

RESEARCH NOTE

# Population structure of *Megabalanus peninsularis* in Malpelo Island, Colombia

Estructura poblacional de *Megabalanus peninsularis* en la isla Malpelo, Colombia

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**Abstract.** - *Megabalanus peninsularis* is a key species in the rocky shore, particularly in Malpelo Island in the Eastern Tropical Pacific (ETP) where it dominates the mesolittoral zone and the infralittoral fringe. The size structure of *M. peninsularis* was determined to infer the population state (pyramid model) by measuring the basal diameter of individuals (n= 837) around the oceanic island. The species population distribution followed a bimodal pattern (class I-II and VII). The pyramid expansive model, with a relatively higher number of juveniles than adults suggests that the population is growing.

**Key words:** Population structure, rocky shore, *Megabalanus peninsularis*, Malpelo, pyramid model

## INTRODUCTION

Barnacles are cosmopolitan organisms that dominate rocky shores around the world, colonizing from the supralittoral to the infralittoral depending on the species and environmental conditions (Chan 2006). These crustaceans can modify the littoral community assemblage due to their particular biological characteristics like rapid growth, high fertility, and high tolerance to extreme weather conditions, which allow them to better compete for space (Penchaszadeh *et al.* 2003, Chan 2006, Tapia & Navarrete 2010).

The life cycle of barnacles comprises a pelagic larval stage and a sessile stage; first as a juvenile and then as an adult when it becomes reproductive (Chan 2006). The duration of the life cycle is highly variable (Muko *et al.* 2001) with reports suggesting 3.75 years on average (Jeffery & Underwood 2001, Chan & Williams 2004, Golléty *et al.* 2008) and up to 7 years (Calcagno *et al.* 1998) for *Balanus amphitre*.

The growth rate and sexual maturity of barnacles (tm) vary according to local environmental conditions (Zvyagintsev & Korn 2003, Heather *et al.* 2005, Chan 2006). Chan & Williams (2004) studied barnacle growth after settlement; *Tetraclita squamosa* grew differently in Middle Bay and Heng Fa Chuen Bay, between 0.8 to 1.16 mm month<sup>-1</sup>, respectively. Similar results were found for *Tetraclita japonica* from 1.0 to 1.4 mm month<sup>-1</sup>. Sexual maturity also changed, individuals of *Capitulum mitella* in Hong Kong reached sexual maturity at 9-12 months, and 2 years in China (Lin 1993). The average size of *B. amphitrite* recruits varied between 3.9 mm (Zvyagintsev & Korn 2003) to 4.8 mm in different locations (El-Komi & Kajihara 1990).

Population structure studies involve measuring a number of individuals and assigning them to a particular size class (frequency), employing a previously defined and ranked independent variable (Akcakaya *et al.* 1999). Three types of population models are proposed in the literature (also called pyramid models), based on the nature of the size class distribution: (i) growing or in expansion, characterized by a high proportion of juveniles compared to other classes (positive skewness), (ii) stable, with a high proportion of adults but a significant relative percentage of juveniles (normal distribution), (iii) regressive, in which adults dominate and the recruitment of new individuals to the population is limited or low (negative skewness; Bühler & Schimid 2001, Hengland *et al.* 2001).

The population structure allows us to infer the population condition (state) and predict population growth (Akcakaya *et al.* 1999). It also serves as a baseline, in monitoring programs, to compare how local changes in climate or oceanographic conditions (new potential habitats) and human impact (*e.g.*, pollutants) affect the reproductive/recruitment success and the viability of the species (Bak & Meesters 1999, Díaz *et al.* 2000, Gori *et al.* 2011). The population structure analysis helps determine the viability of the population through time (Bühler & Schimid 2001, Hengland *et al.* 2001, Rockwood 2006).

According to Gilmore (2004) and Macpherson & Scrosati (2008), the population structure of a particular species is specific to the area studied (location and depth) at the moment that it is measured. For key species (ecosystem functioning), the population size structure and the pyramid model have been used

as cost-effective indicators of population health (Minchinton & Scheibling 1991, Kipson *et al.* 2014). This data will enable the implementation of adaptive management strategies to safeguard local populations; this is one of the objectives of conservation (Babcock *et al.* 2010, Linares *et al.* 2012, Santangelo *et al.* 2012).

*Megabalanus peninsularis* is the dominant cirriped of the rocky shore in Malpelo Island (Mayor *et al.* 2007, García *et al.* 2012), a Fauna & Flora Sanctuary -UNESCO located in the Eastern Tropical Pacific-ETP. This species has been reported in the ETP from Cabo San Lucas, Mexico to the Galapagos Islands in Ecuador (Gómez 2003, Witman & Smith 2003, Lozano-Cortés & Londoño-Cruz 2013). Research on the rocky shore ecosystem is limited in the Colombian Pacific as well as in Malpelo Island; most studies are taxonomic registers (García *et al.* 2012) with no ecological data. For this area of Colombia, only 6 studies related to coastal species taxonomy have been published; none of them related to population structure (Venail 2002, Zapata & Vargas-Angel 2003, Rodríguez-Rubio & Giraldo 2011, Sánchez *et al.* 2011, Velasco *et al.* 2011, Zapata *et al.* 2011, Lozano-Cortés & Londoño-Cruz 2013). Policy makers and managers have recognized the need for baseline studies on rocky shore organisms to know their abundance, spatial distribution, population structure, size, and status of key ecological species (INVEMAR 2009, 2010) to enable the design of management efforts in the rocky shore ecosystem. The previous information highlights the importance of this study; the first on barnacles in Malpelo Island. Our approach relies on the barnacles' benthic stage as there are limited techniques to follow and quantify gametes, embryos, and the variety of larval stages (Akcakaya *et al.* 1999, MacPherson & Scrosati 2008). Our main objective was to characterize the population size structure of the dominant species, *M. peninsularis*, to infer its state around the island (4.0 km perimeter; INVEMAR 2015).

## MATERIALS AND METHODS

Malpelo is located at 4°00'08"N and 81°36'3"W, in the central region of the Colombian Pacific Basin. The island and its islets are part of the Malpelo Wildlife Sanctuary (Mayor *et al.* 2007) and the marine conservation corridor of the Eastern Tropical Pacific (CMAR; Rodríguez-Rubio & Giraldo 2011) that extends 6.5 km<sup>2</sup> (Mayor *et al.* 2007). The island is volcanic, composed of rugged basalt rocks (Caita & Guerrero 2000)<sup>1</sup>; its perimeter is entirely rocky coastline, predominantly upper slopes averaging 40 degrees (Brando *et al.* 1992, López-Victoria & Estela 2007, Mayor *et al.* 2007).

Here, the North Equatorial Counter Current (NECC), which drags warm waters of the Indo-Pacific converges with the Panama Cyclonic Current (PCC) coming from the north, the north-south Colombia Current (COLC) (passing by Gorgona Island, a continental island of Colombia), the Humboldt Current (HC) and the South Equatorial Current (SEC; Brando *et al.* 1992, Bessudo *et al.* 2005; Fig. 1). This convergence of oceanic and coastal currents make the fauna in Malpelo compelling from an ecological (stepping-stone island between central and eastern Pacific, for pelagic larval dispersal; Corredor-Acosta *et al.* 2011) and evolutionary (endemic species) standpoint.

Sea surface temperatures vary between 23 and 28°C (Rodríguez *et al.* 2007). Storms in the area produce waves that exceed 5.0 m in height. These strong waves impact the littoral most of the year with enough energy to erode the rock and remove sessile organisms, and affect the succession cycle in the rocky shore. Tides in Malpelo are semi-diurnal, varying between 0.6 and 5.0 m (Bessudo *et al.* 2005). The datum for the rocky shore has never been calculated in the study area. Waves and tides create a wide supra and the mesolittoral zones around Malpelo Island.

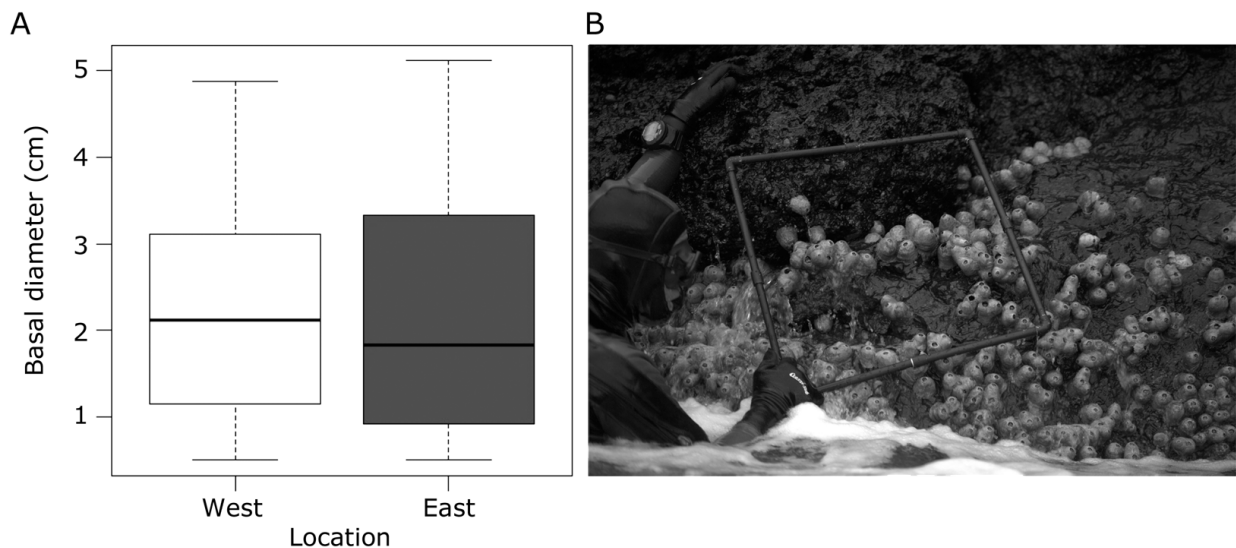
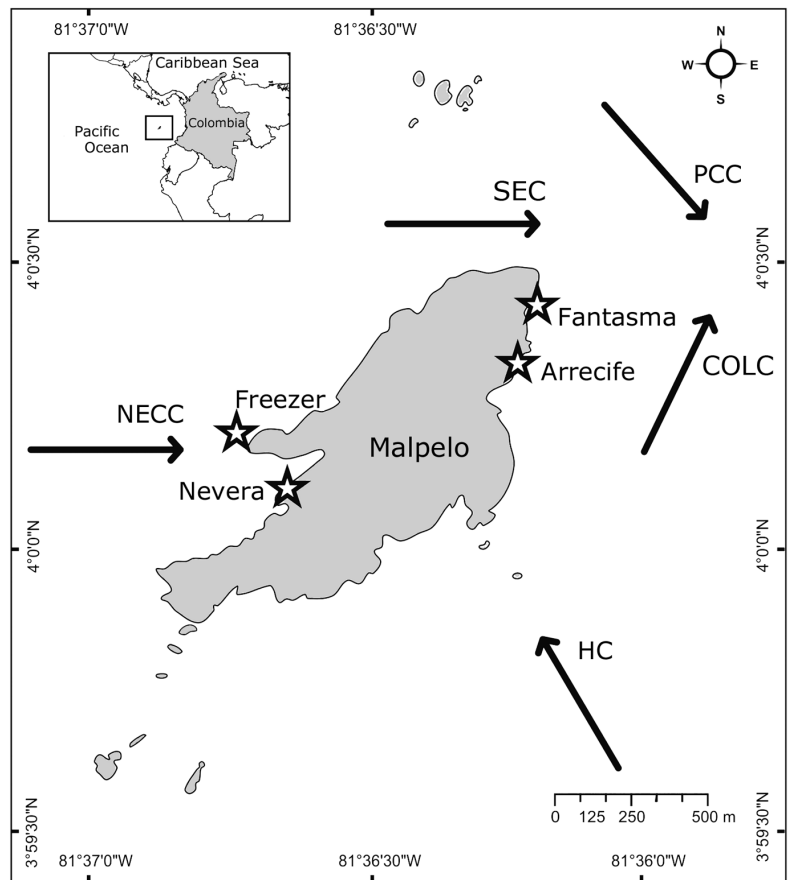
The East and West sides of Malpelo are exposed to leeward or windward conditions depending on seasonality (dry, wet, and wind pattern). In February 2011, 4 zones of the island were sampled, 2 on the East side (Arrecife and Fantasma) and 2 on the West side (Freezer and Nevera; Fig. 1). These sites were selected because, in a preliminary sampling they showed the greatest density and coverage of *M. peninsularis* in the island.

Using a grid situated randomly on the rocky shore 84, 93, 40 and 68 plots of 50 x 50 cm (Fig. 2) were situated in Arrecife, Fantasma, Nevera, and Freezer, respectively. The unequal number of plots between locations reflects the relative density of *M. peninsularis* at each site. All individuals within the plots were sampled: 171 in Arrecife, 288 in Fantasma, 169 in Freezer, and 209 in Nevera. We used a Kruskal-Wallis non-parametric test for two independent samples to determine if there were differences in the diameter of the individuals sampled (population structure) in the West and the East, also to compare each class size between sites. The basal diameter of 837 individuals was measured using a gauge with a precision of  $\pm 0.05$  mm. The species were identified using taxonomy keys (Henry & McLaughlin 1986, Gómez 2003) and consulting a specialist, Dr. Romanus Prabowo<sup>2</sup>.

<sup>1</sup>Caita C & R Guerrero 2000. Geología de la Isla Malpelo. Trabajo de pregrado, Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá, 127 pp.

<sup>2</sup>Dr. Romanus Prabowo. Universitas Jenderal Soedirman. Purwokerto. Indonesia.

**Figure 1. Sampling sites (East: Arrecife, Fantasma, West: Nevera, Freezer) around Malpelo Island and main ocean currents direction that affect the island; North Equatorial Counter Current (NECC), South Equatorial Current (SEC), Humboldt Current (HC) Panama Cyclonic Current (PCC) and Colombia Current (COLC). Figure modified from Mateo López / Sitios de muestreo (East: Arrecife, Fantasma, West: Nevera, Freezer) alrededor de la isla de Malpelo y la dirección de las principales corrientes oceánicas y el efecto en la isla; Contracorriente Ecuatorial del Norte (NECC), Corriente Ecuatorial del Sur (SEC), Corriente de Humboldt (HC) Corriente Ciclónica de Panamá (PCC) y la Corriente Colombia (COLC). Figura modificada de Mateo López**



**Figure 2. A. Comparison of basal diameters between East and West, non-statistical differences were found; B. Sampling method, plots of 50 x 50 cm. The lower box boundary, midline and upper box boundary, correspond to the 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup>, percentiles respectively / A. Comparación de diámetros basales entre Este y Oeste, no se encontraron diferencias significativas; B. Método de muestreo, cuadrantes de 50 x 50 cm. El límite inferior, medio y superior corresponden a los percentiles 25, 50 y 75 respectivamente**

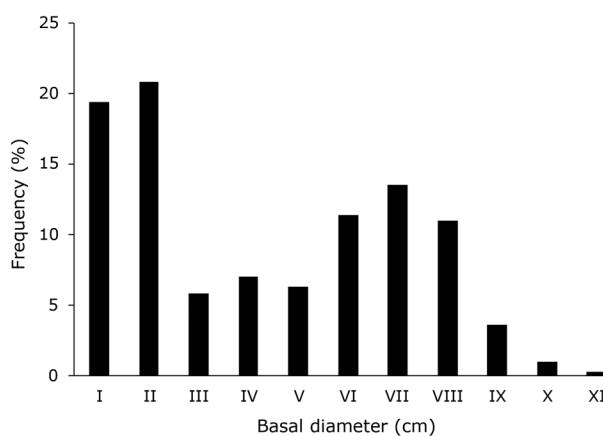
The sampling setup was not designed to compare depths (meso vs. infralittoral) or measure the population in the supralittoral zone, first, because it is not the ideal habitat for this species and, second for safety reasons. High waves (3-8 m) did not allow us to remain stationary to measure the organisms, and the steep rock slope ( $> 40^\circ$ ) also hindered our efforts (Fig. 2). The population size structure of individuals from the mesolittoral zone to the infralittoral fringe was quantified by diving mainly during high tide and in calm water.

Based on basal diameter, 11 categories of size classes were selected using the Sturges rule. Class I: basal diameter between 0.5-0.92 cm, Class II: 0.93-1.35 cm, Class III: 1.35-1.78 cm, Class IV: 1.79-2.21 cm, Class V: 2.22-2.64 cm, Class VI: 2.65-3.07 cm, Class VII: 3.08-3.5 cm, Class VIII: 3.51-3.93 cm, Class IX: 3.94-4.36 cm, Class X: 4.37-4.79 cm, and Class XI: 4.8-5.11 cm. The diameter of individuals oscillated between 0.5 (minimum) to 5.1 cm (maximum). The frequency of the individuals' basal diameters was used to create histograms of the population structure. Descriptive statistics were calculated, and the population distribution was described according to Vermeij & Bak (2000).

## RESULTS AND DISCUSSION

The densities found at each sampled site were Arrecife 50.3 ind  $m^{-2}$ , Fantasma 91.4 ind  $m^{-2}$ , Freezer 55.0 ind  $m^{-2}$ , and Nevera 64.6 ind  $m^{-2}$ . Non statistical differences were found in the diameter of the East and West individuals (Kruskal-Wallis test= 2.76,  $P= 0.096$ ,  $n_{west} = 378$  individuals,  $n_{east} = 459$ , Fig. 2); this allowed us to pool the data to infer about the whole population. Additionally, no statistical differences were observed when we compared each size class between West and East (Kruskal-Wallis test,  $P > 0.05$ ).

The overall size structure of *M. peninsularis* was bimodal with a mode in class I and II (0.5-0.92, 0.93-1.35 cm) and class VII (3.08-3.5 cm; Fig. 3). Our results are consistent with the bimodal distributions of *Tetraclita squamosa* found in Hong Kong, *Chamaesipho tasmanica* reported in New South Wales, and *Pollicipes polymerus* in California (Jeffery & Underwood 2001, Chan & Williams 2004). The bimodal distribution of sizes frequencies in the studied population suggested reproductive-spawning pulses (Minchinton & Scheinling 1991, Zvyagintev & Korn 2003) and successful recruitment (Minchinton & Scheibling 1991, Menge 2000, Jeffery & Underwood 2001, Chan & Williams 2004). The new recruits can be produced by adults within the same local population (self-seeding), or can arrive from distant source populations via dispersal (Zvyagintev & Korn 2003, Chan & Williams 2004, Miller 2013).



**Figure 3.** Frequency distributions of basal diameter of *M. peninsularis* (cm). N= 837. Intervals of basal diameter: I= 0.5-0.92, II= 0.93-1.35, III= 1.36-1.78, IV= 1.79-2.21, V= 2.22-2.64, VI= 2.65-3.07, VII= 3.08-3.5, VIII= 3.51-3.93, IX= 3.94-4.36, X= 4.37-4.79, XI= 4.8-5.11 / Distribución de frecuencias del diámetro basal de *M. peninsularis* (cm). N= 837. Intervalos de diámetros basales: I= 0,5-0,92, II= 0,93-1,35, III= 1,36-1,78, IV= 1,79-2,21, V= 2,22-2,64, VI= 2,65-3,07, VII= 3,08-3,5, VIII= 3,51-3,93, IX= 3,94-4,36, X= 4,37-4,79, XI= 4,8-5,11

The relatively low frequency of the classes III-V could reflect low recruitment in the past or high mortality rates among these classes. According to the theory, low recruitment in some years could be explained by limited suitable habitat to be colonized by larvae due to adults or other benthic colonizers (Gilmore 2004, Macpherson & Socrati 2008, Suárez & Arrontes 2008, Cruz *et al.* 2010) and La Niña years (*e.g.*, 2011) in which oceanographic conditions changed in the ETP. Lower temperatures curtail reproductive output and recruitment (Romero *et al.* submitted). Higher precipitation during La Niña causes an osmotic shock, affecting feeding, food efficiency and survival (Sanford *et al.* 1994, Burrows *et al.* 2010); this may be the case in Malpelo Island.

The survival rates of some classes decreased with high densities of individuals (class IX-XI) that produce intraspecific competition for space, overgrowth, and smothering (Schubart *et al.* 1995, Chan & Williams 2004). The individuals of *M. peninsularis* in Malpelo showed overgrowth of the same species and competition for space with *Tetraclita transversus*, *Tetraclita panamensis*, and *Chthamalus* sp. (Brando *et al.* 1992, García *et al.* 2012). High predation also decreases survival rates; this was measured in populations of *Balanus glandula* and *Diadema antillarum* (Menge 2000, Forero 2006), predators are drawn to intermediate size prey; small individuals offer smaller sources of energy (cost-benefit), large individuals

escape predation (size refuge); this may explain the low frequency found in classes III-V. Lastly, storms and high waves detach layers of superimposed barnacles from several cohorts and of different size classes). Malpelo's rocky shore is exposed to high hydrodynamics that are produced by a combination of factors such as waves (over 5.0 m), tides (3.0-5.0 m), oceanic currents, and frequent storms that generate enough energy to erode the rock and detach *M. peninsularis* from the littoral zone (Bessudo *et al.* 2005). Heavy storms could reduce the frequency of larger individuals (*e.g.*, Class X: 4.37-4.79 cm and Class XI: 4.8-5.11 cm), creating space for new recruits.

*M. peninsularis* has a growth rate of 2.08 mm month<sup>-1</sup> in the ETP (Galápagos Islands, Witman & Smith 2003). We used this data to calculate the age of individuals belonging to a particular size class (population structure based on age; Akcakaya *et al.* 1998). Based on this data, individuals of the first size class, with a basal diameter between 0.5-0.92 cm (Fig. 3), correspond to 1.0 to 4.4 months old, Class II to 4.5 to 6.4 months, Class III 6.5-8.4 months, Class IV to 8.5-10.5 months, Class V to 10.6-12.5 months, Class VI: 12.6-14.6 months, Class VII: 14.7-16.6 months, Class VIII to 16.7-18.6 months, Class XI to 18.7-20.7 months, Class X to 28.8-22.7 months, and Class XI to 22.8-24.8 months. All the calculations are assuming similar growth rate among size classes. The distribution curve based on age for *M. peninsularis* followed the same frequency and bimodal pattern in Fig 3. We also used the sexual maturity age of 6 months for *M. peninsularis* proposed by Chan (2006) to estimate the proportion of immature and mature individuals in the Malpelo population. This value allowed us to infer that the size frequency of classes I and II could be juveniles (non-reproductive individuals), which corresponds to 40.1 % of the population. Classes III to XI correspond to adults (59.9% potentially reproductive). In that scenario, adult organisms that die could easily be replaced by new juveniles (Grigg 1975, Oostermeijer *et al.* 1994, Rodríguez *et al.* 2007). The juvenile to adult ratio in barnacles may indicate equilibrium in the population (Burrows *et al.* 2010).

According to our calculations, *M. peninsularis* recruitment (classes I and II) in Malpelo could occur between July and September 2010, nearly 6 months previous to sampling. In Malpelo Island, benthic populations were influenced by El Niño events in 2009 and 2010 in which sea surface temperatures rose 1.0 to 1.5°C (IDEAM 2009, León 2010<sup>3</sup>). The successful

recruitment observed in classes I and II could be the result of high sea surface temperature during April and May 2010 (IRI 2015)<sup>4</sup>.

El Niño may have improved dispersal, and long distance connectivity, as well as the recruitment of larvae dispersing from downstream populations, increasing the frequency of individuals in the first classes, and playing a role in the genetic pool of target species. Higher current velocity (Fig. 1) during El Niño may have increased the probability of larval dispersal from as far as the Central Pacific to Malpelo Island (Corredor-Acosta *et al.* 2011). Similarly, the high temperatures during May and June 2009 could have generated the high frequency of individuals found in age classes VI-VIII (12.6-18.6 months; IRI 2015)<sup>4</sup>. Comparable settlement peaks were reported for other barnacle species during the warmer months of the year (García & Moreno 1998, Dionisio *et al.* 2007, Suárez & Arrontes 2008, Savoya & Schwindt 2010). El Niño events in 2009 and 2010 could be associated with the bimodal pattern found for *M. peninsularis* in Malpelo. These explanatory hypotheses should be tested in future studies; population structure and dynamics has been related to local oceanographic conditions, as demonstrated for *Chthamalus stellatus*, *Chthamalus dalli*, *Notobalanus flosculus*, *Semibalanus balanoides*, and *Balanus glandula* (Berger *et al.* 2006, Macpherson & Scrosati 2008, Suárez & Arrontes 2008, Tapia & Navarrete 2010).

The last two classes of *M. peninsularis* presented limited individuals. Based on our estimations, older individual (class X-XI) are around 2.5 years old. We hypothesize that the life cycle of *M. peninsularis* could be close to 2-3 years, likewise to the succession cycle in the rocky environment due to high hydrodynamic conditions in the littoral.

In conclusion, the population of *M. peninsularis* in Malpelo Island is growing. The high frequency of juveniles suggests a resilient population, as they can replace dead individuals.

#### ACKNOWLEDGMENTS

To Sandra Bessudo and German Soler (Fundación Malpelo) for financing the field trip to the island. Romanus E. Prabowo for helping in the identification of species, Mauricio Romero for the comments to improve the manuscript and to Marly Rincón for help in the editing process.

<sup>3</sup>León G. 2010. Aspectos de la circulación atmosférica de gran escala sobre el Noroccidente de Suramérica asociada al ciclo ENOS 2009-2010 y sus Consecuencias en el régimen de precipitación en Colombia. <[http://www.cambioclimatico.gov.co/documents/21021/418818/Circulaci%C3%B3n+Atmosf%C3%A9rica+ENOS++2009-2010\\_GloriaLeon.pdf/b4345abd-fcef-461d-8053-44614dc67d07](http://www.cambioclimatico.gov.co/documents/21021/418818/Circulaci%C3%B3n+Atmosf%C3%A9rica+ENOS++2009-2010_GloriaLeon.pdf/b4345abd-fcef-461d-8053-44614dc67d07)>

<sup>4</sup>IRI. 2015. Climate Monitoring: Monthly Sea Surface Temperature. <[http://iridl.ldeo.columbia.edu/maproom/Global/Ocean\\_Temp/Monthly\\_Temp.html?bbox=bb%3A-85.142%3A-2.945%3A-70.728%3A14.727%3Abb](http://iridl.ldeo.columbia.edu/maproom/Global/Ocean_Temp/Monthly_Temp.html?bbox=bb%3A-85.142%3A-2.945%3A-70.728%3A14.727%3Abb)>

## LITERATURE CITED

- Akcakaya H, M Burgman & L Ginzburg. 1999.** Applied population ecology. Principles and Computer Exercises using RAMAS EcoLab 2.0, 285 pp. Sinauer Associates, Sunderland.
- Babcock R, T Shearsb, A Alcalac, N Barrettd, G Edgard, K Laffertye, T McClanahanf & G Russg. 2010.** Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academy of Sciences of the United States of America. 107: 18256-18261.
- Bak R & E Meesters. 1999.** Population structure as a response of coral communities to Global Change. American Zoologist 39(1): 56-65.
- Berger M, A Darrah & R Emlet. 2006.** Spatial and temporal variability of early post-settlement survivorship and growth in the barnacle *Balanus glandula* along an estuarine gradient. Journal of Experimental Marine Biology and Ecology 336: 74-87.
- Bessudo S, G Soler, M Silva, Y Lefèvre & H Zambrano. 2005.** Santuario de fauna y flora Malpelo. Plan de manejo versión institucional, 45 pp. Fundación Malpelo y Otros Ecosistemas Estratégicos. Bogotá. <<http://www.parquesnacionales.gov.co/portal/wp-content/uploads/2013/12/IslandeMalpelo.pdf>>
- Brando A, H Prah & J Cantera. 1992.** Malpelo, isla oceánica de Colombia, 195 pp. Banco de Occidente, OP Gráficas, Bogotá.
- Bühler C & B Schimd. 2001.** The influence of management regime and altitude on the population structure of *Succisa pratensis*: implications for vegetation monitoring. Journal of Applied Ecology 38: 689-698.
- Burrows M, S Jenkins, L Robb & R Harvey. 2010.** Spatial variation in size and density of adult and post-settlement *Semibalanus banalanoides*: effects of oceanographic and local conditions. Marine Ecology Progress Series 398: 207-219.
- Calcagno J, L López & A Tablado. 1998.** Population dynamics of the barnacle *Balanus amphitrite* in an intertidal area affected by sewage pollution. Journal of Crustacean Biology 18(1): 128-137.
- Chan B. 2006.** Ecology and biodiversity of rocky intertidal barnacles along a latitudinal gradient: Japan, Taiwan and Hong Kong. The Nagisa World Congress 1(10): 1-8.
- Chan B & G Williams. 2004.** Population dynamics of the acorn barnacles *Tetraclita squamosa* and *Tetraclita japonica* (Cirripedia: Balanomorpha) in Hong Kong. Marine Biology 146: 149-160.
- Corredor-Acosta A, A Acosta, P Gaspar & B Calmettes. 2011.** Variation in the surface currents in the Panama Bight during El Niño and La Niña events from 1993 to 2007. Boletín de Investigaciones Marinas y Costeras 40: 33-56.
- Cruz T, J Castro & S Hawkins. 2010.** Recruitment, growth and population size structure of *Pollicipes pollicipes* in SW Portugal. Journal of Experimental Marine Biology and Ecology 392: 200-209.
- Díaz S, C Mercado & S Alvarez-Cardenas. 2000.** Structure and population dynamics of *Pinus lagunae* M. - F. Passini. Forest Ecology and Management 134: 249-256.
- Dionisio M, A Rodríguez & A Costa. 2007.** Reproductive biology of *Megabalanus azoricus* (Pilsbry), the Azorean Barnacle. Invertebrate Reproduction and Development 50(3): 155-162.
- El-Komi M & T Kajihara. 1990.** Observation on the Settlement and Growth of Barnacles in Tokyo Bay, Japan. Marine Fouling 8(1/2): 1-8.
- Forero G. 2006.** Estado, distribución espacial y uso de hábitat de la población del erizo negro *Diadema antillarum* (Philippi) en el archipiélago de nuestra señora del rosario (Caribe colombiano). Trabajo de pregrado, Facultad de Estudios Ambientales y Rurales, Pontificia Universidad Javeriana, Bogotá, 74 pp.
- García G & I Moreno. 1998.** Recruitment, growth, mortality and orientation patterns of *Balanus trigonus* (crustacea; Cirripedia) during succession on fouling plate. Scientia Marina 62(1-2): 59-64.
- García S, A Acosta, E Londoño-Cruz & J Cantera. 2012.** Organismos sésiles y móviles del litoral rocoso en el Pacífico Colombiano: Una guía audiovisual para su identificación. INVEMAR Serie de Documentos Especiales 26: 1-134. Unión Gráfica, Bogotá.
- Gilmore J. 2004.** Size-structure of populations of the mushroom coral *Fungia fungites*: the role of disturbance. Coral Reefs 23: 493-504.
- Golléty C, F Gentil & D Davoult. 2008.** Secondary production, calcification and CO<sub>2</sub> fluxes in the cirripedes *Chthamalus montanguis* and *Elminius modestus*. Oecologia 155: 133-142.
- Gómez L. 2003.** Sistemática de los Balanomorfos (Cirripedia, Thoracica) de la Región Sur de la Península de Baja California, México. Tesis de Maestría, Departamento Plancton y Ecología Marina, Instituto Politécnico Nacional, La Paz, 102 pp.
- Gori A, S Rossi, C Linares, E Berganzo, C Orejas, M Dale & J Gili. 2011.** Size and spatial structure in Deep versus shallows populations of the Mediterranean gorgonian *Eunicella singularis* (Cap de Creus, northwestern Mediterranean Sea Marine). Marine Biology 158: 1721-1732.
- Grigg R. 1975.** Age structure of a longevous coral: A relative index of habitat suitability and stability. The American Naturalist 109(970): 647-657.
- Heather L, E Breck, F Chan, J Lubchenco & B Menge. 2005.** Barnacle reproductive hotspots linked to nearshore ocean conditions. Proceedings of the National Academy of Sciences of the United States of America 102(30): 10534-10539.

- Hengland S, M Van Leeuwen & G Oostermeijer. 2001.** Population structure of *Salvis pratensis* in relation to vegetation and management of Dutch dry floodplain grasslands. *Journal of Applied Ecology* 38: 1277-1289.
- Henry D & P McLaughlin. 1986.** The recent species of *Megabalanus* (Cirripedia: Balanomorpha) with special emphasis on *Balanus tintinnabulum* (Linnaeus) Sensu Lato. *Zoologische Verhandlungen* 235: 1-58.
- IDEAM. 2009.** Boletín informativo sobre el monitoreo del fenómeno de 'El Niño'. Número 1. Septiembre 17 de 2009. Instituto de Hidrología, Meteorología y Estudios Ambientales. Oficina del Servicio de Pronóstico y Alertas, Bogotá.
- INVEMAR. 2009.** Informe del Estado de los Ambientes y Recursos Marinos y costeros en Colombia Año 2008. Serie de Publicaciones Periódicas 8: 1-243. INVEMAR, Santa Marta.
- INVEMAR. 2010.** Informe del Estado de los Ambientes y Recursos Marinos y costeros en Colombia Año 2009. Serie de Publicaciones Periódicas 8: 1-319. INVEMAR, Santa Marta. <[http://www.invemar.org.co/redcostera1/invemar/docs/IER\\_2009.pdf](http://www.invemar.org.co/redcostera1/invemar/docs/IER_2009.pdf)>
- INVEMAR. 2015.** Informe del estado de los ambientes y recursos marinos y costeros en Colombia: AnPo 2014. Serie de Publicaciones Periódicas 3: 1-176. INVEMAR, Santa Marta. < [http://www.invemar.org.co/publicaciones/-/asset\\_publisher/SfkbM8hfCgNW/content/informe-del-estado-de-los-ambientes-y-recursos-marinos-y-costeros-en-colombia-2014?inheritRedirect=false](http://www.invemar.org.co/publicaciones/-/asset_publisher/SfkbM8hfCgNW/content/informe-del-estado-de-los-ambientes-y-recursos-marinos-y-costeros-en-colombia-2014?inheritRedirect=false)>
- Jeffery C & A Underwood. 2001.** Longevity determines sizes of an adult intertidal barnacle. *Journal of Experimental Marine Biology and Ecology* 256: 85-97.
- Kipson S, C Linares, H Cizmek, E Cebrian, E Ballesteros, T Bakran-Petricioli & J Garrabou. 2014.** Population structure and conservation status of the red gorgonian *Paramuricea clavata* (Risso, 1986) in the Eastern Adriatic Sea. *Marine Ecology* 1-12.
- Lin G. 1993.** A preliminary study on the reproductive biology of *Pollicipes mitella*. Thesis PhD, Fujian Normal University, Fuzhou, 210 pp.
- Linares C, J Garrabou, B Hereu, D Diaz, C Marschal, E Sala & M Zabala. 2012.** Assessing the effectiveness of marine reserves on unsustainably harvested long lived sessile invertebrates. *Conservation Biology* 26: 88-96.
- López-Victoria M & F Estela. 2007.** Aspectos sobre la ecología del Piquero de Nazca *Sula granti* en isla Malpelo. En: DIMAR-CCCP & UAESPNN-DTSO (eds.). Santuario de Fauna y Flora Malpelo: descubrimiento en marcha, pp. 131-142. Dirección General Marítima (DIMAR), Bogotá.
- Lozano-Cortés D & E Londoño-Cruz. 2013.** Checklist of barnacles (Crustacea; Cirripedia: Thoracica) from the Colombian Pacific. *Marine Biodiversity* 43: 463-471.
- Macpherson E & R Scrosati. 2008.** Population structure of the barnacle *Semibalanus balanoides* (Cirripedia, Thoracica), across intertidal environmental stress gradients in northern Nova Scotia, Canada. *Crustaceana* 81(6): 725-736.
- Mayor G, C Acevedo & S Bessudo. 2007.** Generalidades. En: DIMAR-CCCP & UAESPNN-DTSO (eds). Santuario de Fauna y Flora Malpelo: Descubrimiento en marcha, pp. 15-28. Dirección General Marítima (DIMAR), Bogotá.
- Menge B. 2000.** Recruitment vs. postrecruitment processes as determinants of barnacle population abundance. *Ecological Monographs* 70(2): 265-288.
- Miller R. 2013.** Larval dispersal and population connectivity: implications for offshore renewable energy structures. PhD Thesis, University of Aberdeen, Aberdeen, 275 pp.
- Minchinton T & R Scheibling. 1991.** The influence of larval supply and settlement on the population structure of barnacles. *Ecology* 71(5): 1867-1879.
- Muko S, K Sakai & Y Iwasa. 2001.** Size distributions dynamics for a marine sessile organism with space-limitation in growth and recruitment: Application to a coral population. *Journal of Animal Ecology* 7(4): 579-589.
- Oostermeijer J, R Van't Veer & J Den Nijs. 1994.** Population structure of the rare, long-lived perennial gentian pneumonanthe in relation to vegetation and management in the Netherlands. *The Journal of Applied Ecology* 31(3): 428-438.
- Penchaszadeh P, M Borges, C Damborenea, G Darrigran, S Obenat, G Pastorino, E Schwindt & E Spivak. 2003.** Especies animales bentónicas introducidas, actual o potencialmente invasoras en el sistema del Río de la Plata y la región costera oceánica alemana del Uruguay y de la Argentina. En: Protección ambiental del Río de la Plata y su frente marítimo: prevención y control de la contaminación y restauración de hábitats, Proyecto PNUD/GEFRLA/99/G31, 357 pp.
- Rockwood L. 2006.** Introduction to population ecology, 339 pp. Blackwell Publishing, Malden.
- Rodríguez A, L Álvarez & I Castañeda. 2007.** La pirámide de población. Precisiones para su utilización. *Revista Cubana de Salud Pública* 33(4). <[http://www.bvs.sld.cu/revistas/spu/vol33\\_4\\_07/spu08407.html](http://www.bvs.sld.cu/revistas/spu/vol33_4_07/spu08407.html)>
- Rodríguez-Rubio E & A Giraldo. 2011.** Características oceanográficas en la isla Malpelo y su relación con la cuenca oceánica del Pacífico Colombiano. *Boletín de Investigaciones Marinas y Costeras* 40(1): 19-32.
- Romero M, A Acosta & EA Trembl. 2016.** The regional structure of spawning phenology and the potential consequences for coral assemblages across the Eastern Tropical Pacific. *Journal of Biogeography*. [submitted]
- Sánchez J, C Gómez, D Escobar & LF Dueñas. 2011.** Diversidad, abundancia y amenazas de los octocorales de la isla Malpelo, pacífico oriental tropical, Colombia. *Boletín de Investigaciones Marinas y Costeras* 40 (Supl. Esp.): 139-154.
- Sanford E, D Bermudez, M Bertness & S Gaines. 1994.** Flow food supply and acorn barnacle population dynamics. *Marine Ecology Progress Series* 104: 49-62.

- Santangelo G, L Ramanti, S Rossi, G Tsounis, I Vielmini, C Lott & JM Gili. 2012.** Patterns of variation in recruitment and post-recruitment processes of the Mediterranean precious gorgonian coral *Corallium rubrum*. *Journal of Experimental Marine Biology and Ecology* 411: 7-13.
- Savoya V & E Schwindt. 2010.** Effect of the substratum in the recruitment and survival of the introduced barnacle *Balanus glandula* (Darwin 1854) in Patagonia, Argentina. *Journal of Experimental Marine Biology and Ecology* 382: 125-130.
- Schubart C, L Basch & G Miysato. 1995.** Recruitment of *Balanus glandula* Darwin (Crustacea: Cirripedia) into empty barnacles test and its ecological consequences. *Journal of Experimental Marine Biology and Ecology* 186: 143-181.
- Suárez R & J Arrontes. 2008.** Population dynamics of the barnacles *Chthamalus montagui* at two spatial and temporal scales in northern Spain. *Marine Biology* 155: 363-374.
- Tapia S & A Navarrete. 2010.** Spatial patterns of barnacle settlement in central Chile: Persistence at daily to inter-annual scales relative to the spatial signature of physical variability. *Journal of Experimental Marine Biology and Ecology* 392: 151-159.
- Velasco L, D Gil-Agudelo & R Nieto. 2011.** Endemic shallow reef fishes from Malpelo Island: abundance and distribution. *Boletín de Investigaciones Marinas y Costeras* 40 (Supl. Esp.) 107-116.
- Venail R. 2002.** Acercamiento a la estructura y composición de la comunidad íctica arrecifal de la Isla de Malpelo, utilizando el censo visual rápido (RVC) en el mes de marzo de 2002. Tesis de Pregrado, Facultad de Ciencias, Pontificia Universidad Javerina, Bogotá, 71 pp.
- Vermeij M & R Bak. 2000.** Inferring demographic processes from population size structure in corals. *Proceedings 9<sup>th</sup> International Coral Reef Symposium*. Bali, Indonesia 23-27 October, 5 pp.
- Witman J & F Smith. 2003.** Rapid community change at a tropical upwelling site in the Galapagos Marine Reserve. *Biodiversity and Conservation* 12: 25-45.
- Zapata F & B Vargas-Ángel. 2003.** Corals and corals reefs of the pacific coast of Colombia. In: Cortés J (ed). *Latin American Coral Reefs*, pp. 419-447. Elsevier, Amsterdam.
- Zapata F, J Jaramillo-González & R Navas-Camacho. 2011.** Extensive bleaching of the coral *Porites lobata* at Malpelo Island, Colombia, during a cold water episode in 2009. *Boletín de Investigaciones Marinas y Costeras* 40 (Supl. Esp.) 185-193.
- Zvyagintsev A & O Korn. 2003.** Life history of the barnacle *Balanus amphitrite* Darwin and its role in fouling communities of the Peter the Great Bay, sea of Japan. *Russian Journal of Marine Biology* 29(1): 41-48.

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Received 19 August 2015 and accepted 5 May 2016

Editor: Claudia Bustos D.