand collected from

TABLE 2

Maximum contribution (%) by the crustacean, annelid, mollusc, and others assemblages to total community (112 spp.) change at the caged and uncaged sampling plots. Punta Morales sand-mud flat (10°04' N-84°58' W), Gulf of Nicoya estuary, Pacific, Costa Rica. February to December 1985

Season	Period	Treatment	Assemblage	%
Dry	Feb-Mar	Caged	Crustacea	62.7
	May-Jun		Annelida	46.7
	May-Jun		Mollusca	17.7
	Feb-Apr		Others	11.4
	Feb-Mar	Uncaged	Crustacea	55.9
	May-Jun		Annelida	55.7
	Feb-Apr		Others	16.3
	Feb-Apr		Mollusca	11.2
Rainy	Aug-Set	Caged	Annelida	53.0
	Nov-Dec		Mollusca	38.2
	Nov-Dec		Crustacea	17.4
	Nov-Dec		Others	5.6
	Aug-Oct	Uncaged	Annelida	62.7
	Nov-Dec		Mollusca	56.3
	Nov-Dec		Crustacea	17.4
	Nov-Dec		Others	4.9

TABLE 3

Total percent community (112 spp.) change at the caged and uncaged sampling plots, and percentages (* = 0.0) of community change due to the abundances of eight molluscan species (*ID codes* as in Table 1). Total % contribution by the eight species is listed in the last column. Dry season (February-June, 1985), rainy season (August-December, 1985). Punta Morales sand-mud flat (10°04' N-84°58' W). Gulf of Nicoya, Costa Rica

Cages on site (months)	% community change		% of community change accounted by each species								Total
	caged	uncaged	45	46	47	49	50	55	83	99	
1 (Feb-Mar)	48		0.3	*	*	*	0.8	0.3	0.3	*	1.7
		29	0.3	*	*	*	1.0	0.3	0.3	*	1.9
2 (Feb-Apr)	39		0.3	0.3	*	*	4.2	1.7	0.2	*	6.7
		27	0.4	0.4	*	*	5.0	1.6	*	*	7.4
3 (Feb-May)	39		*	*	*	0.5	1.0	4.1	0.3	*	5.9
		60	0.2	*	0.2	*	0.2	2.5	0.2	*	3.4
1 (May-Jun)	31		*	*	0.6	1.8	1.2	6.5	*	*	10.1
		39	1.2	1.1	0.6	1.7	*	8.0	0.6	*	13.2
1 (Aug-Sep)	53		*	*	*	*	*	5.4	0.4	2.1	7.8
		54	*	*	*	0.5	0.9	10.0	*	0.9	12.3
2 (Aug-Oct)	55		0.4	*	*	*	*	10.0	0.4	0.4	11.2
		59	0.6	*	*	*	0.3	8.0	*	0.6	9.5
3 (Aug-Nov)	70		0.2	0.1	*	*	0.3	2.0	*	0.5	3.1
		58	0.3	1.3	*	0.3	*	4.7	0.3	0.5	7.3
1 (Nov-Dec)	30		0.5	2.4	0.5	0.5	0.9	2.4	1.4	1.4	9.9
		35	*	1.6	*	0.4	0.4	1.6	1.2	1.6	6.9

intertidal to 8m depth in Golfo Dulce (Pacific, Costa Rica), with 14 species in the Vitrinellidae and 13 in the Pyramidellidae, and the genus *Turbonilla* alone represented by 13 species.

Sampling during three years allowed the identification by Vargas (1987, 1988) of seasonal oscillations of the community, with samples from the rainy seasons being more similar to each other than those from the dry seasons. The Gulf of Nicoya estuary is seasonal in rainfall (May to November), which in turn influences salinity fluctuations (Voorhis *et al.* 1983). At the population level, Vargas (1987, 1988) also identified groups of species characterized by peaks of abundance coinciding either with the dry or the rainy seasons. For *L. asperrima*, Palacios *et al.* (1986) point out that a strong decrease in salinity in the Gulf of Nicoya late in the rainy season (October-November), coincided with the spawning peak of this species. The mangrove cockle, *Anadara tuberculosa* has its period of greatest spawning activity from May to September (early to mid rainy season) at Punta Morales (Cruz 1984). As a contrast, the razor clam, *Tagelus peruvianus* has a reproductive peak during January and February (mid dry season) at the intertidal sand flats of Puntarenas, East of Punta Morales (Rojas *et al.* 1988).

Other species showed variations in abundances which could not be directly related to seasonal cycles. Two species of echinoderms found at the flat were also patchy in their temporal distribution (Vargas & Solano 2011). The application of GAModels allowed the identification of three abundance trends: peaks during the rainy seasons and a maximum centered at mid 1985 (*T. bourgeoisae*, Figs., 1, 2, 4A), and an oscillation with periods longer than the annual cycle (*T. rubescens*, Fig. 4B). Thus, the molluscan fauna at the flat is composed of seasonal and non-seasonal species, whose appearance in the samples might be related to the vagaries of recruitment, immigration and emigration, small scale sediment patchiness, predation impacts, or some combination of these factors. McIntyre (1970), in a study of *Tellina tenuis* from different intertidal habitats in England, found that variable recruitment

from year to year was influenced by biotic and abiotic factors affecting the spawning, planktonic, settlement, and post-settlement phases of this bivalve.

The list (Table 1) of molluscan species revealed different feeding modes, as well as biogenic processes (sediment reworking, mucous-lined tracks, fecal pellet and empty shell productions). Comparisons of tidal flat faunas based on species occupying similar niches, or on unrelated species playing analogous ecological roles, are useful to understand the functioning (energy flow), and structuring (species diversity and abundance), of these ecosystems (Reise 1991). Vargas (1996) pointed out that the mollusks, *N. unifasciata*, *N. luteostomus*, *T. bourgeoisae* and *T. rubescens* from the Gulf of Nicoya (10°N, Costa Rica) may play similar ecological roles as the temperate (31°N, USA) species, *Polinices duplicatus*, *Nassarius obsoletus*, *Solen viridis* and *Tellina texana*, respectively. Roles in common include: predation, scavenging, filter and deposit feeding, sediment reworking and formation of feeding tracks. These roles indicate that energy is being transferred by the molluscan assemblage along similar pathways at both latitudes. Moreover, Dittman & Vargas (2001) compared the faunas of tidal flats in the estuaries of Haughton (19°S, Australia) and the Gulf of Nicoya. Although there were no molluscan species in common, they found species of the genera *Natica* and *Nassarius* at both flats.

N. unifasciata has been reported by Gonor (1965) to prey mainly on *N. luteostomus* at the intertidal flats of Golfito bay, an small embayment on the Northern shore of the Golfo Dulce deep anoxic basin (Pacific coast of Costa Rica). *N. unifasciata* was observed at low tide carrying either a clam or a *Nassarius* and crawling on the surface for about a meter, then slowly burrowing into the sediment to drill the shell and consume the prey. Hughes (1985) reports that *N. unifasciata* does not forage when covered by the tide in the Pacific coast of Panama, and takes about 50 hours to consume a small *Nerita funiculata* snail, with most of this time spent drilling through the shell of the prey.

At the Punta Morales site larger specimens of *N. unifasciata* were observed crawling on the sediment surface but most of the specimens captured by the corer were below the sediment surface. The cores also yielded many empty shells of *C. modesta*, lower number of *N. luteostomus* and a few of *T. rubescens* bearing boreholes (Fig. 6). Naticacean boreholes are characterized by smooth walls, beveled outer edges, decreasing diameter with depth, circular, and being perpendicular to the prey shell surface (Carriker 1981). Hughes (1985) has pointed out that dietary conditioning and relative abundance of prey items may account for local preferences of *N. unifasciata* over certain prey species. This may be the case with *N. luteostomus* in Golfoito bay, and with *C. modesta* at the Punta Morales flat. However, drilled shells of *T. rubescens* were scarce at Punta Morales in spite of the relative higher abundance of this clam (Figs. 1, 2). No bored shells of *T. bourgeoisae* were found during the survey.

At low tide the tidal flats of the Gulf of Nicoya are feeding grounds for resident and migratory shore birds. At the sand-mud flat of Punta Morales 13 species of birds were observed foraging at low tide (Vargas 1988). On a nearby sand flat Pereira (1990) recorded 27 species of birds with *Numenius phaeopus*, *Limnodromus griseus* and *Catoptrophorus semipalmatus* being most numerous throughout the year. These species capture and ingest mainly crustaceans, but also other prey items including bivalves, gastropods, brittle stars, gobiid fish, and worms. To test for the impact of bird foraging on the benthos Pereira (1990) fenced 25m² plots with five nylon ropes to a height of 25cm. This design restricted the access of birds, and the number of invertebrates inside plots was found to be significantly higher than outside.

The use of cages in experiments to test the impact of predators on the benthos in temperate latitudes has produced, with few exceptions significant increases on the number of individuals and species inside the caged areas. For instance, in Northern Germany the bivalve *Cerastoderma edule* reached densities of 513 individuals under a 400cm² area protected

by a 1mm mesh cage, while only three clams were found in a 400cm² of ambient mud (Reise 1985). The response of tropical benthos to caging appears to be dependent on a more complex set of factors and interactions (Vargas 1988, 1996). Cages also affect the hydrodynamic environment inside the caged area; therefore, the observed changes are difficult to relate only to the exclusion of macro-predators (Hall *et al.* 1990). At high tide the flats around Punta Morales host an assemblage on more than 60 species of fish (Phillips 1983), some of which may feed on the benthos. Vargas (1988, 1996) concluded that the relative importance of birds, fish and crabs as predators regulating community structure was not a key factor as evidenced by the results of the caging experiments. However, among the mollusks only *T. bourgeoisae* showed an increase in the number of individuals inside cages (Fig. 5).

The relative importance of the molluscan assemblage in the percent numerical change inside and outside caged areas, increased at the end of the rainy season of 1985 with maximum values of 38.2 and 56.3, respectively (Table 2).

Red tide events were observed in the Gulf of Nicoya between April and November of 1985, with dense patches found in July within a small estuary a few hundred meters from the Punta Morales flat. These outbreaks were caused by several species of toxic and non toxic dinoflagellates and diatoms associated mainly to blooms of *Cochlodinium catenatum*, but with an outbreak of *Gymnodinium catenatum* located near the study site in November (Viquez & Hargraves 1995). Fish mortality (corbinas, croakers and drums) was reported from near Punta Morales during September-October of 1985 (Szelistowski & Garita 1989). Moreover, toxic red tides are known to have had a negative impact on the benthos of Wellington Harbour (41°S, New Zealand) where the polychaetes were affected most, but with important changes in species composition and numerical abundance in the mollusks, crustaceans and echinoderms (Wear & Gardner 2001). The fact that a few gaping *T. rubescens* were found on August 19th, 1985 lying on the

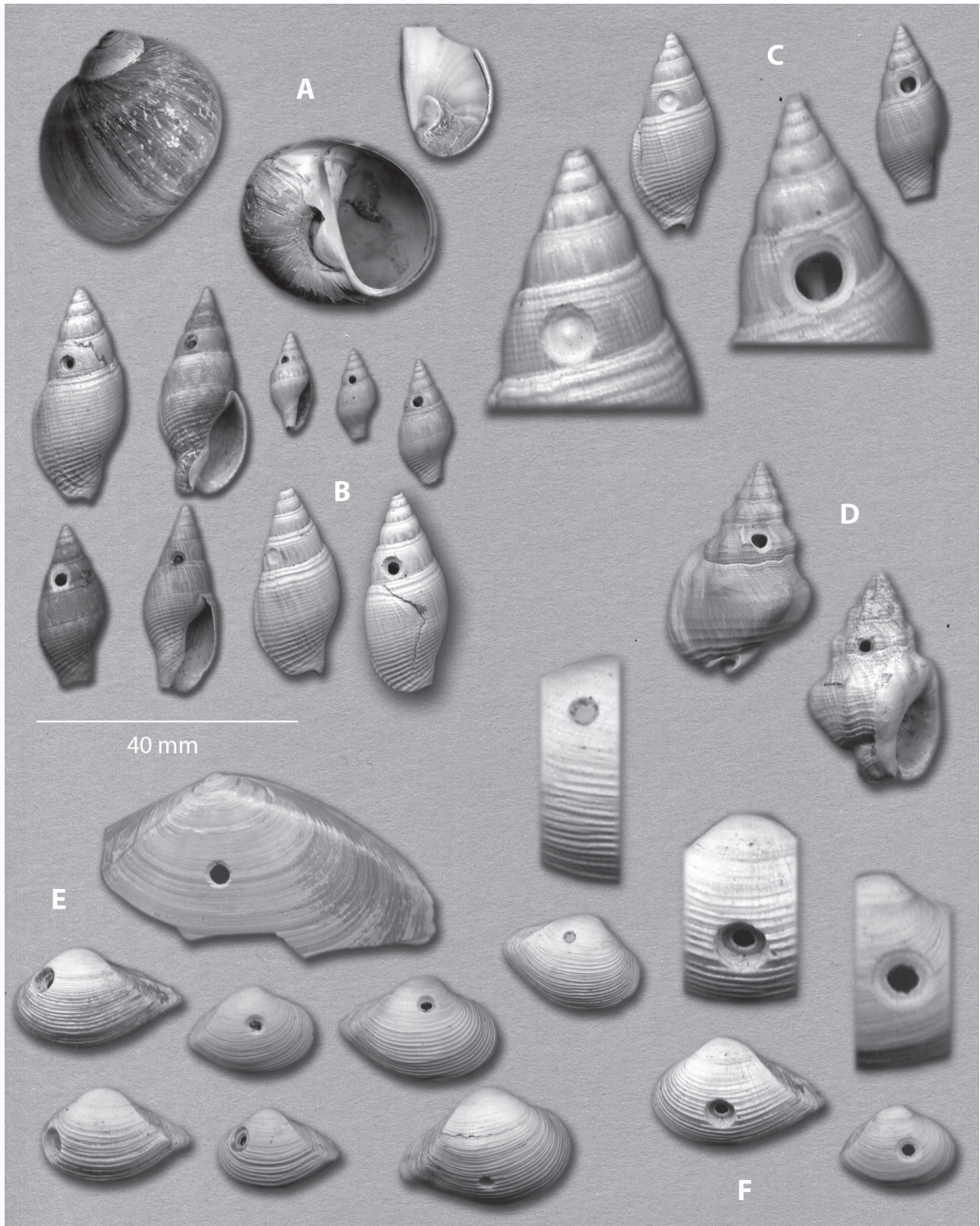


Fig. 6. A. Shell and operculum of *Natica unifasciata*. B. Shells of *Cosmioconcha* sp., with boreholes. Note that the position of the borehole appears constant. C. Details of incomplete and complete boreholes. Note the center boss characteristic of incomplete naticacean boreholes. The complete borehole allows the view of the columella, site of attachment for the foot retractor muscle. D. Two shells of *Nassarius luteostomus* with boreholes. E. Shells of *Tellina* sp., (top left) and *Corbula* sp., with boreholes. F. Details. Punta Morales sand-mud flat (10°04' N-84°58' W), Gulf of Nicoya estuary, Pacific, Costa Rica.

sediment surface at Punta Morales is relevant in this context. Based on the available data, the possibility could not be ruled out that red tides in the Punta Morales region during 1985 also had impacted the molluscan populations.

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RESUMEN

La disponibilidad de datos con una cobertura mayor al año es rara para ambientes tropicales. Avances en computación y programas de cómputo facilitan el re-análisis de antiguos datos y la identificación de patrones ocultos en ellos. Desde febrero de 1984 hasta abril de 1987 (49 fechas de colecta), muestras de barreno (17.7cm², 15cm de profundidad) fueron recolectadas durante la marea baja en una planicie arenosa-fangosa en la región media del estuario del Golfo de Nicoya, Costa Rica. Experimentos de exclusión de depredadores (jaulas 0.5x0.5x0.2m, malla galvanizada, poro de 5mm), fueron realizados en el sitio en 1985 (estación seca vs estación lluviosa). Las muestras fueron preservadas con formalina al 5% en agua de mar teñida con Rosa de Bengala y lavadas después de 24 horas en un tamiz de 500 micras de poro de malla. Los 1 120 barrenos produjeron un total de 112 especie morfológicas, de las cuales los moluscos estuvieron representados por 23 especies que incluyen los bivalvos: *Tellina rubescens*, *Tagelus bourgeoisae*, *Dosinia dunkeri* y *Leukoma asperrima*, y los gastrópodos, *Natica unifasciata*, *Nassarius luteostomus*, *Costoanachis rugosa* y *Turbonilla* sp. Las 23 especies son indicadoras de una fauna de moluscos relativamente rica. *T. bourgeoisae* presentó una oscilación estacional, con mayor abundancia durante la estación de lluvias. *T. rubescens* no fue estacional, pero presentó una oscilación con máximos a intervalos de cerca de 1.5 años. Muchas conchas vacías de *Cosmioconcha modesta*, un poco menos de *N. luteostomus* y unas pocas de *T. rubescens* fueron encontradas con perforaciones hechas por el depredador *N. unifasciata*. *T. rubescens* no fue significativamente más abundante dentro o fuera de las jaulas. *T. bourgeoisae* mostró una falta de abundancia estacional, pero una densidad significativamente mayor dentro de las jaulas. Las fluctuaciones poblacionales de los moluscos fueron más importantes durante la estación de lluvias cuando se les compara con las fluctuaciones de los poliquetos, crustáceos

y otros grupos. Mareas rojas en el Golfo de Nicoya durante 1985 podrían haber tenido un impacto en la dinámica de las poblaciones de moluscos.

Palabras clave: *Natica*, *Nassarius*, *Costoanachis*, *Turbonilla*, *Tagelus*, *Tellina*, *Dosinia*, *Leukoma*, bentos, estuario, planicies de marea, jaulas, perforaciones, Golfo de Nicoya, Costa Rica.

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