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Occurrence, demography, and habitat features of *Pollicipes elegans* (Pollicipedidae: Scalpelliformes) an amphitropical species at a rocky intertidal shore, Costa Rica

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Abstract
Clumps of the gooseneck barnacle *Pollicipes elegans* were found in the Central Pacific on a rocky shore of Costa Rica. This species is known to be abundant in northern and southern latitudes of the Eastern Tropical Pacific. The present study describes aspects of its demography, size structure, as well as habitat features in Costa Rica. The clumps were on vertical rocky substrates, generally, with a negative slope and an average height of 1.70 m above the Lowest Astronomical Tide. Two cohorts were found in the rocky shore in 2014. An important decline of abundance and density of clumps was found between July and October of 2014. Additional clumps were found in September 2016. Based on the previous evidence we present hypotheses about how this species became established in Costa Rica and why a decline of the clumps was observed.

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Introduction

Four species of gooseneck barnacles of the genus *Pollicipes* (Pollicipedidae: Scalpelliformes) inhabit the wave-exposed rocky shores around the world (Van Syoc et al. 2010). In previous biogeographical reports, *Pollicipes elegans* (Lesson, 1831) is abundant only in amphitropical areas at transition zones in the Eastern Tropical Pacific (ETP), between Baja Californian-Mexican (26˚N and 19˚N) and Panamic-Peruvian region (3˚S and 12˚S) to the northern Chile coast. The species was described from a specimen of Paita, Peru, where it is common and commercial (Lesson 1831, Laguna 1985). In the north of Baja California, *P. elegans* overlaps with *Pollicipes polymerus* Sowerby, 1833, a northernmost species of the ETP (Barnes 1996, Fhyn et al. 1972). The region between 20° and 14° N seems to act as a barrier to the dispersion of marine species in the transition of zoogeographical regions between the Mexican Province (Gulf of California to Tehuantepec) and Panamanian Province (El Salvador to Ecuador) (Briggs 1974, Laguna 1990, Marchant et al. 2015).

Compared to *P. polymerus* and *Pollicipes pollicipes* (Gmelin, 1790), little is known about the natural history, distribution, anatomy, and development of *P. elegans* (Barnes 1966). In Central America, *P. elegans* has been reported in El Salvador (Laguna 1985, Van Syoc 1994). The previous report of the species in Costa Rica was three specimens from the locality of Jesús María, Tivives, Puntarenas in 1927 (deposited by M. Valerio in the National Museum of Natural History: USMN 61749), and by personal communication of Villalobos in Laguna (1985). Additional material from this locality was deposited in the Museum of Zoology, Universidad de Costa Rica (MZUCR 160-001) by E. Solís in 1965. Bernard (1988) mentions that in Costa Rica, *P. elegans* supported a small-localized fishery, but he did not mention any other information. Marchant *et al*. (2015) presented a map with mention of a population in Nicoya peninsula, and indicated an absence in the South Pacific of Costa Rica. However, a specimen of Caña Agria, Punta Burica, South Pacific of Costa Rica was collected in January of 2008 by J. Sibaja and deposited in the Museum of Zoology, Universidad de Costa Rica (MZUCR 3442-01) (Fig. 1). Other than the above reports, no other scientific records of this species or its biology are available for Costa Rica. The objectives of the this study are to report the occurrence of a population of the gooseneck barnacle *P. elegans* on the Central Pacific of Costa Rica, and describe aspects of its demography, size structure, and habitat features.

<<Fig. 1 near here>>

MATERIALS AND METHODS

All the gooseneck barnacle patches found were sampled and photographed at an intertidal rocky shore on Jaco beach, in the Central Pacific of Costa Rica (09°37'19N, 84°38'37W), on July 31 and October 11 of 2014, and on September 6 of 2016. The clumps were located directly on the east side of the rocky shore near the mouth of an estuarine system (Quebrada Bonita and Quebrada Doña María). In the laboratory, specimens were identified using the drawings from Newman (1987) and Barnes (1996), the key in Laguna (1985) and the original description of Lesson (1831). The specimens were deposited in the Museum of Zoology, Universidad de Costa Rica.

The clumps of gooseneck barnacles were observed from the west to east side of the rocky shore. The density (ind/m^2) was estimated in October by systematic adaptive cluster sampling (with quadrants of 25cm x 25cm placed at 10 m intervals on a shoreline of 110m) (Krebs 1999). For each clump (clump: group of individuals close to one another but apart from other groups), the upper and lower vertical limits were measured using the distance and inclination of the beach during low tide. These limits were corrected by the tidal level at Lowest Astronomical Tide (LAT) (0 cm). The inclination of the rocky walls was measured with a clinometer on the right-hand side (RHS) and left-hand side (LHS) of each clump to determine the vertical angle of preference by this population. The horizontal angle in the rock with clumps was also measured. In all sampling dates, digital pictures of each clump were taken with a scale and included height, width, area and number of individuals. Each clump was measured using UTHSCSA Imagetool 3.0 software.

A random sample of 35 individuals was taken between and within the clumps in October 2014. Another 40 individuals were sampled in September 2016. On these individuals a Vernier caliper was used to measure the total individual length (from the base of peduncle to the apex of the tergum), the diameter of the peduncle, and length and width of the capitulum.

Data analysis.

All statistical analyses were carried out using PAST software (Hammer et al. 2001).

Density, inclination and vertical limits

The density was calculated by using adaptive cluster sampling as in Krebs (1999). The upper and lower limits of the clumps were estimated and the degree of inclination of the rock in LHS and RHS of the clumps were compared with a paired t test. The mean degree of inclination in the rock was determined by circular statistic using the Watson's goodness-of-fit test for von Mises distribution (U2)(Hammer et al. 2001, Zar 1999). A Spearman rank correlation was used to determinate the influence of the slope of the beach in the upper and lower limits of vertical distribution of the clumps.

Morphometry

A mixture analysis for each morphological characteristic (Fig. 2) was carried out to determine the number of groups of individuals with a normal distribution. The isometric growth was tested with a Reduced Major Axis (RMA) of log-log data for the length of the peduncle with the width (Rostro-Carina) or length of the capitulum. A value of the slope (a) equal to 1 indicates isometric growth, while a value greater than 1 indicates allometric growth (Krebs 1999, Hammer et al. 2001).

<<Fig. 2 near here>>

Temporal variation

For temporal variation of the clumps in the rocky shore, paired tests were carried out to compare the mean value of coverage area and the number of individual per clump between July and October 2014. The mean values of these variables, height and width of clumps present in the rock were compared with data taken on September 2016 by ANOVA.

RESULTS

Density, vertical limits, and rock inclination

The mean density was 40 ind/m^2. However, the patches ranged between 2 to 240 individuals. The intertidal zone ("fringe") occupied by this species was 4.5 cm wide, and *P. elegans* had a mean upper limit of vertical distribution of 1.74 m ± 0.29 m above the LAT, and a lower limit of 1.69 m ± 0.28 m, with a range from 0.85 to 3.00 m. An increase in the height above the low tidal level was found from west to east of the rocky shore (Fig. 3).

<<Fig. 3 near here>>

The inclination of the sandy beach below the rocky shore also increased (from 5 to 7°) in the same direction except in the region of clumps 23 and 24 with 4° (Fig. 3). A positive correlation was found between height of clumps and beach slope (rs=0.38, d.f.=23, p<0.01). A higher correlation was found when clumps 23 and 24 were taken as outliers (rs=0.82, d.f.=21, p<0.001). The vertical orientation in which clumps were located on the rocks did not follow a random pattern (Circular statistic: U^2_{RHS}=0.26, p<0.005; U^2_{LHS}=0.28, p<0.005). The mean inclination was -59.4º at RHS and -43.2º at LHS of the clumps, but these values were not statistically different (t: -1.19, d.f.=21, p=0.247). Around 75% of the clumps were found at -33º to -89º inclination along the rock wall (Fig. 4A-C). Few individuals were found on rock having a positive inclination (Fig. 4A-C). Clumps tended to be in corners having a horizontal aperture with a mean angle of 99º as well as avoiding flat exposed rock surfaces and narrow crevices (Circular statistic: U^2: 2.92, p<0.005, Fig. 4D).

<<Fig. 4 near here>>

Morphometry

In October of 2014 the length measures of morphological characters showed one normally distributed group (Table 1, Fig. 5A, C, E). However the width (Rostro-Carina) of capitulum and diameter of the peduncle presented two groups of gooseneck barnacles by their size (Table 1, Fig. 5B, D). The length of capitulum showed two modal peaks at 14-17 and 23-26 mm (Fig. 5A). During September of 2016 the population of *P. elegans* showed three cohorts according to the width (Rostro-Carina) of capitulum, diameter of the peduncle, and total length (Table 1, Fig. 6 B, D, E). The individuals with lowest values of width in capitulum and peduncle were located peripherally in the clumps and larger specimens tended to occur in the central zone of the clumps.

In the present study, a positive relationship was found between the peduncle length and capitulum size (Fig. 5F, G, 6F, G). In both cases for 2014 data the 95% confidence intervals of the slope are above 1 (length peduncle: length capitulum: 1.25 and 2.44, $p<0.006$, width capitulum: 1.25 and 2.45, $p<0.002$). This was not the same for the 2016 data (length peduncle: length capitulum: 0.604 and 2.18, $p<0.001$ width capitulum: 0.91 and 2.33, $p<0.001$) but the mean slope values were still over 1. These values of slope regression indicated that the growth of the peduncle is faster than the growth of the capitulum in this population (Fig. 5F, G, 6F, G).

<<Fig. 5 and 6 near here>>

<<Table 1 near here>>

Temporal variation The area of the clumps showed a reduction from 25.9±11 cm^2 in July to 11.0 ±6.74 cm^2 in October 2014 ($t=4.06$, $d.f.=39$, $p<0.001$). The average number of individuals was reduced from 34 ±17.02 to 10 ± 6.35 per clump between July to October 2014, respectively ($t=3.37$, $d.f.=39$, $p<0.001$). This reduction in the size of the clumps is shown in figure 7A, B for some of the clumps found in the rock. In Figure 7B the erosion of the sand bottom and decrease in algae and gooseneck barnacle cover is evident in comparison to figure 7A. The species was found in September 2016 forming new clumps in the intertidal zone (Fig. 7C). Considering the sampling done in September 2016, a similar mean was found in length and width of the clumps (Table 2). The mean coverage area and the number of individuals of the clumps were similar between dates (Table 2).

<<Fig. 7 near here>>

<<Table 2 near here>>

DISCUSSION

The specimens found in Jaco, Costa Rica, (museum catalog code: MZUCR 3382-001) presented a peduncle with small calcareous scales. The morphology of these specimens was concordant with the characteristics indicated by Lesson (1831), and Laguna (1985) for the species *P. elegans* (Fig. 1). The current report of *P. elegans* in Costa Rica represents an extension of the biogeography of the species.

Walther et al. (2013) found differences in the tolerance of larvae of *P. elegans* from different places of ETP. Larvae from Peruvian populations have a narrow optimum range in comparison with Mexican populations, while larvae from El Salvador presented resistance to a wider range of temperatures. The critical temperature for *P. elegans* was beyond the range used in the experiment (Walther et al. 2013). In this way, some populations seem to resist higher temperatures as Salvadorian and Costa Rican populations reported in this paper. Moreover, Van Syoc (1994), and Marchant et al. (2015) studied the genetic relations between populations of *P. elegans* from Mexico, El Salvador, and Peru. These studies found a relationship of populations located in El Salvador and Perú. This result as well as the report in Costa Rica indicates that the species could expand its distribution from Perú to Central American shores (Marchant et al. 2015). Especially when seasonal upwelling systems in Panama, Papagayo or Tehuantepec are relaxing (Walther et al. 2013). It will be necessary to analyze Costa Rican samples to determine their genetic relation to populations from other sites in the ETP.

Density, vertical limits and rock inclination

The mean density (40 ind/m^2) was lower than in Peruvian coast where patches consisted of between 176 a 3744 ind/m^2 (Kameya and Zeballos 1988). These authors also found this species between 1 to 4 m above the low tide level in Peru, similar to the range of vertical distribution found here. The vertical limits of sessile fauna in rocky shores tended to increase with the influence of exposure (Little and Kitching 1996), and this was the case with *P. elegans* in Jaco. This rocky shore presented a sandy beach in the lower intertidal. The slope of this sandy beach increased to the east in the direction of an estuary mouth; the height of the clumps increased in the same way. The final clumps of the transect were at >2.8 m above low tide level, within the estuarine channel where the slope was low again, but during the high tide, the waves flow in this estuarine channel create a rip-tide that increases the exposure there (Fig. 3).

Kameya and Zeballos (1988) found that clumps of *P. elegans* were common in vertical rock walls. In contrast, we found the clumps on the rock walls with a mean of 51º negative inclination. According to measures of inclinations and rock exposure where the clumps where found, the recruits can better survive to adults in the abrasion notch of the rock platform than on the exposed surface of the rock wall.

Morphometry

The bimodal distribution of sizes found in Jaco in 2014 represents two separate age classes of *P. elegans*. A new cohort with lower values of these morphological characters is apparent in the data from September of 2016, and possibly some survivors of the previous two samplings were also persistent (Fig. 6, B, D, E). The presence of juvenile and adult individuals evidences healthy reproduction, recruitment and an establishment population, as opposed to ephemeral individuals. This is similar to results of Cruz et al. (2010), who found two cohorts of *P. pollicipes* individuals in Portugal during some periods of the year, and populations from Portugal are clearly permanent.

The distribution of juveniles at edges of clumps could mean that adult individuals aggregations help larvae to recruit. Cruz et al. (1993) explains that *P. pollicipes* larvae find a tridimensional habitat next to adult conspecifics. Recruits of *P. pollicipes* occur mainly in patches with lower density of adults, because the basal area of the stalks is more accessible for settlement (Cruz et al. 2010). The same can happen with *P. elegans*, which has the same tendency of aggregation and patch expansion.

Studies in *P. polymerus* and *P. pollicipes* explain that variation in factors such as immersion time (linked to food resources), and light intensity, result in an increase of the length of gooseneck barnacles (Cruz 1993). Additionally, Marchinko and Palmer (2003) indicated that water velocity explains 92% of peduncle variation. The fast growth of the peduncle and the distribution of adults in the center of clumps can facilitate space for recruits and reduce competition between established and new cohorts.

Temporal variation

An evident reduction in the population of this species was found between July and October of 2014. One possible cause of this reduction could be the climatic conditions, which increased erosion in the rocky shore. During this time period two storm surges with wave heights between 2.2 to 2.4m and peak wave periods of 20 to 24 seconds reached the Central Pacific Coast (Omar Lizano, pers. Com., http://www.miocimar.ucr.ac.cr). However, one of these storms occurred in the first week of July and the second storm was in the middle of September. It is possible that each storm has removed individuals from the rocky littoral as it was observed during this study between sampling events.

This species is uncommon in the Pacific coast of Costa Rica and it is not a traditional food source as in Perú and Portugal (Laguna 1985, Cruz et al. 1993). Although, other invertebrates such as mollusks are a focus of extraction in rocky shores of Costa Rica; e.g. the pulmonate limpet *Siphonaria gigas* G. B. Sowerby I, 1825 and the neritid *Nerita scabricosta* Lamarck, 1822 (Ortega 1987), which implies regular harvesting of invertebrates in the littoral. The locality of Jaco beach is an important tourist hotspot with high human infrastructure. Because of this, human harvesting is a possible factor explaining the reduction of the population.

According to Crickenberge et al. (2015) larval populations of *P. elegans* from Mexico tolerate warm temperatures better than populations found in Peru. The abundance of this species in Peru was low during El Niño 1982-1983 due to factors such as high temperature, increase in sea level, and oxygen in the water (Van Syoc 1994). The decline found in the population of Jaco could be due in part to low tolerance of adults and recruits to high sea surface temperature (SST). Van Syoc (1994) points out that SST in Costa Rica and Panama can reach >28°C during El Niño. We recorded values of 32 and 34ºC in July and October of 2014 in Punta Morales, a locality about 60 km north of Jaco. Data for anomalies in SST of the region oscillated between 0.45-0.86°C from May to October indicating El Niño conditions (http://www.cpc.ncep.noaa.gov/data/indices/), possibly with deleterious effects on larvae or recruits. The structures of the remnant or new clumps did not change drastically over two years (2014 to 2016). Remnant clumps can repopulate the intertidal as has been reported for other barnacles such as *Tetraclita* in Costa Rica (Villalobos 1980, Sutherland 1987).

Conclusions

Pollicipes elegans in Costa Rica inhabit rocks with negative vertical inclination (abrasion notches along rocky shores). The population in the locality studied may have been influenced by wave exposure, storm surges, El Niño events, or by human harvesting. The presence of separate size classes and the persistence of the population between years indicates that this is an established and reproductive population.

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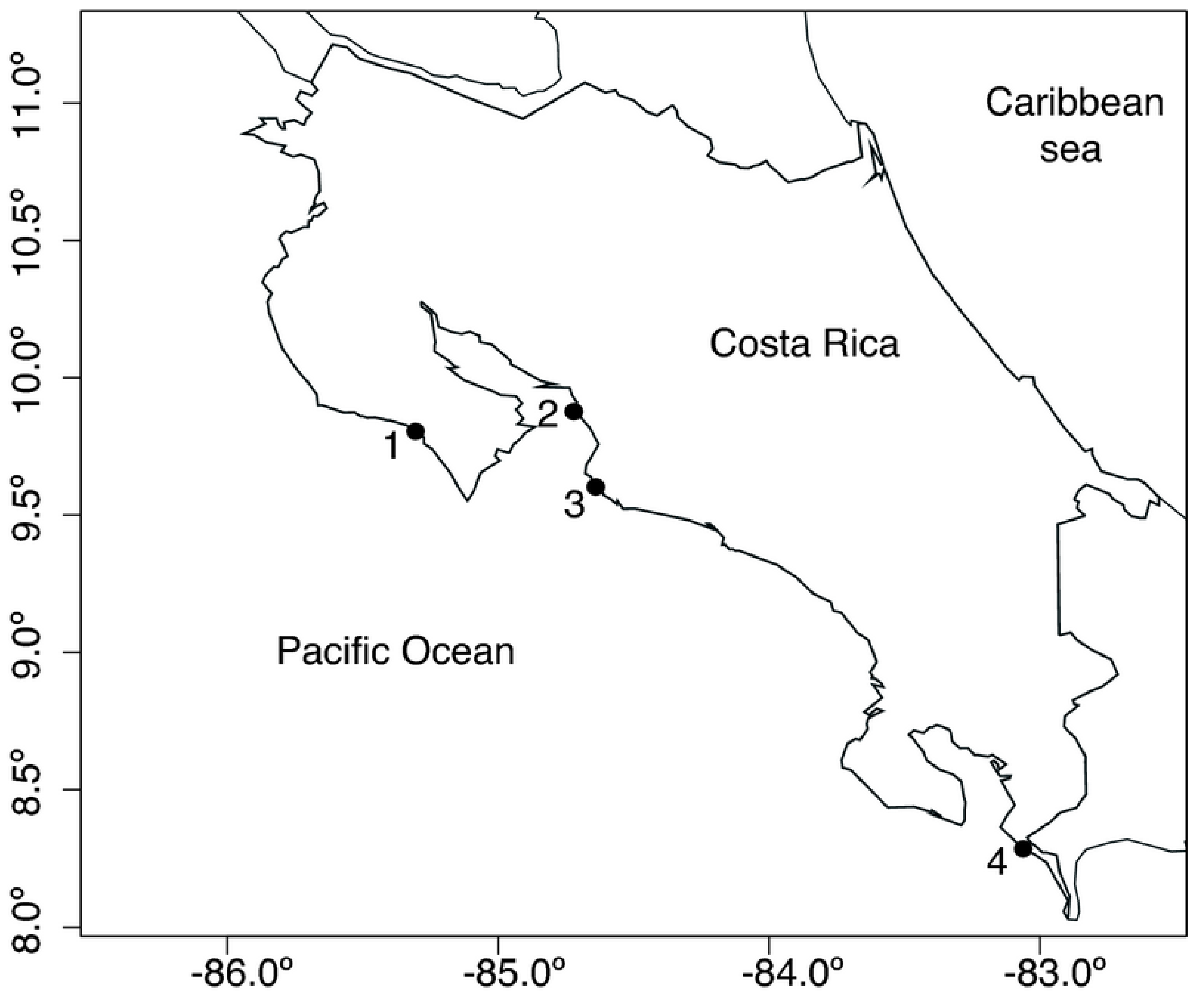


Caribbean
sea
Costa Rica
Pacific Ocean
1
2
3
4
11.0º
10.5º
10.0º
9.5º
9.0º
8.5º
8.0º
-86.0º
-85.0º
-84.0º
-83.0º

Fig. 1 Map of Costa Rica showing distribution of *Pollicipes elegans*. 1: Nicoya (Marchant et al. 2015). 2: Tivives (USMN 61749, MZUCR 160-001, and Laguna 1985). 3: Jaco (Present study), 4: Punta Burica (MZUCR 3442-01).

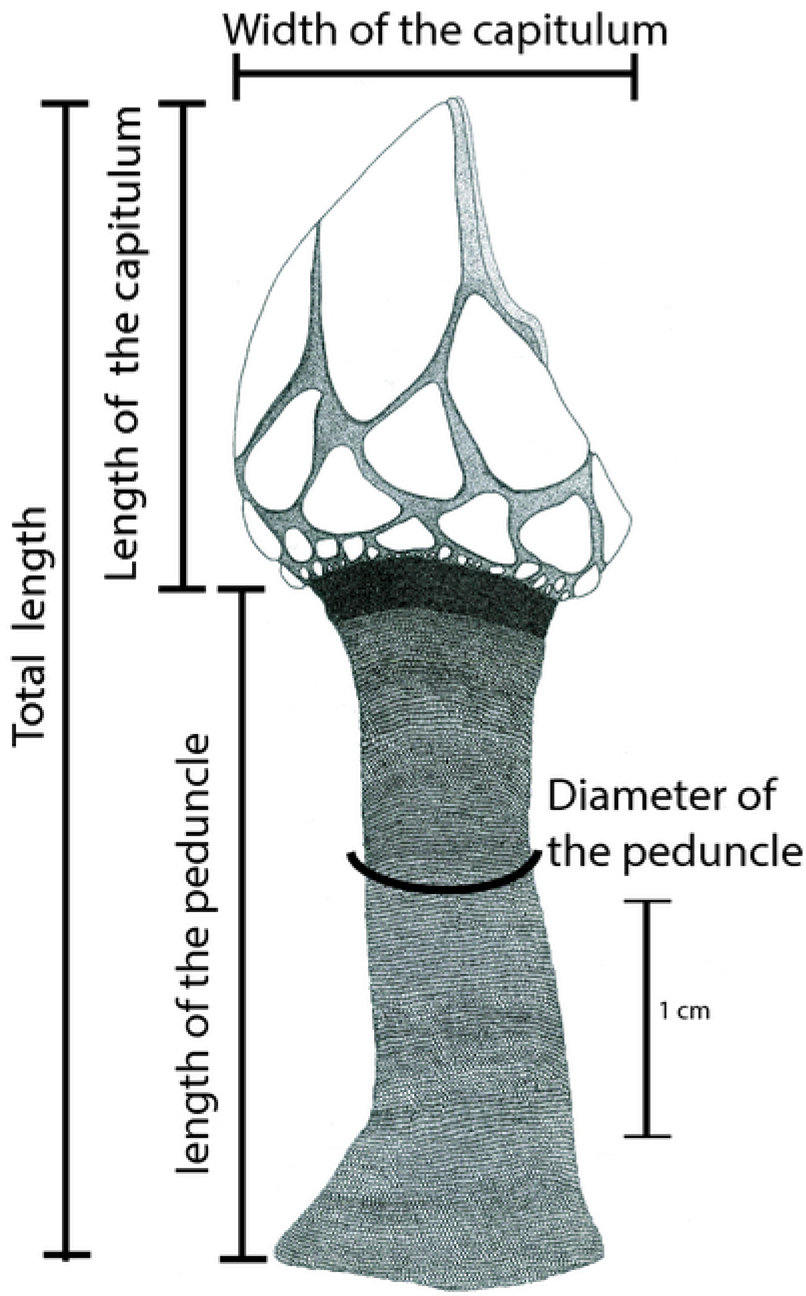
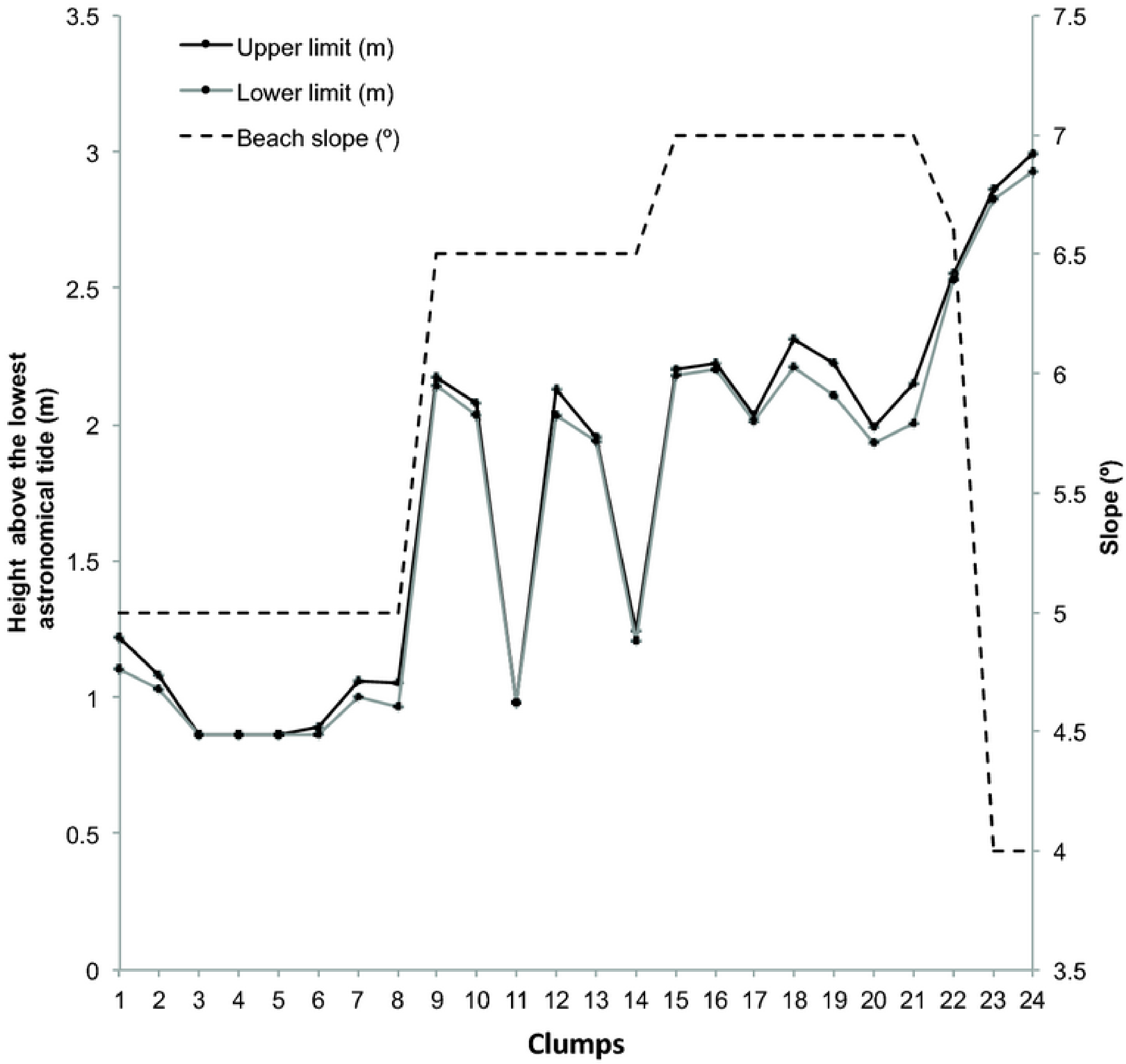


Figure 2. Morphological measures of *Pollicipes elegans* Lesson, 1831. Draw by J.D. Barquero-Bolaños



Upper limit (m)
Lower limit (m)
Beach slope (º)
Height above the lowest astronomical tide (m)
Slope (º)
Clumps
3.5
3
2.5
2
1.5
1
0.5
0
7.5
7
6.5
6
5.5
5
4.5
4
3.5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24

Figure 3. Vertical limits of *Pollicipes elegans* and beach slope in a rocky shore of Jaco beach, Costa Rica, October 2014. The clumps number 1 to 24 indicated the west-east orientation in the shore.

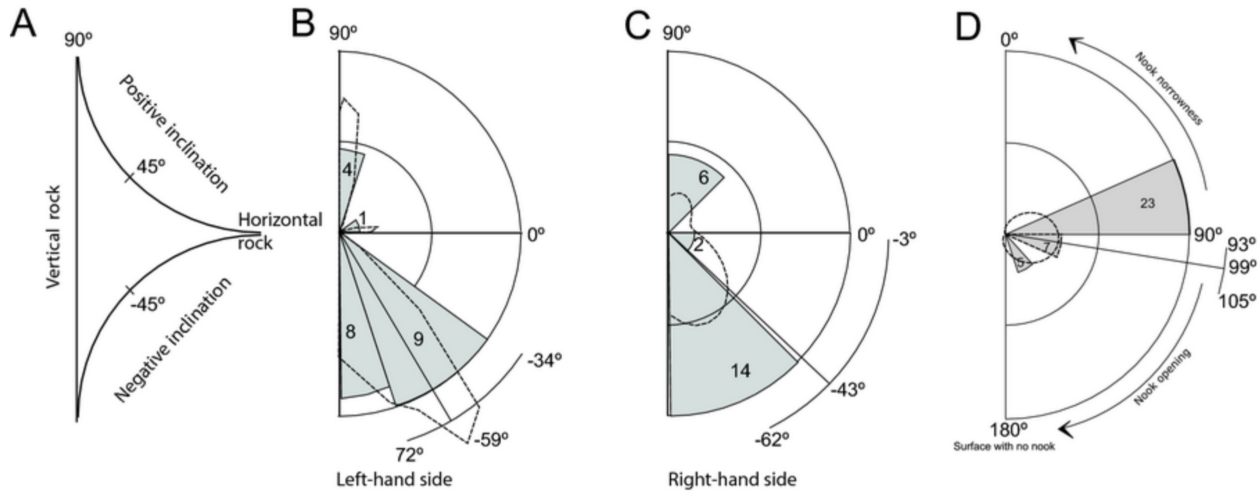
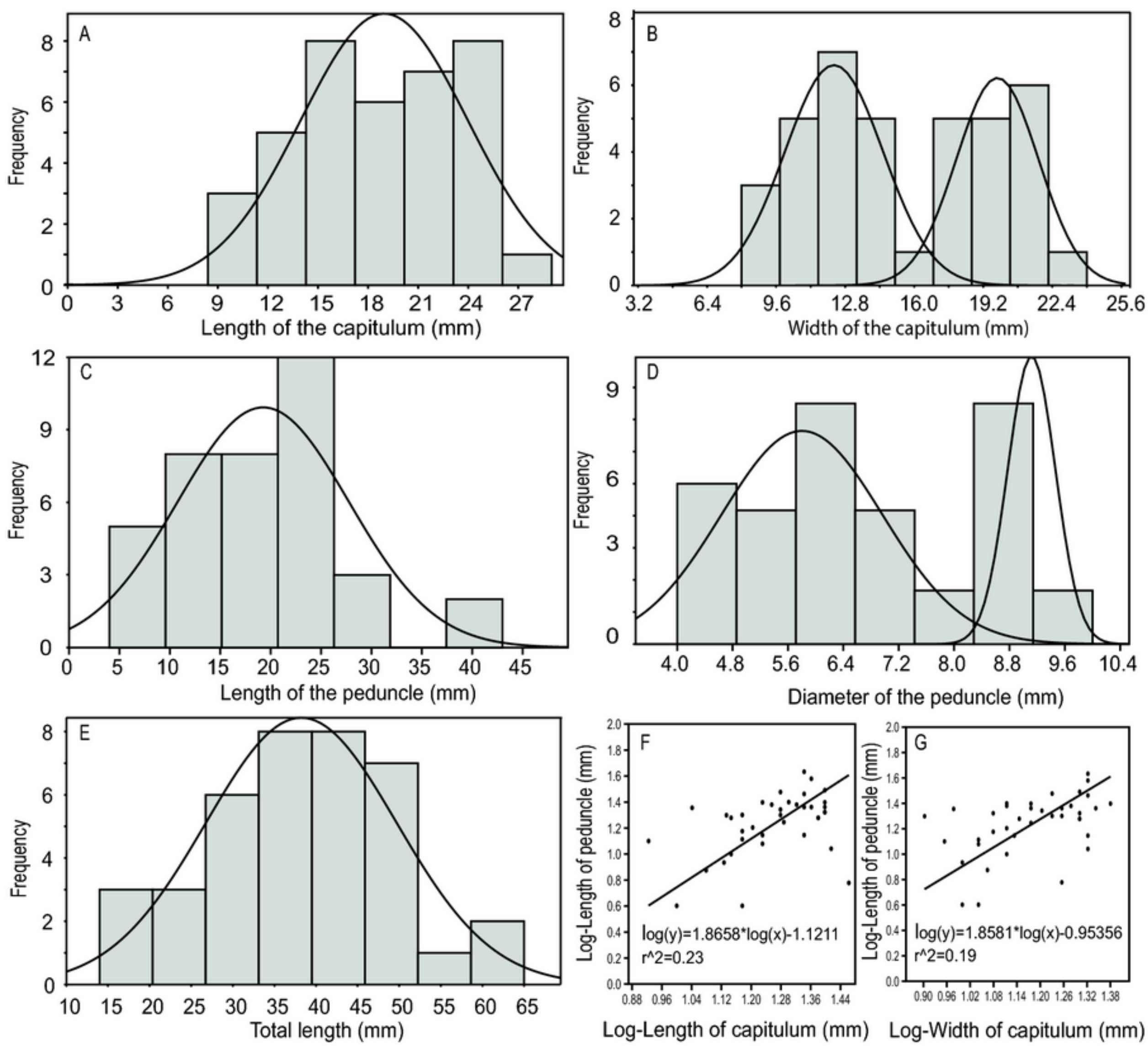


Figure 4. Angle of inclination in the rock wall with patches of *Pollicipes elegans* in Jaco, Costa Rica. October 2014. A) Profile of rock inclination of a rocky shore. Distribution of clumps by B) Vertical angle at left-hand side of the clump, C) Vertical angle at right-hand side of the clump, and D) Horizontal angle of the rock with clumps present. Mean inclination and their bootstrapped 95% limits are presented. Gray zones represent number of clumps and dashed line is the Kernell density.



A
Frequency
Length of the capitulum (mm)
B
Width of the capitulum (mm)
C
Length of the peduncle (mm)
D
Diameter of the peduncle (mm)
E
Total length (mm)
F
Log-Length of peduncle (mm)
log(y)=1.8658*log(x)-1.1211
r^2=0.23
Log-Length of capitulum (mm)
G
log(y)=1.8581*log(x)-0.95356
r^2=0.19
Log-Width of capitulum (mm)

Figure 5. Mixture analysis (A-E) and Reduced Major Axis regression (F-G) of the morphological characteristics of *Pollicipes elegans* of Jaco, Costa Rica. October 2014. A) length and B) Width of the capitulum; C) Length and D) Diameter of the peduncle; E) total length; F) linear regression of length of peduncle with length of capitulum, G) linear regression of length of peduncle-width of capitulum.

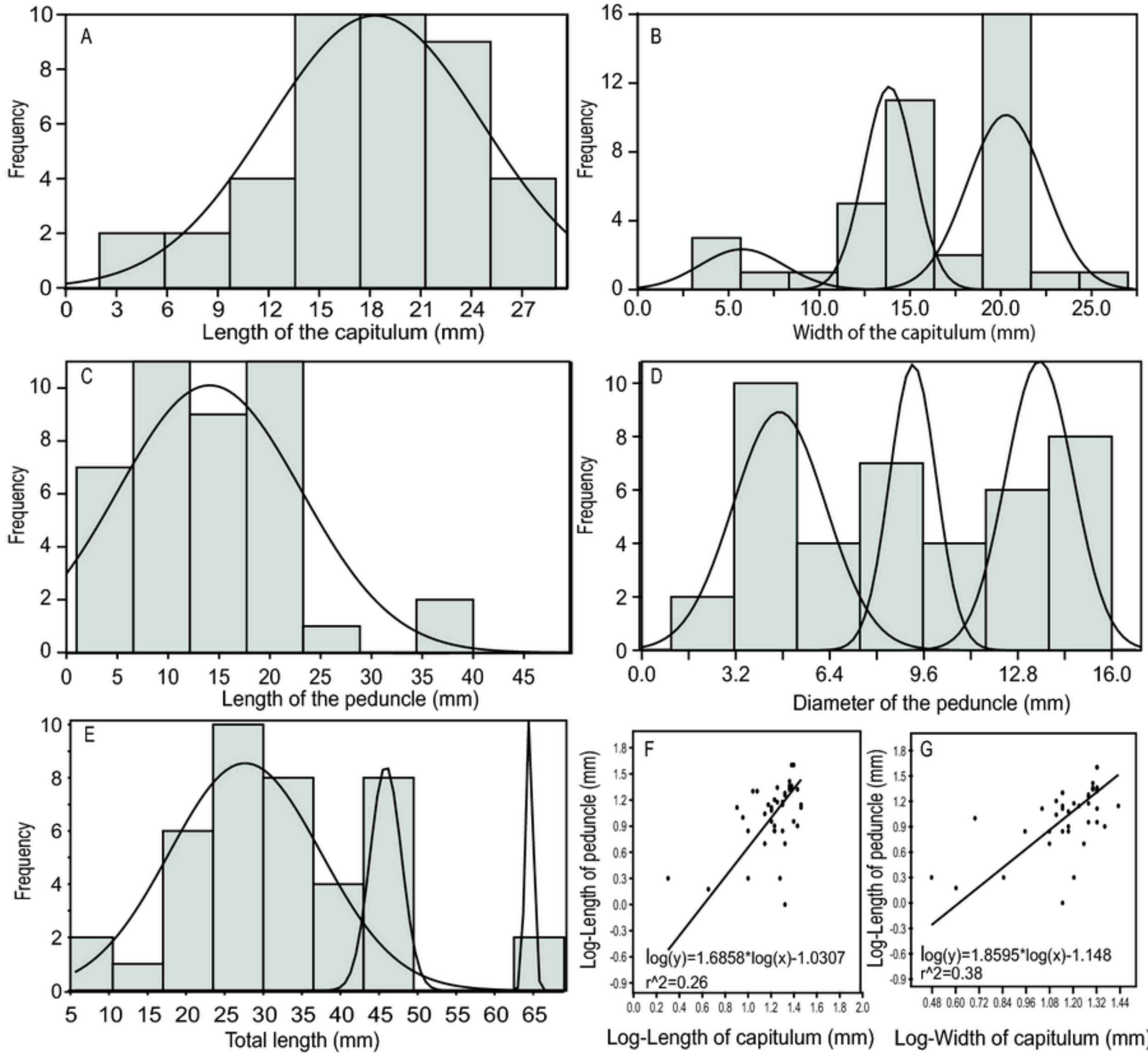

A
Frequency
Length of the capitulum (mm)
B
Frequency
Width of the capitulum (mm)
C
Frequency
Length of the peduncle (mm)
D
Frequency
Diameter of the peduncle (mm)
E
Frequency
Total length (mm)
F
Log-Length of peduncle (mm)
log(y)=1.6858*log(x)-1.0307
r^2=0.26
Log-Length of capitulum (mm)
G
Log-Length of peduncle (mm)
log(y)=1.8595*log(x)-1.148
r^2=0.38
Log-Width of capitulum (mm)

Figure 6. Mixture analysis (A-E) and Reduced Major Axis regression (F-G) of the morphological characteristics of *Pollicipes elegans* of Jaco, Costa Rica. September 2016. A) length and B) Width of the capitulum; C) Length and D) Diameter of the peduncle; E) total length; F) linear regression of length of peduncle with length of capitulum, G) linear regression of length of peduncle-width of capitulum.

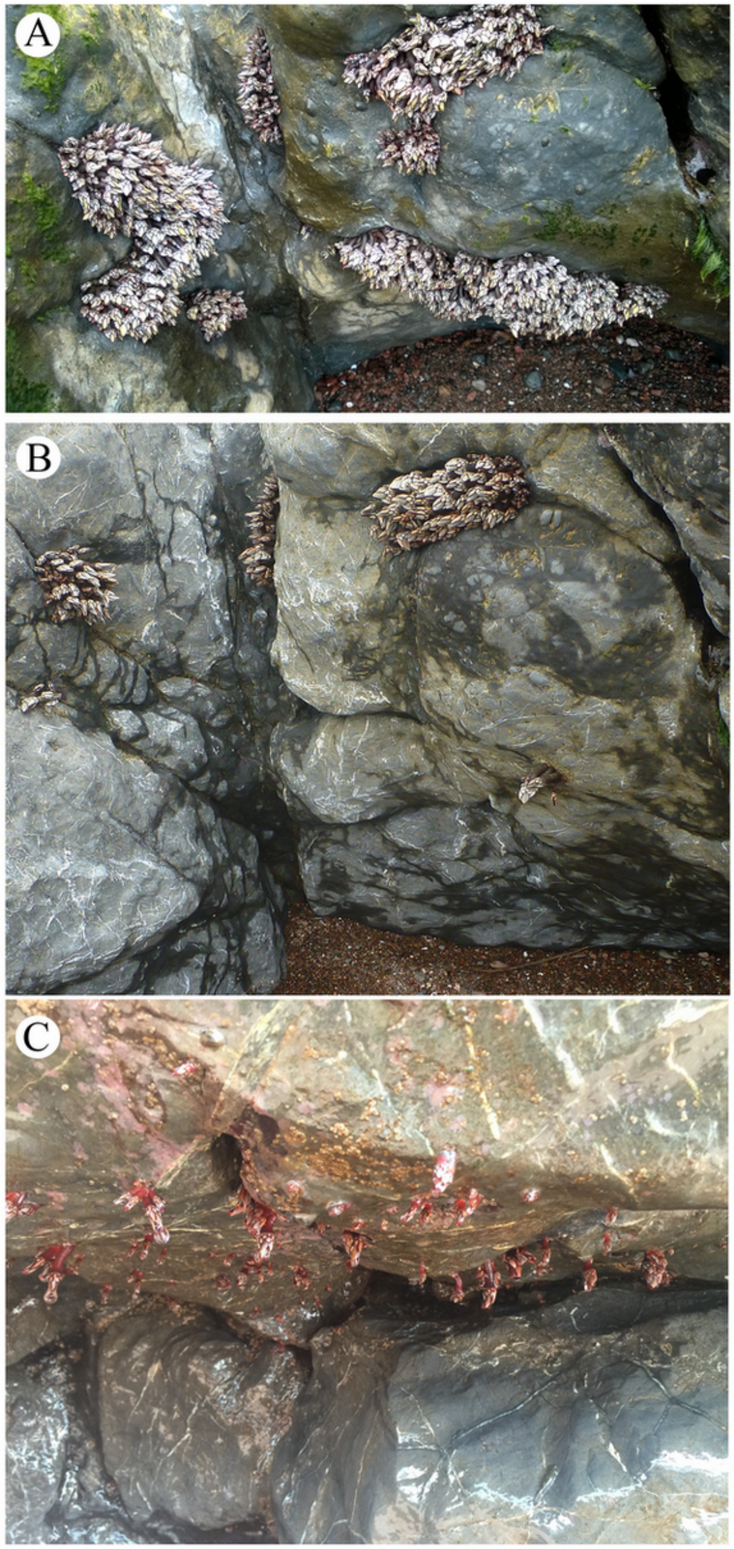

A
B
C

Figure 7. Some clumps of the gooseneck barnacle *Pollicipes elegans*. A) June 2014, B) October 2014, both in the same rocky intertidal section, C) August 2016, new clumps in the rocky intertital of Jaco, Costa Rica.

Table 1. Mixture analysis to determine the mean, standard deviation (sd) and probability of each group of individuals of *Pollipes elegans* from Jaco, Costa Rica, October 2014 and September 2016; that follow a normal distribution within each morphological variant. The model fitness was measured by Log Iikelihood value and Akaike Information Criterion (AIC).

October 2014	Group (Cohort)	p	Mean	sd	LogIikelihood	AIC
Total length (mm)	I	1.000	38.20	11.45	-111.70	227.60
Length of the capitulum (mm)	I	1.000	18.97	5.01	-80.26	164.90
Length of the peduncle (mm)	I	1.000	19.26	8.50	-100.30	205.00
Width of the capitulum (mm)	I	0.559	12.28	2.28	-69.76	148.70
	II	0.441	19.86	1.91		
Diameter of the peduncle (mm)	I	0.714	5.80	1.16	-32.90	75.02
	II	0.286	9.12	0.35		
September 2016						
Total length (mm)	I	0.790	27.65	9.82	-118.50	251.60
	II	0.049	64.50	0.50		
	III	0.161	45.88	2.03		
Length of the capitulum (mm)	I	1.000	18.31	6.33	-96.18	196.70
Length of the peduncle (mm)	I	1.000	14.09	9.02	-110.70	225.70
Width of the capitulum (mm)	I	0.374	13.85	1.38	-81.83	178.10
	II	0.502	20.30	2.15		
	III	0.125	5.74	2.32		

Diameter of the peduncle (mm)	I	0.236	9.26	0.79	-71.04	156.05
	II	0.434	4.55	1.78		
	III	0.330	13.58	1.18		

Table 2. Structure features of clumps of *Pollicipes elegans* between 2014 and 2016 in Jaco, Costa Rica. x̄= mean, U = upper confident limit, L= lower confident limit, F=Fisher value of one way ANOVA, p=probability of the same mean.

Clump feature/ Date	Length (cm)			Width (cm)			Area (cm^2)			Individuals per clump		
	x̄	L	U	x̄	L	U	x̄	L	U	x̄	L	U
July 2014	5.36	4.17	6.56	5.46	3.78	7.15	25.86	14.5	37.23	34.15	16.57	51.74
October 2014	5.16	3.54	6.76	5.06	3.17	6.69	22.67	9.97	35.36	20.58	8.43	32.73
September 2016	6.76	3.56	9.96	7.72	1.84	13.61	43.72	10.42	77.02	35.44	9.04	61.85
F*	0.55			0.80			1.35			0.60		
p	0.58			0.45			0.26			0.55		

*Degrees of freedom=2,72