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# Changes in rocky intertidal communities after the 2015 and 2017 El

## Niño events along the Peruvian coast

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Científica del Sur, Perú

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27

28 **Keywords: Humboldt current ecosystem, Macrobenthos, Biogeography, Community structure,**

29 **Thermal anomaly, latitudinal pattern**

30

31 **Highlights**

- 32 • Rocky intertidal communities' response to El Niño in a latitudinal transect
- 33 • Community changes driven by ecological processes rather than thermal tolerance
- 34 • Biogeographical patterns are persistent to El Niño

35

36 **Abstract**

37 The Peruvian coast experiences the largest interannual variability of sea surface temperature in the  
38 world due to the combined influence of the coastal upwelling and El Niño Southern Oscillation  
39 (ENSO). Although biological impacts of El Niño events have been widely reported, their effects on  
40 rocky intertidal communities remains largely unknown in Peru. Herein, we analyze the results of two  
41 biological surveys of rocky intertidal communities, conducted along 1400 km of the Peruvian coast.  
42 The first survey was conducted in 2015 yielding a snapshot of the distribution of rocky intertidal  
43 communities after 17 years of stable La Niña-like conditions. The second survey was carried in

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3 44 October 2017, after the 2015-16 and the 2017 El Niño events, which produced warm sea surface  
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5 45 temperature (SST) anomalies up to 6°C on the Peruvian coast. We find no changes throughout the  
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7  
8 46 latitudinal transect in taxonomic richness but an important turnover of species, especially marked in  
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10 47 the transition zone (~4-8°S) between the Panamic and the Humboldt provinces. Temperature-related  
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12  
13 48 southward migration of species was evidenced in a few sites but did not explain the large-scale  
14  
15 49 change in communities observed from 2015 to 2017, primarily driven by large changes in the  
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18 50 distribution of a few ecologically important species across the Panamic and Humboldt provinces. A  
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20 51 primary environmental impact on some ecologically key species likely triggered a chain of secondary  
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22 52 impacts through ecological relationships which lead to a complex change independent from SST  
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25 53 gradients. Further studies are needed to better characterize and disentangle the seasonal and  
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27 54 interannual variability of the rocky intertidal communities and their drivers. When this interannual  
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30 55 variability is integrated, the nine study sites show a highly persistent community structure determined  
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32 56 by the latitudinal SST gradient along the Peruvian coast.  
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## 38 58 **1. Introduction**

39  
40 59 El Niño Southern Oscillation (ENSO) is responsible for approximately 85% of the interannual  
41  
42 60 climatic variability along the Peruvian coast (Carré *et al.*, 2013). El Niño, the warm phase of ENSO,  
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44 61 generates sea surface temperature (SST) anomalies that are larger in Peru than anywhere else in the  
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46 62 world, with widespread effects on marine ecosystems. During ENSO-neutral conditions of oceanic  
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48 63 circulation and considering the low latitude, coastal waters are relatively cold (16-20°C) due to  
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50 64 coastal upwelling. During El Niño events, the thermocline deepens in the Eastern Pacific preventing  
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52 65 the upwelling of deeper cold and nutrient-rich waters to the surface. As a result, primary productivity  
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54 66 is reduced and SST increases considerably between 3 to 18 months depending on the magnitude of  
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56 67 the event (Wyrтки, 1975; Cane, 1983). Temperature anomalies can reach up to 8°C during extreme  
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3 68 events like those that occurred in 1982/83 and 1997/98 (Carré *et al.*, 2013). These interannual marine  
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5 69 temperature anomalies are the largest in the world and, coupled with others abiotic cofactors (e.g.,  
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8 70 rainfall and salinity changes), can have significant impacts on the coastal biodiversity either directly  
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10 71 or indirectly (Barber and Chavez, 1983; Paredes *et al.*, 1998; Espino, 1999; Arntz *et al.*, 2006;  
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12 72 Camus, 2008). The opposite phase of ENSO referred to as La Niña, is characterized by cooler  
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15 73 conditions related to a shallower thermocline and an intensification of the coastal upwelling. These  
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18 74 cold anomalies have lower amplitude, favor primary productivity, and are generally not considered as  
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20 75 stressful conditions for the coastal Peruvian ecosystem (Wang and Fiedler, 2006).

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22 76 To date, no continuous, periodic and comparable observations of rocky shores biological  
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25 77 communities along the Peruvian coast and continental margin are available. Several studies document  
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27 78 the biological effects of El Niño in Peruvian coastal ecosystems during the extreme 1982-83 and the  
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30 79 1997-98 events (Arntz, 1986; Glynn, 1988; Castilla and Camus, 1992; Arntz *et al.*, 1988; Tarazona *et*  
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32 80 *al.*, 1988a; Tarazona *et al.*, 1988b; Tarazona *et al.*, 2003; Thiel *et al.*, 2007; Camus, 2008) but focus  
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35 81 on site specific variability. Information about the influence of ENSO on rocky intertidal benthic  
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37 82 fauna and flora in Peru is thus scarce and has never been investigated along a latitudinal gradient.

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39 83 Recently, Ibañez-Erquiaga *et al.* (2018) proposed a biogeographic zonation of rocky intertidal  
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42 84 communities along the Peruvian coast based on a latitudinal survey performed from February to May  
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44 85 2015 in 41 coastal sites. The authors defined three biogeographic units: (1) a tropical, Panamic  
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47 86 province (3.5 - 4.5° S), (2) a transitional zone (5 - 5.5° S), and (3) a temperate, Humboldt province (6  
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49 87 - 13.5°S). The model proposed by Ibañez-Erquiaga *et al.* (2018) provides a snapshot of the latitudinal  
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52 88 distribution of rocky intertidal communities after 17 years of relatively cool and stable La Niña-like  
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54 89 conditions after the strong 1997-98 El Niño event. Herein, we add data from a survey performed in  
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57 90 October 2017 at 9 sites (among those sampled by Ibañez-Erquiaga *et al.*, 2018) distributed along  
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59 91 1400 km of the Peruvian coast (from 3.7 to 13.9° S) (Figure 1). Thus, we assumed that ecosystems

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3 92 had fully recovered from the 1998 El Niño disturbance and were under the long-term influence of La  
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5 93 Niña conditions in Peru.  
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8 94 Two El Niño events occurred between surveys. The 2015-16 El Niño is considered among the most  
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10 95 powerful of the last decade (Huang *et al.*, 2016), with a maximum anomaly located in the central  
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12 96 Pacific region and a moderate warming in the Eastern tropical Pacific and in the Peruvian coast  
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15 97 (Figure 2). Soon after, a short-lasting El Niño event occurred from January to May 2017 (known as  
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17 98 coastal El Niño), characterized by a much larger temperature anomaly but restricted to the coast off  
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20 99 Peru and Ecuador (Echevin *et al.*, 2018; Garreaud, 2018). In central Peru, SST anomalies reached 6°  
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22 100 C (Figure 2) and together with catastrophic rainfall and floods across the coast (Rodríguez-Morata *et*  
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24 101 *al.*, 2018). Although not as severe as the extreme 1982-83 and 1997-98 events, the 2017 coastal El  
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27 102 Niño event has been considered as a strong but localized event for the amplitude of the temperature  
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30 103 anomaly on the Peruvian coast (Echevin *et al.*, 2018; Garreaud, 2018). Our second survey was  
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32 104 conducted in October, about 4 months after the end of this event. Therefore, this second survey is  
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35 105 ideal to assess long-lasting impacts of El Niño environmental variability in biological communities  
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37 106 after a long period of being predominantly under rather cool neutral or La Niña conditions.  
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39 107 Ibañez-Erquiaga *et al.* (2018) showed that temperature and nutrients are strongly linked with the  
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41  
42 108 biogeographic zonation of benthic rocky communities. Since surface warm water masses are also  
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44 109 characterized by low nutrient concentration, here we use SST anomalies as an integrated indicator of  
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47 110 the oceanographic state on the Peruvian coast. We expected long-lasting impacts of El Niño on the  
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49 111 rocky shore communities including changes in the species diversity and in the latitudinal pattern of  
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52 112 community composition due to mortality, southward migration, and a southward shift in species  
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54 113 recruitment.  
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56 114 The objective of this study is twofold. First we aimed to evaluate the cumulative impact of the 2015-  
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59 115 16 and 2017 El Niño events on species diversity and geographic distribution of benthic rocky  
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61 116 intertidal communities across the Peruvian Pacific coast, by assessing changes in the characteristics  
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3 117 and latitudinal patterns in the communities before and after the El Niño events in relationship with  
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5 118 SST anomalies along the coast. Because earlier systematic records of rocky shore communities are  
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8 119 not available in Peru, our approach lacks referential observations, but is also the first study of rocky  
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10 120 intertidal communities' response to El Niño in a latitudinal transect. Our second aim was to assess  
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13 121 the robustness of the bioregionalization to inter-annual variability, as well as the relative influence of  
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15 122 mean SST conditions versus El Niño-related SST anomalies as long-term abiotic drivers of the  
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17  
18 123 biogeographic zonation of rocky intertidal species along the Peruvian coast, comparing the  
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20 124 biogeographic zonation of rocky shore communities with latitudinal gradients in long-term statistics  
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22 125 of coastal SST including ENSO-related variability.  
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## 28 127 **2. Materials and Methods**

### 31 128 **2.1. Study area, site selection and sampling design**

34 129 We studied nine rocky shore sites of the Peruvian coast, from Acapulco (3.74° S, 80.77° W) to La  
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36 130 Mina (13.91° S, 76.31° W) encompassing a 1400 km stretch of coastline (1200 km in direct line), or a  
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39 131 variation of 11.63° latitude and 6.14° longitude (Figure 1). These nine sites were selected among the  
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41 132 41 sites survey performed between February and May of 2015 by Ibañez-Erquiaga *et al.* (2018)  
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43  
44 133 allowing a direct comparison in these localities. Sites were separated by 0.5 to 2.8° of latitude with a  
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46 134 shorter distance between northern sites where gradients are steeper and where the transition between  
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49 135 the Panamic and the Humboldt ecoregion was reported (Figure 1, Table 1). Fishing, recreational, or  
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51 136 urban areas were avoided to minimize the anthropogenic influence in community composition.  
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54 137 Selected sites were rocky shore, with wave-exposed platforms from 25 m<sup>2</sup> to ~1000 m<sup>2</sup>. The slope of  
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56 138 the rock platform did not exceed 45°. Caves and crevices were not surveyed to keep a homogeneous  
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59 139 flat sampling area. At each site, observations were performed in a representative sample of the  
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61 140 intertidal zone through a total of 16 quadrats distributed in four haphazardly-distanced (in a range of  
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3 141 3-10m) transects of four quadrats distributed from the upper intertidal to the lower intertidal zones.  
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5 142 We used a 0.25 m<sup>2</sup> quadrat of 0.50 m x 0.50 m with a 100-intersection grid. In each transect 4  
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8 143 intertidal fringes were identified according to the presence of litorinids (upper), sessile barnacles  
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10 144 (mid-high), mussels (mid-low) and macroalgae and anemones (low) following the sampling method  
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13 145 presented in Broitman *et al.* (2001), Rivadeneira and Fernandez (2005) and Ibañez-Erquiaga *et al.*  
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15 146 (2018). Within each fringe and along the transect, one quadrat was randomly placed on plain rock  
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18 147 surface. We used a 0.25 m<sup>2</sup> quadrat of 0.50 m x 0.50 m with a 100-intersection grid. Each site  
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20 148 sampling cover thus a total surface area of 4 m<sup>2</sup> and 1600 point-intersects, which is similar to  
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23 149 previous rocky shore studies in the Pacific (Broitman *et al.*, 2001; Blanchette *et al.*, 2008;  
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25 150 Rivadeneira and Fernandez, 2005; Ibañez-Erquiaga *et al.*, 2018). Sampling was conducted during the  
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27 151 lowest tide at daytime and lasted about 3 hours per site.  
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33 153 **Table 1.** Study sites coordinates and sampling dates

Site name	Sitecode	Latitude °N	Longitude °E	1 <sup>st</sup> sampling	2 <sup>nd</sup> sampling
Acapulco	ACA	-3.74	-80.77	22/02/2015	2/10/2017
PuntaVeleros	PVE	-4.17	-81.14	21/02/2015	6/10/2017
PuntaBalcones	PBA	-4.68	-81.32	1/03/2015	5/10/2017
Yacila	YAC	-5.12	-81.16	3/03/2015	3/10/2017
PuntaAguja	PAG	-5.80	-81.08	15/03/2015	4/10/2017
Puemape	PUE	-7.51	-79.54	10/03/2015	7/10/2017
Tamborero	TAM	-10.32	-78.05	8/04/2015	8/10/2017
Pucusana	PUC	-12.47	-76.79	17/04/2015	13/10/2017
La Mina	MIN	-13.91	-76.31	8/05/2015	18/10/2017

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53 155 The zonation pattern for the region sampled has been described in Paredes (1974) for the central  
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55 156 coast, and further characterized by Ibanez-Erquiaga *et al.* (2018). These authors describe for the  
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58 157 rocky intertidal of the Panamic Province, the predominance of *Jehlius cirratus* and *Austrolittorina*  
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60 158 *araucana* for the upper intertidal level, *Ulva* spp. for the middle level, and *Semimytilus algosus* with  
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3 159 *Grateloupia filicina* in the low level. In the Transition Zone, *J. cirratus* and *Echinolittorina* spp. are  
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5 160 predominant in the upper intertidal level, *Ulva* spp. and *Phragmatopoma* spp. characterize the middle  
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8 161 level, and *G. filicina* with *Ahnfeltiopsis durvillaei* are predominant in the lower level. For the  
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10 162 Humboldt ecoregion, *J. cirratus* and *Echinolittorina* spp. are predominant in the upper intertidal  
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13 163 level, *Perumytilus purpuratus* and *Ulva* spp. characterize the middle level, and *S. algosus* the lower  
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15 164 level.

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## 19 20 21 166 **2.2. Data collection at the rocky intertidal habitat**

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24 167 A commonly used minimum size of 0.5 cm was chosen as size limit for individuals to be counted.  
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26 168 Mobile species (e.g. limpets, snails, crabs, mobile polychaetes) were counted as individuals present  
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29 169 within the quadrats (4m<sup>2</sup> in total), and their abundance was reported in number of individuals per  
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31 170 square meter. The abundance of sessile species (e.g. mussels, barnacles, algae, anemones, sessile  
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34 171 polychaetes) was measured as a percentage of coverage using a 100-point grid within quadrats (1600  
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36 172 intercept points in total). Percentage of rocky and sandy substratum was also quantified. When full  
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39 173 taxonomic identification was not achieved *in situ*, specimens were collected in 96% alcohol  
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41 174 (invertebrates) or 4% formalin (algae) for further examination in the laboratory. Some genera include  
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44 175 species that cannot be differentiated visually in the field, such as *Scurria* or *Ulva*, which means that  
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46 176 their identification and quantification in the laboratory would require the collection of all individuals  
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49 177 in the field. This option was not chosen because of its high environmental impact, so that these  
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51 178 genera are not resolved here to the species level. *Scurria* species have been shown to be separated by  
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53 179 small scale processes rather by large scale biogeographic features (Aguilera et al. 2013), so that this  
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56 180 taxonomic limitation is not expected to induce any significant bias in our study. Collected samples  
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58 181 were deposited at the collection of the Marine Biology Laboratory of the Universidad Peruana  
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61 182 Cayetano Heredia in Lima, Peru. In the laboratory, a stereoscope or microscope was used to sort  
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3 183 specimens into major taxa and then identified to the lowest possible taxonomic level. When possible,  
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5 184 Holothurian ossicles were extracted and observed to identify to the species level. Where the  
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8 185 taxonomic uncertainty persisted, species were pooled into genera. Taxonomic identification was  
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10 186 double checked for consistency.  
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### 16 188 **2.3. Temperature data**

19 189 Sea surface temperature (SST) data was obtained from the Multi-scale Ultra-high Resolution (MUR)  
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21 190 SST Analysis fv04.1, Global, 0.01°x0.01° (Vazquez *et al.*, 1998; JPL MUR MEaSURES Project,  
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24 191 2015). The monthly time series covers the period from June 2002 to April 2018. This dataset was  
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26 192 chosen because coastal features can be captured by the ultra-high spatial resolution of ~1 km. In  
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29 193 figure 3, we show maps of (A) mean annual SST, (B) annual SST range, (C) mean July SST, (D)  
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31 194 mean February SST, and (E) the influence of ENSO estimated by the variance (squared standard  
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34 195 deviation) of SST anomalies. SST statistics were calculated over the 2002-2018 period. Monthly  
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36 196 anomalies were calculated in reference to the 2003-2016 period. For all these variables, the trend  
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39 197 observed along the coastline was plotted vs. latitude. Monthly time series of SST anomalies  
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41 198 calculated for each sampling sites are shown in figure 2. The map of SST anomalies observed in  
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43 199 March 2017 (Figure 3F) shows the spatial pattern of the maximum temperature stress of the 2017  
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46 200 Coastal El Niño event.  
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### 52 202 **2.4. Data analysis**

54  
55 203 A sampled based rarefaction analysis (Gotelli and Colwell, 2001) was performed to assess the  
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57 204 sampling representativeness for the nine sampled localities. Taxa composition (presence/absence),  
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60 205 abundance (number of individuals per square meter for mobile species, or percentage of coverage for  
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3 206 sessile species) and the Chao2 estimator of species richness (Chao et al., 2009) were calculated for  
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5 207 each site and each survey. Chao2 index values were calculated with presence/absence data of all taxa  
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8 208 using the R package SpadeR (Chao et al., 2016).  
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11 209 Non-metric multi-dimensional scaling (nMDS) was used to build ordination plots calculated from the  
12  
13 210 Sorensen-Dice similarity matrices. The nMDS analyses were conducted with the presence-absence  
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15  
16 211 data set of sessile and mobile species using the R package 'vegan' (Oksanen *et al.*, 2010). The nMDS  
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18 212 analysis was first applied to the full 2015 presence/absence dataset (41 sites) together with the 2017  
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21 213 dataset (9 sites) to assess the dissimilarity between these two periods and test if the samples from  
22  
23 214 2017 fit in the 2015 latitudinal pattern. The same analysis was repeated without singletons (taxa that  
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25 215 have been recorded in only one site and one year) to assess the effect of rare species (Supplementary  
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27  
28 216 information). The difference between abundance data and presence-absence data in the sites surveyed  
29  
30 217 in 2015 and 2017 was calculated to detect species with large changes in their abundance or spatial  
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33 218 distribution (Tables S1 and S2). We evaluated the median latitude of the distribution before and after  
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35 219 the El Niño events for each species observed both in 2015 and 2017. We compared median latitudes  
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38 220 in 2015 to those observed in 2017 using a paired t-test to assess a potential latitudinal shift in species  
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40 221 distributions.  
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43 222 Observations of 2017 were then combined with those obtained in 2015 in the same sites to test  
44  
45 223 whether the biogeographical zonation is robust to interannual variability. A second nMDS analysis  
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48 224 was performed for the combined dataset using the same methodology (Bray–Curtis similarity  
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50 225 matrices using presence-absence data). The influence of temperature on the rocky intertidal  
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53 226 biogeography was evaluated by least square linear regressions between the principal axis of this  
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55 227 second nMDS ordination and SST statistics calculated over the 2002-2018 period (annual mean,  
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58 228 February mean, July mean, and the variance of SST anomalies).  
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3 229 A power analysis was performed using the G\*Power 3.1 software (Faul et al., 2009) when no  
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5 230 correlation was detected between two variables. Post hoc evaluations were performed for bivariate  
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8 231 regression assuming normal distribution, using a 0.05  $\alpha$  significance level, and correlation coefficient  
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10 232  $R = 0$  as null hypothesis. We report  $R_{P0.8}$ , the minimum value of the true correlation coefficient so  
11  
12 233 that the dataset statistical power is above 0.8. In other words,  $R_{P0.8}$  represents the correlation  
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15 234 coefficient that the dataset can reject with a type II error probability less than 0.2, which is the  
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18 235 recommended threshold in statistical power analysis (Peterman, 1990). We also report the achieved  
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20 236 post-hoc power.

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23 237 Linear correlations were tested for spatial autocorrelation by evaluating the significance of the  
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25 238 Moran's I coefficient through Monte Carlo and normal distribution (Supplementary information).  
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28 239 When strong autocorrelations were found, generalized least squares (GLS) models were calculated so  
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30 240 the influence of the spatial structure was incorporated into the linear regression model through the  
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33 241 residual terms (Diniz-Filho et al., 2003). Different correlation spatial structures were tested, and the  
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35 242 best fitting model was defined using the lowest Akaike Information Criterion (AIC) along with the  
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38 243 less negative Log-Likelihood (LogLik) values (Supplementary information). Finally, a cluster  
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40 244 analysis using Sorensen-Dice index was performed, using the software 'PAST' (Hammer *et al.*,  
41  
42 245 2000), to study the similarity between study sites using presence-absence data of mobile and sessile  
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44  
45 246 species. Robustness of tree topologies was assessed through 10000 bootstrap replications. All  
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47 247 statistics, except when noted, were done using R 3.5.0 (R-Core Team, 2018), through the *spdep*  
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49  
50 248 (Bivand et al., 2013), *nlme* (Pinheiro et al., 2018), and *MuMIn* (Barton, 2020) packages.

### 51 52 53 249 54 55 250 **3. Results**

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58 251 Sites are listed in table 1 and hereafter referred to in the text and figures by their acronym and  
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60 252 latitude. The 2017 dataset is composed of 1076 observations (an observation being the  
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3 253 documentation of the presence of any given species within a set quadrat) resulting in 79 taxa, while  
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5 254 924 observations, resulting in 69 taxa were obtained in the same sites in 2015. Due to spring tides,  
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7  
8 255 hazardous swell or other logistic constrains, data from 13 quadrats (1 in PVE[4.17°S], 3 in  
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10 256 TAM[10.32°S], and 8 in PUC[12.47°S], representing 9.0% of the sampled surface) in 2015 and data  
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13 257 from one quadrat (PBA[4.68°S], representing 0.7 % of the sampled surface) in 2017 could not be  
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15 258 sampled. Observations obtained in 2015 and 2017 for the nine analyzed sites are reported in the  
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18 259 online supplementary data Table S1 as abundance data and in Table S2 as presence/absence data. The  
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20 260 complete 2015 dataset (41 sites) is available online in Ibañez-Erquiaga *et al.* (2018). Sampled-based  
21  
22 261 rarefaction analysis showed that the number of taxa is reasonably close to the asymptotic maximum  
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25 262 in the nine locations and both surveys, indicating that sampling effort was enough for obtaining an  
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27 263 acceptable representation of the taxonomic richness (Figure 4), thus supporting the validity of the  
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30 264 following analyses.

### 31 32 33 265 **3.1. Species incidence and abundance**

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35 266 In this study 104 taxa were identified, of which 79 were identified to the species level. 40 species  
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38 267 were observed only once in the 9 study sites.

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41 268 The most abundant sessile species was the barnacle *Jehlius cirratus* (19.5% of total coverage in 2015  
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43 269 and 13.6% in 2017). Other species with high abundance include the green algae *Ulva* spp., and the  
44  
45  
46 270 encrusting algae *Lithophyllum* spp.. The most abundant mobile species were the periwinkle  
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48 271 *Echinolittorina* spp. (accounting for 46.8% of total abundance in 2015 and 24.3% in 2017, reaching  
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50  
51 272 top densities of 521.3 individuals per m<sup>2</sup> in TAM[10.3°S] in 2015, the limpet *Scurria* spp.. The  
52  
53 273 periwinkle *Austrolittorina araucana*, highly abundant and characteristic of the upper intertidal zone  
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55  
56 274 in 2015 had disappeared in these sites in 2017 (Table S1).

57  
58 275 Among the 24 most abundant taxa (each representing over 1% of the total abundance or coverage), a  
59  
60  
61 276 majority was ubiquitous: *Echinolittorina* spp., *Jehlius cirratus*, *Scurria* spp., *Ulva* spp., *Tegula* spp.,  
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3 277 *Lithophyllum* spp., *Corallina officinalis*, encrusting brown algae. The anemone *Oulactis concinnata*  
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5 278 was the most abundant sessile species in the two northernmost sites ACA[3.7°S] and PVE[4.2°S].  
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8 279 Taxa with high abundance and only occurring in the Humboldt province include the mussel  
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10 280 *Perumytilus purpuratus*. Taxa with high abundance occurring only in the transition zone were the  
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13 281 snail *Stramonita haemastoma* and the red algae *Gelidium pusillum*.  
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19 283 We now report changes in taxa presence, abundance, and distribution between 2015 and 2017. 44  
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21 284 taxa have been identified both in 2015 and 2017. 25 taxa were observed in 2015 in those sites but not  
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23 285 in 2017, while conversely, 35 taxa were only observed in 2017. Among those 60 taxa that appeared  
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26 286 or disappeared, most (65%) are rare (observed only once). However, some of them, were widespread  
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28 287 and/or abundant in one of the surveys.  
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30  
31 288 Among the taxa that disappeared, 3 were widespread in 2015. The most notorious is *Austrolittorina*  
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34 289 *araucana*, abundant in all sites of the northern and central coast of Peru in 2015 in the upper  
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36 290 intertidal zone. The macroalgae *Grateloupia filicina*, abundant in 2015 in the central coast, from 5 to  
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38  
39 291 10°S, was not observed in 2017. The snails *Diloma nigerrimum* and *Prisogaster niger*, present in  
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41 292 2015 in the southern sites, disappeared in 2017. *Polysiphonia* spp. observed in 3 sites at different  
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43 293 latitudes in 2015 was absent in 2017. Important taxa whose distribution was strongly reduced in 2017  
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45  
46 294 include the limpet *Siphonaria* spp. which disappeared from 5 sites but curiously appeared in great  
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48 295 abundance in 2017 in PAG[5.8°S]. The algae *Gymnogongrus durvillei*, the anemone *Phymanthea*  
49  
50  
51 296 *pluvia*, and the mussel *Semimytilus algosus* disappeared from 4 sites, which shifted their distribution  
52  
53 297 southward by 4.8°, 6.4°, and 1.8° of latitude, respectively. *Jehlius cirratus*, the most abundant sessile  
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56 298 species of the Peruvian rocky shores, showed a decreased coverage in most sites in 2017.  
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58  
59 299 The 2017 survey also showed remarkable increases in some taxa. 4 taxa appeared in 3 to 6 sites in  
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61 300 2017: the snails *Mitrella baccata* and *Stramonita biserialis* in the northern sites, the cucumber  
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3 301 *Patallus mollis* in the south, and the sea anemona *Phymactis clematis* from 4.7° to 13.9°S. *Fissurella*  
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5 302 spp., restricted to 2 northern sites in 2015, spread in 5 sites down to the southernmost site. The chiton  
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8 303 *Acanthopleura echinata* was observed in 3 more sites. The limpet *Scurria spp.*, as well as the algae  
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10 304 *Corallina officinalis* and the encrusting brown algae (possibly *Ralfsia sp.*) became more widespread  
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13 305 and abundant and tend to expand their distribution northward.  
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15 306 We thus observe that some taxa shifted their distribution southward while others shifted northward.  
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18 307 The average latitudinal shift (estimated by the change in the median latitude of taxa presence) of all  
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20 308 taxa is not significant (t-test). Among the 9 main taxa that showed an increased abundance and  
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23 309 distribution, 6 are mobile and 3 are sessile. On the contrary, among the 8 main taxa that showed a  
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25 310 decreased abundance and distribution, a majority is sessile (5) and a minority is mobile (3).

28 311 Table 2. Summary of taxa richness and changes from 2015 to 2017  
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Number of taxa	ACA* [3.7°S]	PVE [4.2°S]	PBA [4.7°S]	YAC [5.1°S]	PAG [5.8°S]	PUE [7.5°S]	TAM [10.3°S]	PUC [12.5°S]	MIN [13.9°S]
In 2015 (N <sub>0</sub> )	24	26	14	25	16	18	25	20	21
In 2017 (N <sub>1</sub> )	9	26	25	22	23	22	22	15	25
appearing (N <sub>a</sub> )	5	13	18	7	13	14	7	7	12
disappearing (N <sub>d</sub> )	20	13	7	10	6	10	10	12	8
persisting	4	13	7	15	10	8	14	8	13
net change	-15	0	11	-3	7	4	-3	-5	4
turnover % **	75.8	50	64.1	36.2	48.7	60	36.2	54.3	43.5

42 312 \* This site was not representative of the rocky intertidal in 2017  
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44 313 \*\*  $100(N_a+N_d)/(N_0+N_1)$   
45 314  
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### 48 315 3.2. Species richness and species turnover

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50  
51 316 The differences in the Chao2 richness estimator from 2015 to 2017 does not show any clear  
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53 317 geographical pattern. When considering all sites together, no significant difference was detected in  
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55  
56 318 species richness between 2015 and 2017, neither for mobile, sessile taxa, or all taxa together  
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58 319 (Wilcoxon signed rank test, and t-test,  $p>0.95$  in all cases). Thus, at regional scale, no significant  
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3 320 increase nor decrease in the taxonomic richness as estimated by the Chao2 index was detected four  
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5 321 months after the El Niño events.  
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8 322 Some substantial changes were site specific. A strong reduction of species richness is observed in  
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10 323 2017 in ACA[3.7°S], which can be explained by a significant increase of sand coverage (t-test,  
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13 324  $p < 0.05$ ) in this site and the subsequent reduction of the rocky intertidal (only two mobile species  
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15 325 were registered while 8.5 mobile species per site were registered in average). In other sites, rock  
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18 326 coverage did not vary among sampling sets (Wilcoxon signed ranks test,  $p = 0.91$ ), and sand coverage  
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20 327 of the rocky shore areas was zero south of 5° S. This change in ACA[3.7°S] was possibly the result  
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22  
23 328 of coastal geomorphological dynamics due to increased river discharge and sandbank movement  
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25 329 during the 2017 El Niño event (Rodríguez-Morata *et al.*, 2018).  
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28 330 The large decrease in species richness observed in the southern site PUL[12°S] is likely related to the  
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30 331 incomplete sampling in 2015 when only 8 out of 16 quadrats could be sampled because of logistics  
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33 332 constraints. This results in a large data dispersal in the Chao2 index for 2015. A significant increase  
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35 333 in species richness is observed in PAG[5.8°S], a site that lies in the biogeographic transition zone.  
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38 334 The number of taxa recorded in this site increased from 16 in 2015 to 23 in 2017 (Table 2). This net  
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40 335 increase is composed by a loss of 6 species (2 mobile and 4 sessile) and a gain of 13 species (7  
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42  
43 336 mobile, 6 sessile). The largest net increase in the number of species is observed in PBA[4.7°S] with  
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45 337 11 additional species in 2017 (2 mobile, 9 sessile) compared to 2015. However, the small difference  
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48 338 in the Chao2 index values suggest this may mainly result from under-representation of the 2015  
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50 339 sample.  
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52  
53 340 The turnover of taxa from 2015 to 2017 is relatively high (Table 2), from 36% taxa in TAM[10.3°S]  
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55 341 (17 taxa appearing or disappearing in the record) to 64% taxa in PBA[4.7°S] (25 taxa appearing or  
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57  
58 342 disappearing in the record). One of the largest change in taxa is observed in the northern site  
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60 343 PVE[4.2°S], with 13 taxa that disappeared and 13 new species in the 2017 record compared to 2015.  
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### 3.3. Dissimilarities of rocky intertidal communities between 2015 and 2017

In the first nMDS ordination analysis, samples from 2017 are dissimilar to 2015 along axis 2, while both datasets are similarly distributed along axis 1 (Figure 6A). This latter result suggests that, in 2015 like in 2017, the communities are primarily structured by the same environmental factors. For instances, sites observed in 2017 after the El Niño events are similar along axis 1 as also observed for 2015. The axis 1, which explains 54% of the variability of the complete dataset, is clearly related to the latitudinal mean SST gradient (Figure 6B). The sites surveyed in 2017 are aligned along a similar relationship with mean annual SST as the 41 sites surveyed in 2015 (Figure 6B) confirming that the rocky intertidal communities are latitudinally structured, as already shown by Ibañez-Erquiaga et al. (2018), and that this latitudinal gradient persisted after the El Niño events.

The axis 2, which explains 33% of the variability, seems largely driven by the difference between 2015 and 2017. All the sites surveyed in 2017 show a positive shift along axis 2 since 2015 (arrows in figure 6A). Because a large proportion of taxa have been observed only once (~40%), we performed a nMDS analysis excluding singletons, which showed a similar pattern (Supplementary information). The separation of the 2015 and 2017 dataset along axis 2 is therefore not related to the occurrence of rare and potentially seasonal species, but rather to the changes in the distribution of important species described in section 3.1. The disappearance of *Austrolittorina araucana*, *Prisogaster niger*, and *Grateloupia filicina* in the 2017 samples together with the widespread apparition of *Mitrella baccata*, *Stramonita biserialis*, and *Phymactis clematis* played in particular a major role. As a consequence, the dissimilarity between the 2015 and 2017 surveys is likely due to environmental factors which may be related to El Niño or to seasonal variations since the 2015 observations were made between February and April while 2017 observations were made in October.

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3 367 The similarity of the 9 sites surveyed in 2017 compared to the 41 sites surveyed in 2015 is observed  
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5 368 in a cluster analysis (Figure 7). Besides two 2105 sites separated because of anthropogenic impact  
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8 369 (ANC and BAR) and ACA[3.7°S] which was covered in sand in 2017, the sites are distributed in 4  
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10 370 groups, which, despite low bootstrap values, are biogeographically consistent. The northernmost site  
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13 371 of 2017 PVE[4.2°S] (pink branch), the Peruvian Panamic province (orange branches) in which  
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15 372 PBA[4.7°S] and PAG[5.8°S] are included in 2017, the transition zone (red) as defined in 2015, and  
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18 373 the Humboldt province in which 4 sites of 2017 are grouped together. All sites of the Humboldt  
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20 374 province in 2015 belong to the Humboldt province of 2017, except for the northernmost,  
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22 375 PAG[5.8°S], which appears in the Panamic province group in 2017. The cluster analysis indicates  
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25 376 that 2017 samples tend to group together within their respective ecological province, which confirms  
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27 377 that the change in rocky intertidal communities from 2015 to 2017 does not correspond to a  
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30 378 replacement of Humboldt communities by Panamic communities, but rather to the emergence of new  
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32 379 taxa assemblages. The outside position of PVE[4.2°S] in 2017 suggests the record of a dissimilar  
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35 380 Panamic community in northern Peru in 2017. This is supported by the fact that among the 13 new  
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37 381 taxa observed in PVE[4.2°S] in 2017, 8 have not been observed in any other site, and 2 were only  
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39 382 observed further north in ACA[3.7°S] in 2015.

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#### 45 384 **3.4. The latitudinal structure of rocky intertidal communities**

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48 385 Whatever their cause, the differences between 2015 and 2017 evidence a strong seasonal to  
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51 386 interannual variability of rocky shore communities. The 2017 observations were pooled with the  
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53 387 2015 observations from the same sites and analyzed to test the robustness of the biogeographical  
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55 388 zonation found in rocky intertidal communities by Ibañez-Erquiaga et al. (2018) to this interannual  
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57  
58 389 variability. The nMDS ordination analysis of the pooled dataset provided a pattern that is consistent  
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60 390 with the site latitudinal sequence (Figure 8A). The nMDS analysis showed a slight horseshoe effect,  
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3 391 which is common in ordination techniques due to the fact that the axes are forced to be uncorrelated,  
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5 392 but are not necessarily independent (Legendre and Gallagher, 2001). The first axis explained 84% of  
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8 393 the ordination and the second axis 1%.

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11 394 We evaluated the relationship between the long-term persisting geographical structure of the rocky  
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13 395 intertidal communities with long-term SST statistics. The first axis was significantly and strongly  
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15 396 correlated with mean annual SST ( $R=0.93$ ,  $p=0.001$ ) (Figure 8B) and mean SST of July (winter)  
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17  
18 397 ( $R=0.89$ ,  $p=0.001$ ). Statistically significant spatial autocorrelations ( $p<0.05$ ) were observed between  
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21 398 these two variables and the first axis, however, in both cases GLS maintain significant correlations  
22  
23 399 ( $p=0.0001$  for the mean annual SST and  $p=0.004$  for the mean SST of July) with lower AIC values  
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25 400 (23.29 and 23.92, respectively) improving the explanatory power of the model (Supplementary  
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27  
28 401 information). The correlation observed between the first axis and with mean SST of February  
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30 402 (summer) ( $R=0.77$ ,  $p=0.195$ ,  $R_{P0.8}=0.79$ ,  $power=0.87$ ) was not significant, suggesting that summer  
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33 403 temperatures are less determinant than winter temperatures in the biogeography of rocky intertidal  
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35 404 species. On the other hand, no correlation was observed between the ordination's first axis and long-  
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38 405 term ENSO-related variability ( $R=0.10$ ,  $p=0.82$ ,  $R_{P0.8}=0.79$ ,  $power=0.06$ ) (Figure 8C) nor with the  
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40 406 mean seasonal SST range ( $R=0.06$ ,  $p=0.872$ ,  $R_{P0.8}=0.79$ ,  $power=0.05$ ).

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43 407 The cluster analysis of the pooled incidence dataset (Euclidian cluster,  $R=0.93$ ) confirms that the  
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45 408 latitudinal organization of rocky intertidal communities found in the snapshot observation of 2015, is  
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48 409 maintained when the interannual variability is integrated (Figure 9). Locations were grouped into two  
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50 410 main branches: the northern branch, corresponding to warm conditions of the Panamic province  
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52  
53 411 includes ACA[3.7°S] and PVE[4.2°S]. The southern branch is itself divided in two groups: the  
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55 412 transition zone, which includes three sites located to the north of the Illescas Peninsula, PBA[4.7°S],  
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58 413 YAC[5.1°S] and PAG[5.8°S], and the Humboldt province which includes the 4 remaining  
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60 414 southernmost sites. High bootstrap scores indicate a robust structure.

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## 4. Discussion

### 4.1. Changes in taxonomic diversity

The effects of El Niño on intertidal communities depend on the intensity and magnitude of the event. Although, the coupled oceanographic-atmosphere variability is similar, the biological responses are not always predictable (Arntz *et al.* 2006). Some responses are similar among events, strong El Niño (1982-83 and 1997-98) increased the diversity of macrobenthos on hypoxic soft-bottoms due to the increase of oxygen concentration, and colonization by low latitude immigrant species in central Peru (Tarazona *et al.* 1988a,b). Also, neritic fish assemblages would add tropical species and cold-adapted fish would extend their distributional ranges down to central Chile (Sielfeld *et al.* 2010). In rocky shore communities the most important change documented is the mass mortality of kelp beds (Martínez *et al.* 2003) which could open rocky primary space in Peru and northern of Chile. This could trigger the colonization and recovery of communities via immigration and settlement of surviving species, but there is no available evidence on how this could affect diversity patterns. Our results indicate that, at the scale of the north-central Peruvian coast, the 2015-2016 and the 2017 El Niño events did not promote an overall change in the taxonomic richness of rocky intertidal communities. The disappearing of species between the two surveys was in average compensated by the occurrence of new species. We tested whether this could mask spatial contrasts related to the fact that the 2017 El Niño SST anomaly was not of equal amplitude along the latitudinal transect of our study. SST anomalies peaked everywhere during March 2017 (Figure 2), but were highest (5-6°C) along the central coast between 5 and 9°S (Figure 3F), and limited to 1-2°C in the northernmost and southernmost sites. No significant relationship is observed between the amplitude of the El Niño 2017 SST anomaly and the Chao2 estimator change, nor with the level of taxa turnover, which may be partly due to the low statistical power resulting from the limited number of sites. However, the

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3 439 largest increase in Chao2 index was observed in PAG[5.8°S], the largest net increase in taxonomic  
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5 440 richness in PBA[4.7°S], and the largest turnover in PBA[4.7°S] and PUE[7.5°S]. All these sites  
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8 441 experienced El Niño SST anomalies larger than 5°C, supporting some level of impact of the 2015  
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10 442 and 2017 El Niño events on rocky intertidal diversity, especially in the transition zone.  
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#### 16 444 **4.2. Changes in species distribution**

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19 445 The warm anomaly associated to an El Niño event may be a stressor for some species and may  
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21 446 favour others, while some El Niño adapted species would show no response at all (e.g. Barahona *et*  
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24 447 *al.* 2019). Overall, it could be predicted that El Niño produces a southward shift of species, either by  
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26 448 inducing mortality in the northern limit of their distribution where conditions would exceed some  
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29 449 physiological or ecological threshold, or by favouring a migration towards higher latitudes (Riascos  
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31 450 *et al.*, 2009; Sotil *et al.*, 2008; Carstensen *et al.*, 2010). Here, we found that the average shift of  
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34 451 incidence median latitude is non-significant for mobile or sessile taxa (t-test). The large distribution  
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36 452 changes observed for some taxa were not all directed southward.  
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39 453 Based on presence/absence analysis a pattern among sites and years emerge. Mobile gastropods such  
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41 454 as *Fissurella* spp., *Mitrella baccata*, *Scurria* spp., *Stramonita biserialis*, and the sea anemone  
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44 455 *Phymactis clemactis* were present in most of the sites sampled in 2017 but almost absent in 2015.  
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46 456 These species are mobile and while they can inhabit exposed rocky surfaces, they can also move into  
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49 457 crevices and sheltered areas of the habitat. Thus, these species may undergo undetected during  
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51 458 sampling, but it is unlikely that this may have happened at multiple sites. The same reasoning applies  
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54 459 to those taxa present in 2015 but absent or strongly reduced in 2017: gastropods *Austrolittorina*  
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56 460 *araucana*, *Prisogaster niger*, *Siphonaria* spp., the anemone *Phymanthea pluvia*, but not for the  
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59 461 mytilid *Semimytilus algosus*, and algae *Grateloupia filicina*, *Gymnogongrus durvillei*, and  
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61 462 *Polysiphonia* spp.. *G. filicina* is considered an annual species, with plants showing higher  
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3 463 abundances and sizes during summer, and re-growing from the perennial attachment disc in spring  
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5 464 after overwintering (Irvine 1983). The absence of *G. filicina* during 2017 spring could be explained  
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8 465 by the fact that the perennial attachment disc is difficult to identify in the field or by the small size of  
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10 466 young plants growing from it. In contrast, *G. durvillei* is usually found all year in central and north-  
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13 467 central coast of Peru (Hidalgo et al. 2008; Li-Alfaro and Zafra-Trelles 2012; Pisfil-Farro 2014;  
14  
15 468 Rojas-Paredes 2014). Its absence in multiple sites during spring 2017 could not be attributed to  
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18 469 seasonality and is likely linked to El Niño events. *S. algosus* (Tarazona et al. 1985) and other  
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20 470 mytilids (e.g., Gamarra and Cornejo 2002; Avendaño and Cantillanez 2011) have been reported to  
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22 471 experience mortality and recruitment failure during and after strong El Niño events.  
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25 472 The ecology and seasonality of most marine species from Peru remains unknown. In the absence of  
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28 473 long-term control observations, we cannot clearly attribute the observed changes in distribution and  
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30 474 abundance to seasonal processes or to El Niño perturbations (Paine, 1986). Sessile taxa should,  
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33 475 however, exhibit less seasonal variation in the presence/absence data and may thus reflect more  
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35 476 closely direct or indirect El Niño impacts. Among widespread sessile species, 2 were completely  
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38 477 absent in 2017 (*G. filicina*, *Polysiphonia spp.*) and 3 were strongly reduced (*G. durvillei*, *P. pluvia*,  
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40 478 and *S. algosus*) and all shifted south, which is consistent with a SST-related stress. Some sites reveal  
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42 479 some interesting changes: the fact that PAG[5.8°S] taxon assemblage belonged to the Humboldt  
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45 480 province in 2015 and to the transition branch after the El Niño events in 2017 (Figure 7) suggests that  
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47 481 the new rocky intertidal community in this site is at least partly due to southward species migration  
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50 482 facilitated by El Niño conditions from 2015 to 2017. The occurrence of 8 new Panamic species in  
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52 483 PVE[4.2°S] in 2017, which places this northernmost assemblage outside the cluster analysis (Figure  
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55 484 7), also supports a southward migration of species consistent with the expected impact of El Niño  
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57 485 events.  
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3 486 Some taxa, on the other hand, do not fit in this scenario. The three sessile taxa that widely spread  
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5 487 from 2015 to 2017 (*Corallina officinalis*, encrusting brown algae, *Phymactis clematis*) are not warm  
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8 488 water taxa but ubiquitous taxa, that expanded in both Panamic and Humboldt provinces. A few  
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10 489 species also show an interesting northward expansion (brown algae *Colpomena tuberculata*,  
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12  
13 490 *Colpomena sinuosa*). The expansion of those species was therefore not caused by favourable physical  
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15 491 conditions during El Niño events, but was more likely an indirect consequence of those events  
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18 492 through a modified ecological network.  
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### 23 494 **4.3. El Niño impacts on community structure**

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26 495 Changes in community structures between 2015 and 2017 are evidenced in the nMDS (Figure 6) and  
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28  
29 496 the cluster analysis (Figure 7). These changes are linked to large changes in the latitudinal  
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31 497 distribution of a few widespread species, likely caused, at least for some of them, by El Niño regional  
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34 498 environmental anomalies occurred in 2015-2016 and 2017. Quantifying how much of the community  
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36 499 change can be attributed to El Niño and how much to seasonal variations will require additional  
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39 500 surveys in those sites.  
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41 501 The change in the communities from 2015 to 2017 was not characterized by a shift along a  
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44 502 temperature-related axis (axis 1 of nMDS analysis, Figure 6) as one could expect from El Niño  
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46 503 impacts. The 2017 communities are thus not simply the result of the southward migration of species  
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48  
49 504 and the replacement of "temperate" taxa by "Panamic" taxa. This process, which has been reported  
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51 505 for earlier extreme El Niño events (Tarazona et al. 1988a,b; Arntz et al. 2006) was only secondary  
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54 506 here, possibly because the amplitude and duration of the temperature anomaly was not as large than  
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56 507 in those extreme events. The primary process responsible for the 2015 to 2017 community change  
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59 508 might thus be ecological.  
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3 509 Since some of the taxa impacted here are major component of the rocky intertidal communities, we  
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5 510 can speculate that their local disappearing or expansion produced a secondary positive or negative  
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8 511 impact on other taxa that had not been directly affected by the physical or chemical anomalies  
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10 512 associated to the El Niño events. In this view, the physico-chemical conditions of El Niño may have  
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13 513 only been the trigger of a chain of impacts across the ecological network of Peruvian rocky shores. A  
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15 514 detailed study of the ecological interactions between the most impacted species would be needed to  
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18 515 test this hypothesis.

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#### 22 23 517 **4.4. Robustness of the biogeographic zonation**

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26 518 Merging the 2015 and 2017 dataset integrates part of the seasonal and interannual variability which  
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29 519 therefore provides us with a dataset that is more representative of the long-term biogeographical  
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31 520 features. The nMDS (Figure 8) and the Euclidian cluster (Figure 9) analyses on the merged dataset  
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34 521 showed a latitudinally coherent pattern of the rocky shore communities, coinciding with the  
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36 522 biogeographic zonation proposed by Ibañez-Erquiaga *et al.* (2018) based on a snapshot picture of the  
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39 523 rocky shore communities before the El Niño event. The coastal sites are divided in 3 groups  
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41 524 belonging to the Panamic province in the north, the Humboldt Province in the central coast, and a  
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43 525 transition zone that shares more similarity with the Humboldt province than with the Panamic  
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46 526 province (Figure 9). The zonation obtained with the joint dataset suggests that the exposition to the  
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48 527 2015-16 and 2017 El Niño events and the change in communities described above did not alter the  
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51 528 biogeographical structure of rocky intertidal species along the Peruvian coast. The dominant axis that  
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53 529 structures the sites in the nMDS analysis is strongly correlated with mean surface temperature  
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56 530 (Figure 8B), especially winter temperature. This is consistent with the fact that the community  
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58 531 change from 2015 to 2017 is described by nMDS axis 2, which is independent from axis 1 related to  
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61 532 mean SST (Figure 6).

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3 533 No correlation is observed with long-term ENSO variance (Figure 8C). This shows that interannual  
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5 534 temperature anomalies, although very high in Peru for the influence of ENSO, do not play a primary  
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8 535 role in the latitudinal structure of rocky intertidal communities in the northern and central coast of  
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10 536 Peru. Additional environmental factors besides SST, wave impact, water oxygen content, nutrient  
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13 537 concentration and air temperature, may be determinant in the biogeographical distribution of the  
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15 538 intertidal rocky communities and require further studies. Broitman *et al.* (2001) showed that more  
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18 539 than mean SST and latitude, the influence of coastal upwelling cells was the driving force in the  
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20 540 geographic patterns in the rocky intertidal of Central Chile. Another comprehensive study in Chile  
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22 541 (assessing about 24° of latitude between 18°S and 42°S) showed a mid-latitudinal peak (at 30-32°S)  
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25 542 in species diversity (Rivadeneira *et al.*, 2002) that could be due to a combination of regional  
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27 543 environmental conditions and local ecological interactions. In the same sense, Ibañez-Erquiaga *et al.*  
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30 544 (2018) found phosphate concentrations to be one of the main potential drivers of biogeographic  
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32 545 patterns at the intertidal communities at the Peruvian coast. Further work, increased sampling  
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35 546 resolution, analysis of additional variables, and long-term ecological records are needed in Peru to  
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37 547 describe more precisely the role of upwelling cells and ecological relationships in the rocky intertidal  
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40 548 communities and disentangle these variables from the SST which is strongly linked to the coastal  
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42 549 upwelling in this region.

## 43 44 45 550 46 47 48 551 **5. Conclusions**

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51 552 We have presented the first insights into the response of the rocky intertidal community to two  
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53 553 successive El Niño event in Peru (2015-16 and 2017) by analyzing the taxonomic diversity of  
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56 554 macrobenthic species, their geographic distribution, and the latitudinal structure of communities  
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58 555 observed in austral fall 2015 after 17 years of stable La Niña conditions and in austral spring 2017,  
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61 556 four months after the end of the 2017 coastal El Niño event. The 2017 El Niño produced during  
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3 557 about three months a strong SST anomaly in the central and northern coast of Peru (Echevin et al.,  
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5 558 2018) that reached 6°C at its maximum and triggered strong rainfalls (Rodríguez-Morata *et al.* 2018).  
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8 559 We find that four months after this violent environmental disturbance, the taxonomic richness has not  
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10 560 significantly changed at the regional scale, but an important turnover of species was observed  
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13 561 everywhere, and especially in the transition zone, where the highest SST anomalies occurred. A  
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15 562 southward migration of taxa, resulting from the southward shift of SST pattern during El Niño events  
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18 563 in this region, has apparently occurred in some sites of northern Peru, especially in PVE[4.2°S]  
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20 564 where eight Panamic species appeared. However, this mechanism did not trigger a strong latitudinal  
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22 565 change on the structure of the communities. While the rocky shore communities are clearly structured  
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25 566 along a latitudinal SST gradient, the change in species assemblages observed in 2017 occurred in a  
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27 567 direction independent from this SST gradient. The change in species assemblages was mainly driven  
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30 568 by the large distribution reduction of some important widespread species (*Austrolittorina araucana*,  
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32 569 *Prisogaster niger*, *Siphonaria* spp., *Grateloupia filicina*, *Gymnogongrus durvillei*, *Phymanthea*  
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35 570 *pluvia*, *Semimytilus algosus*) and the spread of some other species (*Fissurella* spp., *Mitrella baccata*,  
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37 571 *Scurria* spp., *Stramonita biserialis*, *Corallina officinalis*, *Phymactis clematis*). In the absence of long-  
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39 572 term record of the rocky intertidal communities in Peru, the change observed from 2015 to 2017  
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42 573 cannot be simply attributed to seasonal variations or to the El Niño events. However, since some of  
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44 574 these important species are clearly not seasonal, we must conclude that at least part of these changes  
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47 575 was caused by large scale regional environmental perturbations associated to the 2015-16 and 2017  
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49 576 El Niño events. The primary environmental impact on some ecologically key species likely triggered  
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52 577 a chain of secondary impacts through ecological relationships which lead to a complex change in  
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54 578 rocky shore communities. Further studies are needed to better characterize the seasonal and  
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57 579 interannual variability of the rocky intertidal communities and their drivers. When this interannual  
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59 580 variability is integrated, the 9 study sites show a very robust structure determined by the latitudinal  
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61 581 SST gradient along the Peruvian coast.  
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### **Author Contributions**

JV and MC conceived the project idea. BI, JV and MPH carried out the field and laboratory work. BI, LW, JV, MPH and AI carried out the invertebrate identification. JAP, JV, BI and LW carried out the algae identification. JV, MC, ASP, BI, DO performed the data analysis. RSG, DO, JC, ASP aided in interpreting the results and worked on the manuscript. All authors discussed the results, provided critical feedback and contributed to the final manuscript.

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### **Conflict of Interest**

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604 The authors declare that the research was conducted in the absence of any commercial or financial  
605 relationships that could be construed as a potential conflict of interest.

606  
**References**

608 Aguilera, M. A., Valdivia, N., Broitman, B. R. (2013). Spatial niche differentiation and coexistence  
609 at the edge: co-occurrence distribution patterns in *Scurria* limpets. *Marine Ecology Progress*  
610 *Series*, 483, 185-198.

611 Arntz, W. E. (1986). The two faces of El Niño 1982-83. *Meeresforschung*. 31( I): 1-46.

612 Arntz, W.E., Brey, T., Tarazona, J., Robles, A. (1987). Changes in the structure of a shallow sandy-  
613 beach community in Peru during an El-Niño event. *S Afr J Marine Sci.* 5, 645–658.

614 Arntz, W.E., Valdivia, E., Zeballos, J. (1988). Impact of El Niño 1982–83 on the commercially  
615 exploited invertebrates (mariscos) of the Peruvian shore. *Meeresforschung*. 32, 3–22.

616 Arntz, W.E., Gallardo, V. A., Gutiérrez, D., Isla, E., Levin, L. A., et al. (2006). El Niño and similar  
617 perturbation effects on the benthos of the Humboldt, California, and Benguela Current upwelling  
618 ecosystems. *Advances in Geosciences. Enrgy Proced.* 6, 243-265.

619 Avendaño, M., Cantillanez, M. (2011). Reestablishment of *Choromytilus chorus* (Molina, 1782)  
620 (Bivalvia: Mytilidae) in northern of Chile. *Lat. Am. J. Aquat. Res.* 39(2), 390-396.

621 Barahona, S.P., Vélez-Zuazo, X., Santa-Maria, M., & Pacheco, A.S. (2019). Phylogeography of the  
622 rocky intertidal periwinkle *Echinolittorina paytensis* through a biogeographic transition zone in  
623 the Southeastern Pacific. *Mar. Ecol.* 00:e12556. <https://doi.org/10.1111/maec.12556>

624 Barber, R.T., Chavez, F.P. (1983). Biological consequences of El Niño. *Science*. 222, 1203-1210.

625 Bivand, RS, Pebesma, E, Gomez-Rubio, V (2013). *Applied spatial data analysis with R*, Second  
626 edition. Springer, NY. <http://www.asdar-book.org/>.

- 1  
2  
3 627 Blanchette, C.A., Melissa Miner, C., Raimondi, P.T., Lohse, D., Heady, K.E.K., Broitman, B.R.  
4  
5 628 (2008). Biogeographical patterns of rocky intertidal communities along the Pacific coast of  
6  
7  
8 629 North America. *Journal of Biogeography* 35, 1593–1607. <https://doi.org/10.1111/j.1365->  
9  
10 630 2699.2008.01913.x  
11  
12  
13 631 Broitman, B.R., Navarrete, S.A., Smith, F., Gaines, S.D., (2001). Geographic variation of  
14  
15 632 southeastern Pacific intertidal communities. *Mar Ecol Prog Ser.* 224, 21-34.  
16  
17  
18 633 Broitman, B.R., Véliz, F., Manzur, T., Wieters, E., Finke, R., Fornes, P., Valdivia, N., Navarrete,  
19  
20 634 S.A. (2011). Geographic variation in diversity of wave exposed rocky intertidal communities  
21  
22 635 along central Chile. *Rev Chil Hist Nat.* 224, 21-34.  
23  
24  
25 636 Castilla, J.C., Camus, P.A. (1992). The Humboldt–El Niño scenario — coastal benthic resources and  
26  
27 637 anthropogenic influences, with particular reference to the 1982/83 ENSO. *S Afr J Marine Sci.*  
28  
29  
30 638 12, 703–712.  
31  
32 639 Camus, P. (2008). Understanding biological impacts of ENSO on the eastern Pacific: an evolving  
33  
34  
35 640 scenario. *Int J Environ Heal R.* 2(1): 5-18.  
36  
37 641 Cane, M. A. (1983). Oceanographic events during El Niño. *Science.* 222, 1189-1195.  
38  
39  
40 642 Carré, M., Sachs, J. P., Schauer, A. J., Rodríguez, W. E., Ramos, F. C. (2013). Reconstructing El  
41  
42 643 Niño-Southern Oscillation activity and ocean temperature seasonality from short-lived marine  
43  
44 644 mollusk shells from Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 371, 45-53.  
45  
46  
47 645 Carstensen, D., Riascos, J. M., Heilmayer, O., Arntz, W. E., Laudien, J. (2010). Recurrent,  
48  
49 646 thermally-induced shifts in species distribution range in the Humboldt current upwelling system.  
50  
51  
52 647 *Marine Environmental Research*, 70, 293- 99. Doi: [10.1016/j.marenvres.2010.06.001](https://doi.org/10.1016/j.marenvres.2010.06.001)  
53  
54 648 Chao, A., Colwell, R.K., Lin, C.-W., Gotelli, N.J. (2009). Sufficient sampling for asymptotic  
55  
56 649 minimum species richness estimators. *Ecology* 90, 1125–1133. <https://doi.org/10.1890/07->  
57  
58  
59 650 [2147.1](https://doi.org/10.1890/07-2147.1)  
60  
61  
62  
63  
64  
65

- 1  
2  
3 651 Chao, A., Ma, K. H., Hsieh, T. C., Chiu, C.H. (2016). SpadeR: Species-Richness Prediction and  
4  
5 652 Diversity Estimation with R. R package version 0.1.1. [https://CRAN.R-](https://CRAN.R-project.org/package=SpadeR)  
6  
7  
8 653 [project.org/package=SpadeR](https://CRAN.R-project.org/package=SpadeR)  
9
- 10 654 Diniz- Filho, J. A., Bini, L. M., Hawkins, B. A. (2003). Spatial autocorrelation and red herrings in  
11  
12 655 geographical ecology. *Global Ecology and Biogeography*, 12(1), 53-64.  
13  
14
- 15 656 Echevin, V., Colas, F., Espinoza-Morriberon, D., Vasquez, L., Anculle, T., Gutierrez, D., 2018.  
16  
17 657 Forcings and Evolution of the 2017 Coastal El Niño Off Northern Peru and Ecuador. *Frontiers in*  
18  
19  
20 658 *Marine Science* 5, 367. <https://doi.org/10.3389/fmars.2018.00367>  
21
- 22 659 Espino, M. (1999) El Niño 1997-98: Su efecto sobre el ambiente y los recursos pesqueros en el Perú.  
23  
24 660 *Rev Peru Biol. Vol. Extraordinario: 97-109*  
25  
26
- 27 661 Faul, F., Erdfelder, E., Buchner, A., Lang, A.-G. (2009). Statistical power analyses using G\*Power  
28  
29  
30 662 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, 41, 1149-1160.  
31
- 32 663 Gamarra, A., Cornejo, O. (2002). Study of the mussel *Aulacomya ater* Molina, 1782 (Bivalvia:  
33  
34 664 Mytilidae) near Santa Rosa Island, Independence Bay, during El Niño phenomenon 1997-98.  
35  
36  
37 665 *Investig. Mar.* 30(Supl. 1) <http://dx.doi.org/10.4067/S0717-71782002030100045>  
38
- 39 666 Garreaud, R. D. (2018), A plausible atmospheric trigger for the 2017 coastal El Niño, *International*  
40  
41  
42 667 *Journal of Climatology*, 38, e1296-e1302.  
43
- 44 668 Glynn, P.W. (1988). El Niño Southern Oscillation 1982–1983 — nearshore population, community,  
45  
46  
47 669 and ecosystem responses. *Ann Rev Ecol S.* 19, 309–345.  
48
- 49 670 Gotelli, N.J., Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the  
50  
51  
52 671 measurement and comparison of species diversity. *Ecol Lett.* 4, 379–391.  
53
- 54 672 Hammer, O., Harper, D.A.T. and Ryan, P.D. (2000). PAST; paleontological statistics software  
55  
56 673 package for education and data analysis. *Palaeontologia Electronica*, 4(1): 9.  
57  
58
- 59 674 Hidalgo, F.J., Firstater, F.N., Fanjul, E., Cielo Bazterrica, M., Lomovasky, B.J., Tarazona, J.,  
60  
61 675 Iribarne, O.O. (2008) Grazing effects of the periwinkle *Echinolittorina peruviana* at a central  
62  
63  
64  
65

1  
2  
3 676 Peruvian high rocky intertidal. *Helgol. Mar. Res.* 62 (suppl 1):S73–S83. doi:10.1007/s10152-  
4  
5 677 007-0086-3  
6  
7  
8 678 Huang, B., L'Heureux, M., Hu, Z.-Z., Zhang, H.-M. (2016). Ranking the strongest ENSO events  
9  
10 679 while incorporating SST uncertainty. *Geophysical Research Letters.* 43, 9165-9172.  
11  
12  
13 680 Ibañez-Erquiaga, B., Pacheco A.S., Rivadeneira, M.M., Tejada, C.L. (2018) Biogeographical  
14  
15 681 zonation of rocky intertidal communities along the coast of Peru (3.5–13.5° S Southeast Pacific).  
16  
17 682 PLoS ONE 13(11): e0208244.  
18  
19  
20 683 Irvine, L. M. (1983). *Seaweeds of the British Isles. Vol 1: Rhodophyta. Part 2A Cryptonemiales*  
21  
22 684 (sensu stricto) *Palmariales, Rhodymeniales.* British Museum, London.  
23  
24  
25 685 JPL MUR MEaSURES Project. 2015. GHRSSST Level 4 MUR Global Foundation Sea Surface  
26  
27 686 Temperature Analysis (v4.1). Ver. 4.1. PO.DAAC, CA, USA. [https://doi.org/10.5067/GHGMR-](https://doi.org/10.5067/GHGMR-4FJ04)  
28  
29 687 [4FJ04](https://doi.org/10.5067/GHGMR-4FJ04).  
30  
31  
32 688 Legendre, P., Gallagher, E.D. (2001). Ecologically meaningful transformations for ordination of  
33  
34 689 species data. *Oecologia.* 129, 271-280. doi:10.1007/s004420100716.  
35  
36  
37 690 Li-Alfaro, G., Zafra-Trelles, A. (2012). Composición, abundancia y diversidad de macroalgas en el  
38  
39 691 litoral de puerto Malabrigo, La Libertad - Perú 2009. *Sciéndo* 15, 33-42.  
40  
41  
42 692 Martínez, A., Cárdenas, L., & Pinto, R. (2003) Recovery and genetic diversity of the intertidal kelp  
43  
44 693 *Lessonia nigrescens* (Phaeophyceae) 20 years after El Niño 1982/83. *J. Phycol.* 39(3), 504-508.  
45  
46  
47 694 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, R.G., O'Hara, B., Simpson, G.L., Solymos, P.,  
48  
49 695 Stevens, H.H. and Wagner, H. (2010). *Vegan: Community Ecology Package*, pp. R package  
50  
51 696 version 1.17-4, <http://CRAN.R-project.org/package=vegan>.  
52  
53  
54 697 Paine, R. T. (1986). Benthic community-water column coupling during 1982-1983 El Niño. Are  
55  
56 698 community changes at high latitudes attributable to cause or coincidence? *Limnol. Oceanogr.*  
57  
58 699 31(2): 351-360.  
59  
60  
61  
62  
63  
64  
65

1  
2  
3 700 Paredes, C. (1974). El modelo de zonación en la orilla rocosa del departamento de Lima. *Rev Peru*  
4  
5 701 *Biol, 1*, 168-191.  
6  
7  
8 702 Paredes, C., Tarazona, J., Canahuire, E., Romero, L., Cornejo, O., Cardoso, F. (1998). Presence of  
9  
10 703 tropical mollusks from the Panamanian province in the central coast of Peru and relation with the  
11  
12  
13 704 events "El Niño". *Rev Peru Biol. 5*(2): 123-128.  
14  
15 705 Peterman, R. M. (1990). Statistical power analysis can improve fisheries research and management.  
16  
17 706 *Canadian Journal of Fisheries and Aquatic Sciences*, 47(1), 2-15.  
18  
19  
20 707 Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2018). nlme: Linear and Nonlinear Mixed  
21  
22 708 Effects Models\_. R package version 3.1-137, <https://CRAN.R-project.org/package=nlme>  
23  
24  
25 709 Pisfil-Farro, J.C. (2014). Distribución de las macroalgas y su potencialidad en la bahía de Tortugas  
26  
27 710 (Casma, Perú) entre Noviembre 2011 y Febrero 2012. Thesis, Universidad Nacional del Santa,  
28  
29  
30 711 Perú. Available on-line:  
31  
32 712 <http://200.37.61.90/bitstream/handle/UNS/2755/27216.pdf?sequence=1&isAllowed=y>  
33  
34  
35 713 R-Core Team, 2013. R: A language and environment for statistical computing, R Foundation for  
36  
37 714 Statistical Computing. URL <http://www.R-project.org/>, Vienna, Austria.  
38  
39  
40 715 Riascos, J. M., Carstensen, D., Laudien, J., Arntz, W. E., Oliva, M. E., Güntner, A., & Heilmayer, O.  
41  
42 716 (2009). Thriving and declining: climate variability shaping life-history and population  
43  
44 717 persistence of *Mesodesma donacium* in the Humboldt Upwelling System. *Marine Ecology*  
45  
46 718 *Progress Series*, 385, 151-163. <https://doi.org/10.3354/meps08042>  
47  
48  
49 719 Rivadeneira, M., Fernández, M., Navarrete S. (2002). Latitudinal trends of species diversity in rocky  
50  
51  
52 720 intertidal herbivore assemblages: spatial scale and the relationship between local and regional  
53  
54 721 species diversity. *Mar Ecol Prog Ser.* 245: 123-131.  
55  
56  
57 722 Rivadeneira, M., Fernandez, M. (2005). Shifts in southern endpoints of distribution in rocky  
58  
59 723 intertidal species along the south-eastern Pacific coast. *J Biogeogr.* 32, 203-209.  
60  
61  
62  
63  
64  
65



- 1  
2  
3 724 Rodríguez-Morata, C., Díaz, H.F., Ballesteros-Canovas, J.A., Rohrer, M., Stoffel, M. (2018) The  
4  
5 725 anomalous 2017 coastal El Niño event in Peru. *Climate Dynamics*. doi: 10.1007/s00382-018-  
6  
7  
8 726 4466-y.  
9  
10 727 Rojas-Paredes, N.L. (2014). Variación del macrobentos en el intermareal rocoso de Puerto Salaverry,  
11  
12 728 Huanchaco y Puerto Malabrigo, Región la Libertad durante Mayo-Julio del 2014. Unpublished  
13  
14  
15 729 Thesis, Universidad Nacional de Trujillo, Perú. <http://dspace.unitru.edu.pe/>  
16  
17 730 Sielfeld, W., Laudien, J., Vargas, M., & Villegas, M. (2010). El Niño induced changes of the coastal  
18  
19  
20 731 fish fauna off northern Chile and implication for ichthyography. *Rev. Mar. Biol. Oceano*. 45(S1),  
21  
22 732 705-722.  
23  
24  
25 733 Sotil, G., Tarazona, J., Alvis, R., Francia, J. C., & Shiga, B. (2008). Comparative evaluation of the  
26  
27 734 DNA damage response in two Peruvian marine bivalves exposed to changes in temperature.  
28  
29  
30 735 *Helgoland Marine Research*, 62(1), 101-105. <https://doi.org/10.1007/s10152-007-0100-9>  
31  
32 736 Tarazona, J., Salzwedel, H., Arntz, W.E. (1988a). Oscillations of macrobenthos in shallow waters of  
33  
34  
35 737 the Peruvian central coast induced by El Niño 1982–1983. *J Mar Res*. 46, 593–611.  
36  
37 738 Tarazona, J., Salzwedel, H. and Arntz, W. (1988b) Positive effects of “El Niño” on macrozoobenthos  
38  
39 739 inhabiting hypoxic areas of the Peruvian upwelling. *Oecologia*. 76, 184–190.  
40  
41  
42 740 Tarazona, J., Gutiérrez, D., Paredes, C., Indacochea, A. (2003). Overview and challenges of marine  
43  
44 741 biodiversity research in Peru. *Gayana*. 67, 206–231.  
45  
46  
47 742 Tarazona, J., Paredes, C., Romero, L., Blaskovich, V., Guzman, S., & Sanchez, S. (1985).  
48  
49 743 Características de la vida planctónica y colonización de los organismos bentónicos epilíticos  
50  
51  
52 744 durante el fenómeno El Niño. *Boletín Instituto del Mar del Perú*, Volumen Extraordinario 41-49.  
53  
54 745 Vazquez, J., Perry, K., Kilpatrick, K. (1998). NOAA/NASA AVHRR Oceans Pathfinder sea surface  
55  
56 746 temperature data set user's reference manual. Jet Propulsion Laboratory Tech Rep. D-14070.  
57  
58  
59 747 Wang, C., Fiedler, P.C. (2006) ENSO variability and the eastern tropical Pacific: A review. *Prog*  
60  
61 748 *Oceanogr*. 69, 239-266.  
62  
63  
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Wyrтки, K. (1975). El Niño—The Dynamic Response of the Equatorial Pacific Ocean to Atmospheric Forcing. *J Phys Oceanogr.* 5, 572-584.

**FIGURE CAPTIONS**

**Figure 1.** Map of the study area across the Peruvian Pacific coast. Black triangles show sampling locations with name, acronym and latitude. Brackets show the two biogeographic provinces.

**Figure 2.** SST anomalies (SSTa) from June 2002 to April 2018 for the 9 study sites, estimated from the Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1. Note the remarkable spatial coherence of SST anomalies along the Peruvian coast. The two El Niño events of 2015/16 and 2017 are represented by the grey shaded bands. Black arrows indicate time intervals of the two sampling campaigns.

**Figure 3.** SST values off Peru from the Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1. Gridded values are represented as shades in the left panels, while the values along the coastline are represented versus the latitude in the right panels. (A) mean annual SST, (B) mean seasonal SST range (shown in black and white, as it does not represent warm and cold waters), (C) mean SST for July (austral winter), (D) mean SST for February (austral summer), (E) SST anomaly variance, (F) SST anomaly of March 2017 (EN event). The 9 circles along the coastline represent sampling locations.

**Figure 4.** Rarefaction curves for the 9 sampling locations in 2015 (circles) and 2017 (triangles).

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**Figure 5.** Species richness estimated by the Chao2 index in nine study sites for 2015 (blue circles) and 2017 (gray triangles).

**Figure 6.** (A) nMDS plot showing the pattern of dissimilarity in community structures using incidence data of the 2015 survey (Ibañez et al. 2018) (black dots, site latitude indicated as gray numbers) and the 2017 survey (blue dots, with site label). Dotted arrows show the change from 2015 to 2017 in the nine study sites. (B) Linear regression (red line) between nMDS scores (Axis 1) and sites' mean annual temperature. (see location codes in Table 1). The correlation coefficient and the p-values are indicated in red.

**Figure 7.** Sorensen-Dice Cluster including the 41 sites surveyed in 2015 (Ibañez-Erquiaga et al., 2018) (black labels) and the nine sites surveyed in 2017 (blue labels) using incidence data of both mobile and sessile taxa. Colors highlight the main clusters: Panamic province (orange), PVE site of 2017 (pink), the transition zone (red), and the Humboldt province (blue). Bootstrap values are indicated at each node.

**Figure 8.** (A) nMDS plot showing the pattern of dissimilarity in community structures of nine localities using 2015 and 2017 combined datasets. Correlation analysis between first Coordinate of nMDS graph with (B) mean annual SST and (C) ENSO-related SST variability.

**Figure 9.** Cluster (based on Sorensen-Dice index,  $R=0.93$ , number of bootstrap replicates: 10000) of the 9 sampling locations combining 2015 and 2017 incidence data of both sessile and mobile species. Bootstrap values are indicated at each node.

FIGURE 1

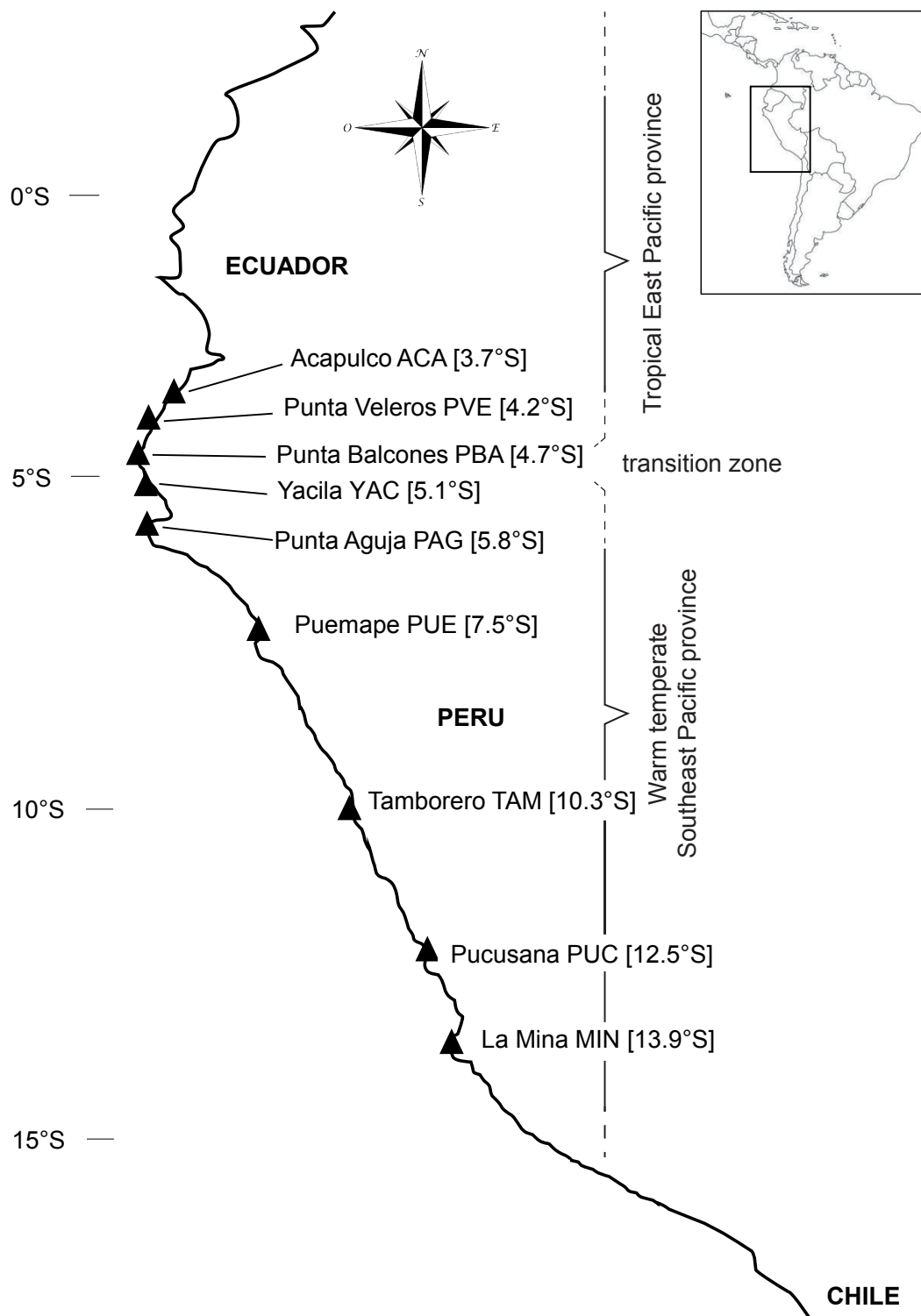


Figure 2

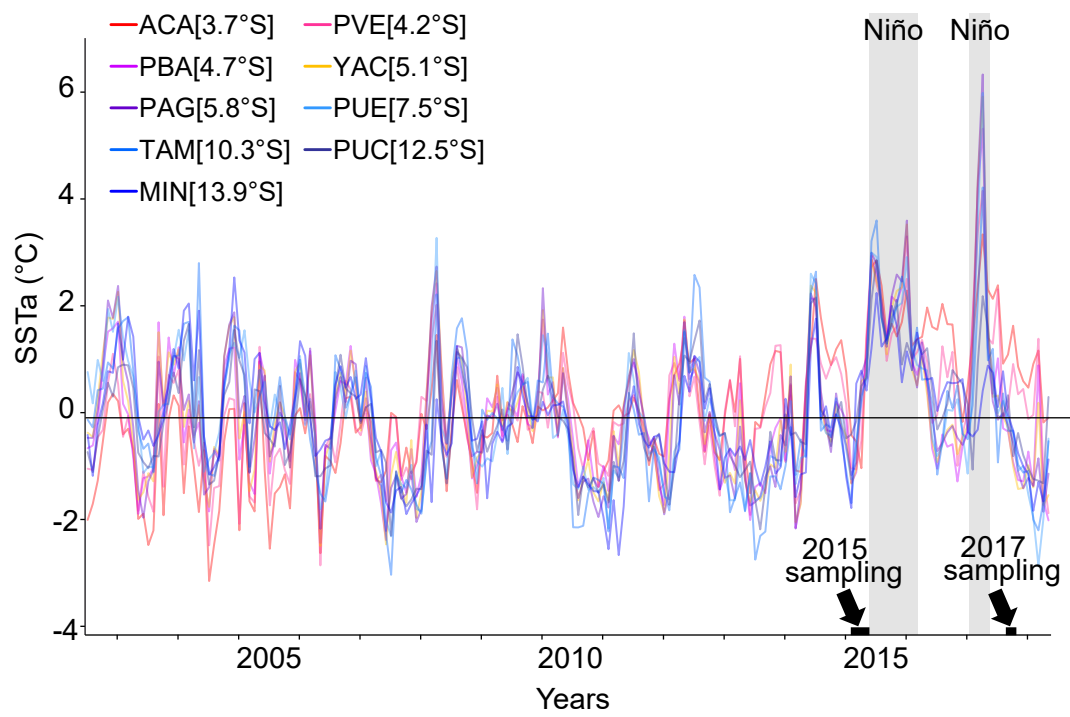


Figure 3

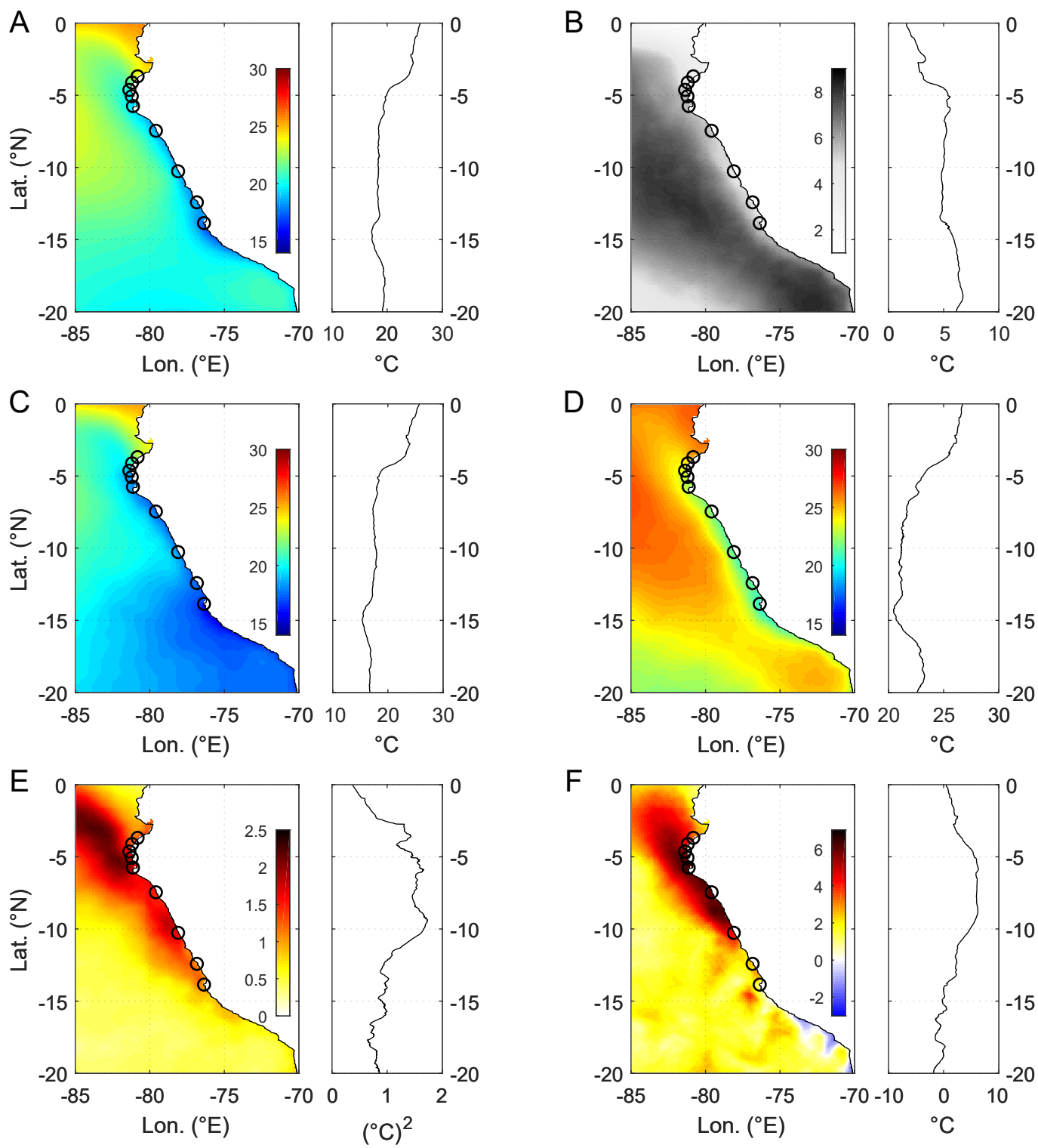


Figure 4

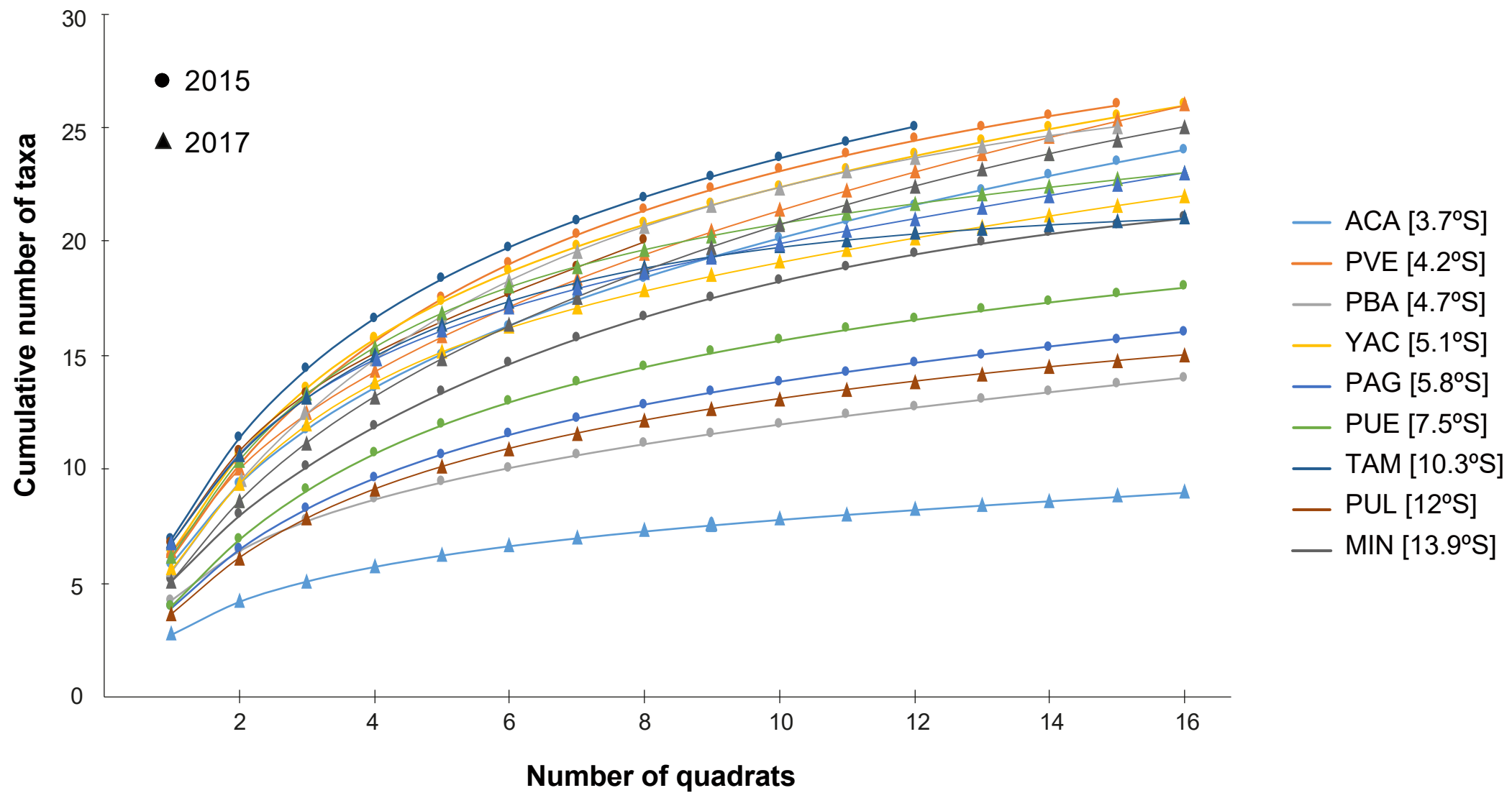


Figure 5

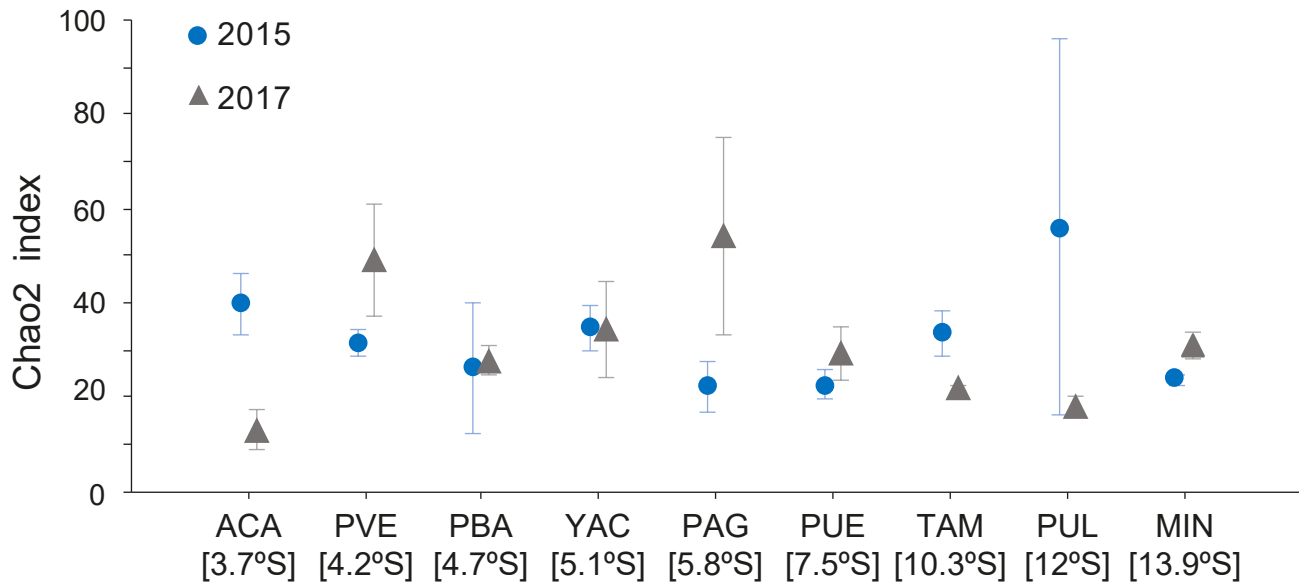








Figure 8

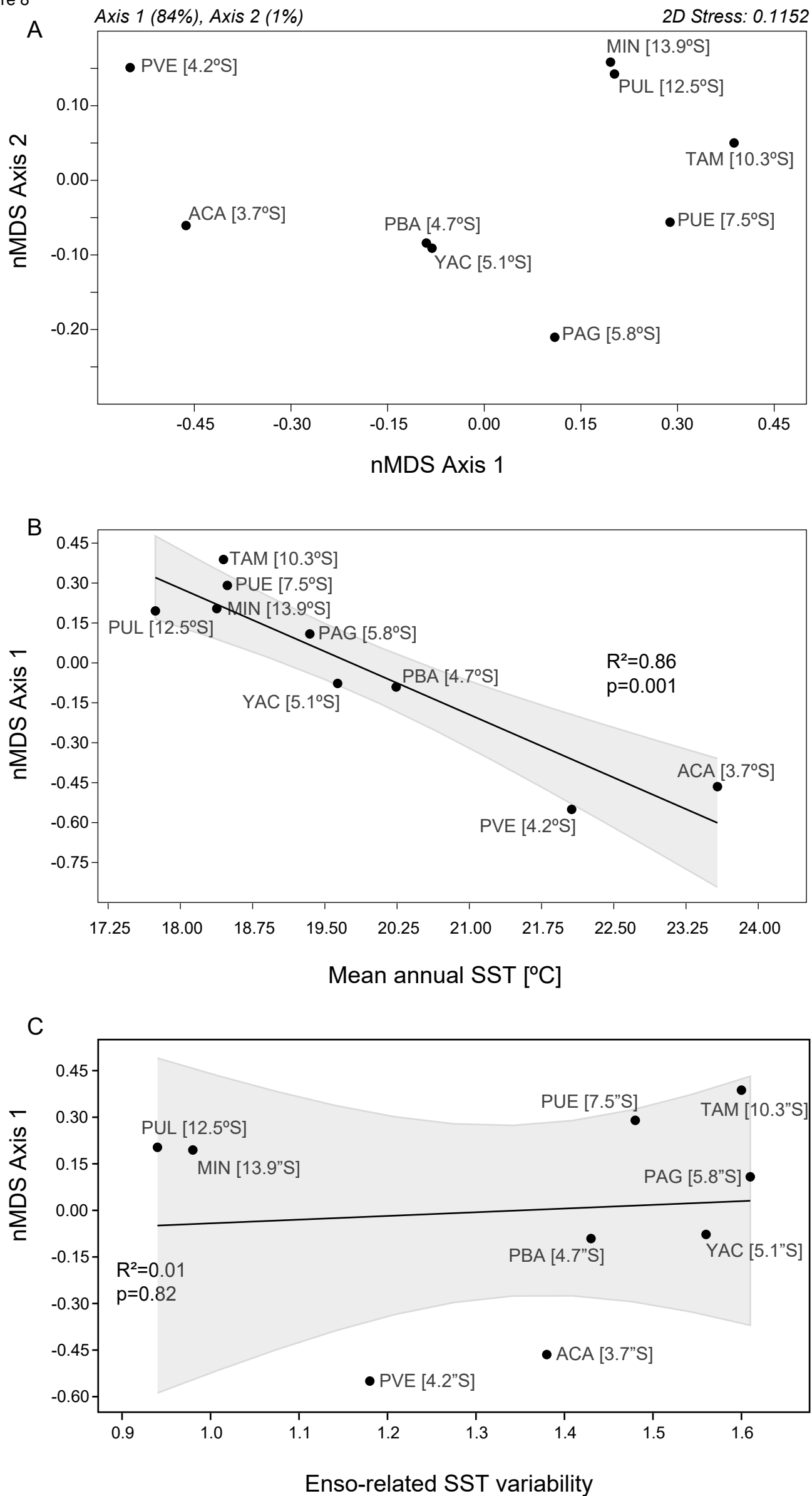
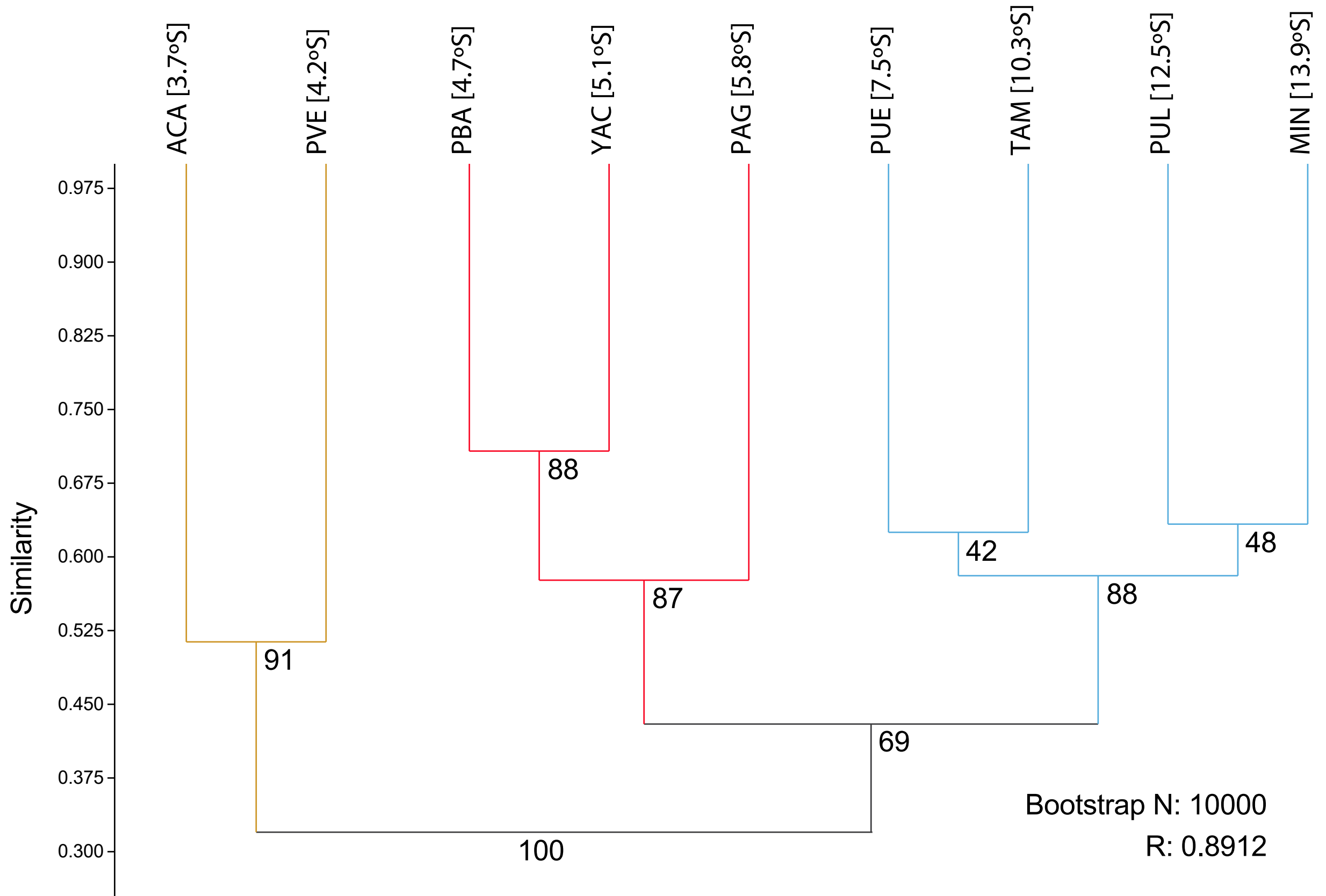


Figure 9



**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

## AUTHORSHIP STATEMENT

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All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this study has not been and will not be submitted to or published in any other publication before its appearance in *Estuarine, Coastal and Shelf Science*.

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