



Latitudinal distribution of polyplacophorans along the South-eastern Pacific coast: unravelling biases in geographical diversity patterns

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Abstract

Latitudinal diversity patterns in marine species are commonly estimated from literature records, which at times are incomplete and/or biased. Advances in molecular phylogenetics have contributed to avoid this bias, clarifying the identity of the species, improving our knowledge of species diversity and distribution. With the aim to identify biogeographic biases, we compiled and compared range distribution data of polyplacophorans along the South-eastern Pacific (SEP) coast (0°–56° S) generated from: (i) literature review (LIT dataset) and (ii) Operational Taxonomic Units (OTUs dataset), based on the analysis of 8949 individuals obtained from field sampling and biological collections. Cytochrome oxidase I (COI) and 16S rRNA of 104 specimens were used for genetic identification of conflictive morphospecies. Multivariate analysis (nMDS, PERMANOVA) were applied to test differences between datasets (LIT, OTUs) and also between biogeographic ecoregions. Just like prior studies based on literature reviews, the richness of LIT species showed an increase with latitude. Contrastingly, OTUs' richness peaked at intermediate latitudes showing a bell-shaped distribution, indicating that the LIT dataset was flawed by inaccuracies in the identification and location of polyplacophoran species on the South-eastern Pacific, causing an overestimation of their geographic ranges. Our results contrast with the previous richness patterns described for the SEP polyplacophorans, where species richness was reported to increase with latitude. Both an overestimation of geographic ranges and inaccuracies in the identification of species cause these differences. Biogeographical studies should be conducted on the basis of a comprehensive review of specimens with verifiable occurrences, and incorporate as far as possible genetic analysis to define the identity of conflicting morphospecies, in order to improve the estimation of species richness and the understanding of marine biodiversity.

Keywords Chitons · Species richness · Biogeography · Latitudinal diversity gradient · Conflicting morphospecies

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Introduction

Large-scale studies in ecology, biogeography and conservation biology are commonly based on data collected from published or unpublished sources, which at times are incomplete and can be biased (Kodric-Brown and Brown 1993). This problem may include marine studies and, as such, claims of large-scale patterns should be evaluated carefully. Specifically, biases can exist due to the collection methodologies used (Camus 2001; Navarrete et al. 2014), which can lead to artefactual trends in diversity reported for certain taxonomic groups.

Biogeographic studies in the South-eastern Pacific (hereafter SEP) have described a classic pattern of decreasing diversity toward higher latitudes for several marine taxa such as chondrichthyans, teleost fishes, decapod crustaceans, prosobranchs, nudibranchs, cephalopods and nematodes (Lancellotti and Vásquez 2000; Ojeda et al. 2000; Astorga et al. 2003; Ibáñez et al. 2009; Lee and Riveros 2012; Navarrete et al. 2014). However, there are several studies that also report the opposite pattern in groups such as seaweeds, polychaetes, amphipods, isopods, echinoderms, polyplacophorans and bivalves (Santelices and Marquet 1998; Lancellotti and Vásquez 2000; Valdovinos et al. 2003; Hernández et al. 2005; Rivadeneira et al. 2011), which exhibit an increasing species diversity toward high latitudes. Studies mentioned above were performed compiling information from literature, and not using, or partially including, empirical data. Therefore all of them should be interpreted carefully due to two reasons: (i) the bias caused by the use of different approaches and collection methods to get samples (Camus 2001; Navarrete et al. 2014) might lead to erroneous interpretations about diversity for certain groups; (ii) the effects of taxonomic accuracy and synonymy over the species number in some places has seemingly generated an increase in the entities during the last two centuries (e.g. Rivadeneira et al. 2011), but the underlying reason is that many of these “new” taxa are just synonyms of the same taxonomic entity, artificially increasing the species richness value, and eventually producing a latitudinal bias. In this sense, advances in molecular biology and phylogenetic analysis in the last decades have revealed ecosystems with under- or overestimation of species diversity (Knowlton 2000; Fouquet et al. 2007; Fonseca et al. 2010; Leray and Knowlton 2015; Tedersoo et al. 2014).

Marine molluscs have been frequently the focus of biogeographical studies, given that they are fundamental parts of marine systems, perform key ecological roles and are economically important (Pérez-Matus et al. 2017; Wanninger and Wollesen 2018). Among molluscs, polyplacophorans have been included on studies using data from literature to determine biogeographic patterns (e.g. Viviani 1979; Brattström and Johanssen 1983; Lancellotti and Vásquez 2000; Valdovinos et al. 2003; Fernández et al. 2009; Pappalardo

and Fernández 2014). Despite the ecological importance of polyplacophorans in rocky shore ecosystems of the SEP coast (Pérez-Matus et al. 2017), the taxonomic identification of species in this group remains problematic. The most complete taxonomical review of Chilean polyplacophorans by Valdovinos (1999) reported at least 60 species of chitons belonging to six families. Nevertheless, recent studies have significantly refined and reduced the taxonomic list to 45 species, currently suggesting an increase of chiton species diversity toward the poles (Valdovinos et al. 2003; Sirenko and Gallardo 2005; Fernández et al. 2009; Schwabe and Sellanes 2010; Pappalardo and Fernández 2014; Sirenko 2015; Sirenko and Sellanes 2016).

In this study we compare the richness, composition and latitudinal distribution of polyplacophoran species along the SEP coast, considering the high variability of biogeographical patterns of marine invertebrate taxa documented for the area, and the incompleteness and biases of the datasets used to build large-scale distribution patterns. To do so, we analyse two datasets compiled from: (i) literature reviews (hereafter LIT), and (ii) direct identification of morphospecies (field sampling and museum collections) aided with genetic identification for conflictive species (hereafter OTUs), comparing the richness of each dataset between biogeographic ecoregions. Here we sought to determine the latitudinal pattern of polyplacophoran species richness along the SEP coast and to quantify biases associated with data collection in order to identify sources that built variance to the observed patterns.

Materials and methods

Datasets

To improve the estimated pattern in polyplacophoran species richness along the SEP coast, we compiled two datasets (Table 1). Together, the datasets include reports and field samplings of coastal chiton species occurrences between 0° and 56° S, covering more than 5000 km of coastline and 56 latitudinal bands (Fig. 1). The first dataset was obtained from a literature review (LIT) compiled from published studies of the SEP region. All chiton species records included in this study are available in Kaas and Van Belle (1987), Bullock (1988a, b), Valdovinos (1999), Sirenko (2006), Kaas et al. (2006), Schwabe et al. (2006), Schwabe (2009) and Ibáñez et al. (2016). Our second dataset included identifications using morphological species (MS) aided with genetic data (determining Operational Taxonomic Units, OTUs). For this, an exhaustive sampling was performed between 2011 and 2016 along the SEP coast (Fig. 1) collecting a total of 6123 chitons belonging to 35 morphospecies. For each sample site, individual chitons were collected from intertidal (highest tidal level) and shallow subtidal (10-m depth) zones by hand during low tide via

Table 1 Distributional range (0–56°south) of polyplacophoran species along the South-eastern Pacific included in the literature richness data (LIT) and operational taxonomic unit's data (OTUs)

Species	Range LIT	Range OTUs	Range difference
<i>Acanthochitona arragonites</i> (Carpenter, 1857)	0–2 ⁽¹⁾		
<i>Acanthochitona ferreirai</i> Lyons, 1988	0–5 ⁽⁸⁾	0–4 ⁽³⁾	1
<i>Acanthochitona hirudiniformis</i> (Sowerby I, 1832)	0–5 ⁽⁷⁾	0–1 ⁽¹⁾	4
<i>Acanthopleura echinata</i> (Barnes, 1824)	4–36 ⁽¹⁷⁾	4–37 ⁽⁹⁾	1
<i>Callistochiton expressus</i> (Carpenter, 1865)	0–3 ⁽²⁾	0–4 ⁽⁴⁾	1
<i>Callistochiton pulchellus</i> (Gray, 1828)	0–33 ⁽¹²⁾	17–20 ⁽¹⁷⁾	30
<i>Callochiton gaussi</i> Thiele, 1908	50–55 ⁽⁴⁸⁾		
<i>Callochiton puniceus</i> (Gould, 1846)	41–55 ⁽³⁷⁾	53–55 ⁽³³⁾	12
<i>Callochiton steinenii</i> (Pfeffer, 1886)	45–55 ⁽⁴¹⁾	54–55 ⁽³⁶⁾	9
<i>Calloplax vivipara</i> (Plate, 1899)	20–35 ⁽²⁷⁾	20–33 ⁽¹⁹⁾	2
<i>Chaetopleura angulata</i> (Spengler, 1797)	45–55 ⁽⁴²⁾		
<i>Chaetopleura benaventei</i> Plate, 1899	15–37 ⁽²⁴⁾	35–46 ⁽²⁸⁾	11
<i>Chaetopleura brucei</i> Iredale in Melville & Standen, 1912	45–55 ⁽⁴³⁾		
<i>Chaetopleura hanselmani</i> (Ferreira, 1982)	0–6 ⁽¹⁰⁾		
<i>Chaetopleura hennahi</i> (Gray, 1828)	11–27 ⁽²¹⁾	12–21 ⁽¹⁴⁾	7
<i>Chaetopleura lurida</i> (G. B. Sowerby I, 1832)	0–18 ⁽¹¹⁾		
<i>Chaetopleura peruviana</i> (Lamarck, 1819)	1–55 ⁽¹³⁾	12–41 ⁽¹⁶⁾	25
<i>Chaetopleura roddai</i> Ferreira, 1983	0–3 ⁽³⁾	0–4 ⁽⁵⁾	1
<i>Chiton bowenii</i> King, 1832 ^a	42–55 ⁽³⁹⁾		
<i>Chiton barnesii</i> Gray, 1828	26–45 ⁽²⁸⁾	27–39 ⁽²²⁾	7
<i>Chiton cumingsii</i> Frembly, 1827	5–45 ⁽¹⁸⁾	5–41 ⁽¹⁰⁾	4
<i>Chiton granosus</i> Frembly, 1827	5–55 ⁽¹⁹⁾	8–45 ⁽¹¹⁾	13
<i>Chiton magnificus</i> Deshayes, 1827	12–55 ⁽²²⁾	27–55 ⁽²³⁾	15
<i>Chiton stokesii</i> Broderip, 1832	0–5 ⁽⁹⁾	0–4 ⁽⁶⁾	1
<i>Enoplochiton niger</i> (Barnes, 1824)	4–30 ⁽¹⁶⁾	12–30 ⁽¹⁵⁾	8
<i>Gallardoia valdiviensis</i> Sirenko, 2007	39–39 ⁽³⁴⁾	39–39 ⁽²⁹⁾	0
<i>Hemiarthrum setulosum</i> Carpenter in Dall, 1876	53–55 ⁽⁴⁹⁾	53–55 ⁽³⁵⁾	0
<i>Ischnochiton dispar</i> (Sowerby in Broderip & Sowerby, 1832)	0–3 ⁽⁴⁾	0–4 ⁽⁷⁾	1
<i>Ischnochiton dorsuosus</i> Haddon, 1886	45–55 ⁽⁴⁴⁾		
<i>Ischnochiton punctulatissimus</i> (Sowerby, 1832)	3–55 ⁽¹⁴⁾		
<i>Ischnochiton pusillus</i> (Sowerby, 1832)	7–20 ⁽²⁰⁾		
<i>Ischnochiton pusio</i> (Sowerby I, 1832)	3–55 ⁽¹⁵⁾	20–41 ⁽²⁰⁾	31
<i>Ischnochiton stramineus</i> (G. B. Sowerby I, 1832)	15–55 ⁽²⁶⁾	33–53 ⁽²⁶⁾	20
<i>Ischnochiton viridulus</i> (Gould, 1846)	54–55 ⁽⁵⁰⁾		
<i>Lepidopleurus cullerti</i> Rochebrune, 1889	45–55 ⁽⁴⁵⁾		
<i>Leptochiton kerguelensis</i> Haddon, 1886	45–55 ⁽⁴⁶⁾	53–55 ⁽³⁴⁾	8
<i>Leptochiton lascrusesi</i> Sirenko, 2015	33–33 ⁽³²⁾	33–33 ⁽²⁵⁾	0
<i>Leptochiton medinae</i> (Plate, 1899)	40–55 ⁽³⁵⁾	42–55 ⁽³⁰⁾	2
<i>Nuttallochiton martiali</i> (Rochebrune, 1889)	42–55 ⁽⁴⁰⁾	52–55 ⁽³¹⁾	10
<i>Plaxiphora aurata</i> (Spalowsky, 1795)	26–55 ⁽²⁹⁾	23–55 ⁽²¹⁾	3
<i>Stenoplax limaciformis</i> (Sowerby, 1832)	0–3 ⁽⁵⁾	0–2 ⁽²⁾	1
<i>Stenoplax rugulata</i> (G.B. Sowerby I, 1832)	0–3 ⁽⁶⁾	0–5 ⁽⁸⁾	2
<i>Stenosemus exaratus</i> (Sars G. O., 1878)	45–55 ⁽⁴⁷⁾		
<i>Tonicia atrata</i> (G.B. Sowerby II, 1840) ^b	27–55 ⁽³⁰⁾		
<i>Tonicia calbucensis</i> Plate, 1897	41–55 ⁽³⁸⁾	18–55 ⁽¹⁸⁾	23
<i>Tonicia chilensis</i> (Frembly, 1827)	12–55 ⁽²³⁾	33–55 ⁽²⁷⁾	21
<i>Tonicia disjuncta</i> (Frembly, 1827)	30–49 ⁽³¹⁾	27–55 ⁽²⁴⁾	9
<i>Tonicia elegans</i> (Frembly, 1827) ^c	15–45 ⁽²⁵⁾		

Table 1 (continued)

Species	Range LIT	Range OTUs	Range difference
<i>Tonicia fremblyana</i> (Kaas, 1957)		11–33 ⁽¹²⁾	
<i>Tonicia lebruni</i> Rochebrune, 1884	40–55 ⁽³⁶⁾	52–55 ⁽³²⁾	12
<i>Tonicia smithi</i> Leloup, 1980 ^d	36–55 ⁽³³⁾		
<i>Tonicia swainsoni</i> (Sowerby in Broderip & Sowerby, 1832)		12–18 ⁽¹³⁾	
Total richness	50	36	

Superscript numbers in parentheses for each database refer to the distribution range represented in Fig. 1. Species with no occurrence in the OTUs data correspond to species with incorrect records from the LIT database

^a Synonymy of *Chiton magnificus* following genetic distances

^b Synonymy of *Tonicia chilensis* following genetic distances

^c Synonymy of *Tonicia calbucensis* following genetic distances

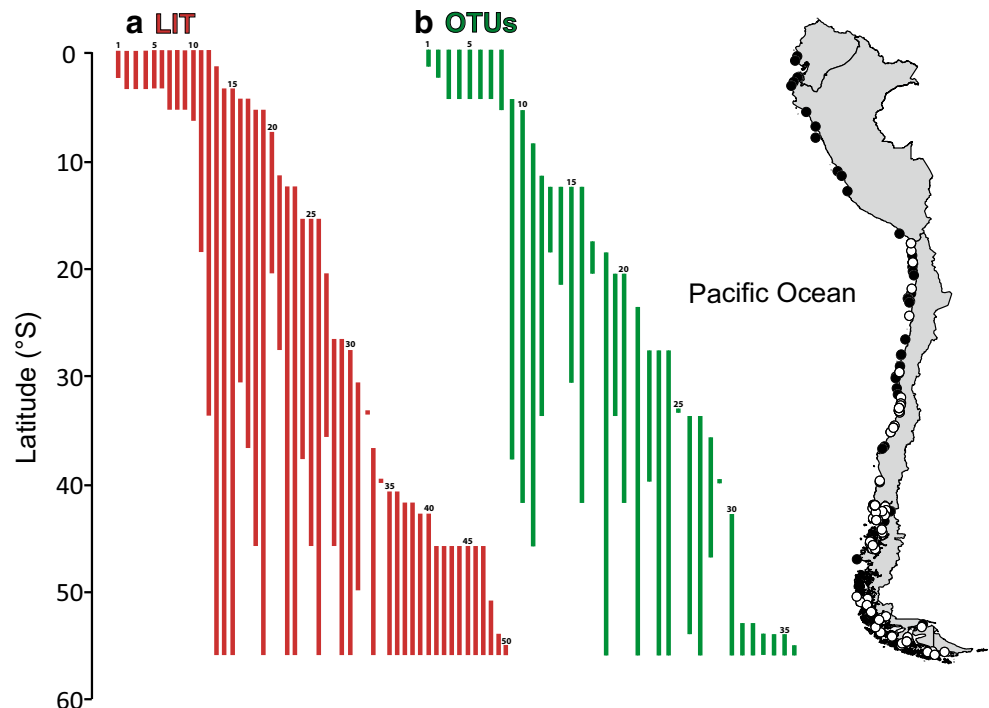
^d Synonymy of *Tonicia disjuncta* following genetic distances

snorkelling and SCUBA diving. All of the specimens collected were identified to species-level following Leloup (1956), Bullock (1988a, b), Kaas et al. (2006), Schwabe et al. (2006), Sirenko (2006) and Schwabe (2009). Some voucher specimens were properly registered and stored at the Museo Nacional de Historia Natural de Chile (MNHNCL) and in the Sala de Colecciones Biológicas Universidad Católica del Norte, (SCBUCN) Coquimbo, Chile (Online Table S1). Additionally, we reviewed 2826 specimens from: Museo Nacional de Historia Natural de Chile, Santiago, Chile (MNHNCL); Collection of Flora and Fauna, Professor Patricio Sánchez from Pontificia Universidad Católica de Chile, Santiago, Chile (SSUC); Instituto de la Patagonia from

Universidad de Magallanes, Punta Arenas, Chile (UMIP); Santa Barbara Museum of Natural History, Santa Barbara, USA (SBMNH); and the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZISP) (Fig. 1). Combining data from all collections and those collected from field sampling, a total of 8949 chitons belonging to 41 morphospecies were utilized to estimate the geographic distribution range of all species (Fig. 1).

To estimate the representativeness of the presence–absence matrix of species distribution and species richness, a species accumulation curve (Colwell et al. 2004) was performed using the software PAST v3.25 (Hammer et al. 2001). The expected number of species was estimated using the Chao 2 algorithm

Fig. 1 Latitudinal distribution ranges of polyplacophoran species along the South-eastern Pacific coast recorded from **a** literature reviews (LIT) and **b** Operational Taxonomic Units (OTUs). The numbers over the latitudinal distribution ranges for each database identify each species included in Table 1. Filled dots drawn along the South-eastern Pacific coast represent sampled localities, and open dots represent records from biological collections



(Colwell et al. 2004), based on the number of latitudinal bands (Fig. 2).

Finally, two absence–presence matrices with a resolution of one degree of latitude were built from the obtained datasets of LIT and OTUs (Table 1).

Phylogenetic analysis

Portions of mitochondrial genes were sequenced, and OTUs were determined. For this, the cytochrome oxidase subunit I (COI) gene was sequenced for 104 specimens belonging to 35 morphological species. In addition, sequences of *Hemiarthrum setulosum* (KJ574095), *Leptochiton medinae* (HQ907865) and *L. kerguelensis* (HQ907864) were obtained from GenBank and incorporated in our analysis. Additionally, the 16S rRNA ribosomal genes (16S) of 45 specimens belonging to 31 morphological species were sequenced.

Total DNA (gDNA) was extracted considering the saline extraction protocol following Aljanabi and Martinez (1997). The polymerase chain reaction (PCR) amplifications were performed using a total reaction volume of 25 μ l, with 2.5 μ l of Buffer 10x (200 mM Tris-HCL using pH=8.4, 500 mM KCL), 2.0 μ l of dNTPs [2.5 mM], 1.0 μ l MgCl₂ [50 mM], 0.3 μ l of Invitrogen™ Platinum™ Taq DNA polymerase (now part of ThermoFisher Scientific), 0.1 μ l of DNA and 0.25 μ l of each primer [10 pmol] (COI primer pair LCO1490–HCO 2198 in Folmer et al. 1994; 16S rRNA primer pair 16Sa–16Sb in Okusu et al. 2003). For amplification, the optimum condition had an initial denaturation at 94 °C for 5 min, followed by 30 cycles of 94 °C (60 s), 50 °C (60 s), and 72 °C (60 s); followed by a final extension at 72 °C during 10 min, using a thermal cycler. Double-stranded PCR products were purified and sequenced in both directions using an abi3730 automatic sequencer (Macrogen, Inc., Seoul, Korea). Sequences were edited and aligned using the MUSCLE software (Edgar 2004a, b) implemented in MEGA 7.0 (Kumar

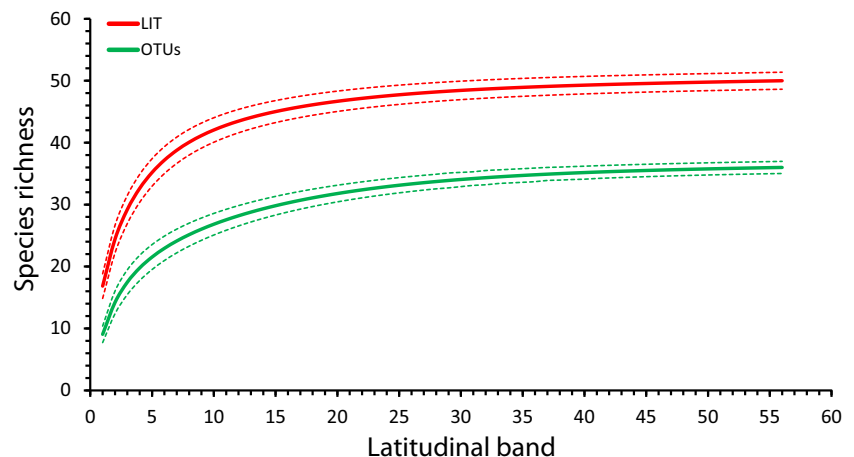
et al. 2016). Sequences extracted in this survey were stored at the GenBank database (Online Table S1).

Bayesian inference was applied to evaluate the phylogenetic relationships among polyplacophorans from the SEP using rRNA 16S and COI separately in the software BayesPhylogenies v1.1 (Pagel and Meade 2004). Three independent analyses were ran using four Markov Chain Monte Carlo (MCMC), each including 5,000,000 generations, and to assure that successive samples were independent, sampling was done every 1000 trees. To assess the stationary distribution of the MCMC we visually inspected the log-likelihood values of the iterations until they reached convergence, removing all of them prior to this burn-in point. Also, a sampling size above 500 was verified. This was done using the software Tracer v1.5 (Rambaut and Drummond 2009). Trees that did not reach convergence (20%) were discarded. Among the remaining trees, 4001 were selected to reconstruct a majority rule consensus tree collapsing nodes above 0.7 posterior probability in the BayesTrees v1.3 software (Meade 2011). We rooted the trees using *Hanleyella oldroydi* (Dall 1919) (16S KJ574077 and COI HQ907874) as outgroup.

Comparison between datasets

To detect differences in species compositions along the SEP coast between the LIT and OTUs datasets, a two-way permutational multivariate analyses of variance (PERMANOVA+: Anderson 2001; Anderson et al. 2008) with 10,000 permutations was performed to test for differences between datasets and ecoregions (after Spalding et al. 2007) along the SEP coast. Ordination analyses were based on the Jaccard similarity index (J_{index}) calculated for all species within each 1° latitude bin. Non-metric multidimensional scaling (nMDS) was performed (Clarke 1993) to visualize potentially distinct clusters along the latitudinal gradient and ecoregions (Spalding et al. 2007). All analyses were performed using the

Fig. 2 Species accumulation curve of the number of coastal polyplacophorans reordered for every band of 1° of latitude along the South-eastern Pacific coast. Solid lines correspond to the average richness of Literature (LIT in red) and Operational Taxonomic Units (OTUs in green), while dashed lines represent the 95% confidence interval



Plymouth Routines in Multivariate Ecological Research (PRIMER v6) software (Clarke and Gorley 2006).

To evaluate the replacement degree in species composition between localities and ecoregions, beta diversity was estimated using the Williams index (Koleff et al. 2003). This analysis was performed only for the OTUs data base.

Results

Morphospecies and OTUs identification

We identified 37 morphospecies from biological collections and field sampling. Not all species were sequenced for COI and 16S, but our results helped improve the taxonomic resolution of the dataset. In relation to genetic results, it was possible to identify 31 OTUs using 104 COI sequences derived from 35 morphospecies with 88.6% certainty. Using the 16S subunit, we identified 26 OTUs from 30 morphospecies with 86.6% certainty. By combining results from both genetic markers (COI and 16S), we identified 32 OTUs from 37 morphospecies sequenced with 86.5% certainty (Fig. 3). The Bayesian phylogenetic trees based on the COI and 16S sequences showed cohesive clusters for most of the species (Fig. 3). The sequences of both genes (COI and 16S) revealed that particular pairs of morphospecies of the genera *Chiton* or *Tonicia* were genetically indistinguishable (i.e. correspond to synonymies) (Fig. 3), where individuals of *Chiton bowenii* were not genetically different with *C. magnificus*, individuals of *T. elegans* were not genetically different with *T. calbucensis*, individuals of *T. smithi* were not genetically different with *T. disjuncta* and individuals of *T. atrata* was not genetically different with *T. chilensis*.

Latitudinal diversity

Each dataset displayed a distinct latitudinal pattern of species richness. For example, species richness increased poleward according to the LIT dataset. Specifically, 12 species were found near the Equator, and a maximum of 26 species were found at $\sim 55^\circ$ S (Fig. 4). The trend was not monotonic as two significant drops in species richness were recorded along the latitudinal gradient. The first drop was observed between $\sim 5^\circ$ S and $\sim 10^\circ$ S with ~ 10 species while the second drop was observed at $\sim 38^\circ$ S with ~ 13 species (Fig. 4). Species richness compiled from OTUs datasets varied significantly along the latitudinal gradient (Fig. 4), tended to increase slightly southwards, and exhibited a bell-shape pattern with species richness reaching a maximum at 33° S. Eight species were found near the Equator, and 12 species were found at $\sim 55^\circ$ S, whereas a maximum of 14 species were found at intermediate latitudes (33° S). Two significant drops in species richness were recorded along the latitudinal gradient. The first drop

was observed between $\sim 5^\circ$ S and $\sim 11^\circ$ S (with 2–4 species) while the second drop was observed between $\sim 45^\circ$ S and 51° S (with 7–8 species) (Fig. 4).

Differences of species ranges between both data sets were around 58%, and one of the main differences was the decrease in range distribution of 23 species (Table 1). Other eight species increased their distribution, and only three had the same distribution in both data sets (Table 1).

Significant differences in species composition were found when we compared the two datasets (Fig. 5). Aligned along a latitudinal gradient, two distinctive clusters were identified from the nMDS ordination, one for each dataset (Fig. 5a), and significant differences were found between each group according to the PERMANOVA ($F = 90.32$, $p_{\text{perm}} < 0.001$) (Table 1). Pairwise comparisons between the LIT and OTUs datasets indicated similarities of $\sim 64.94\%$ (J_{index}).

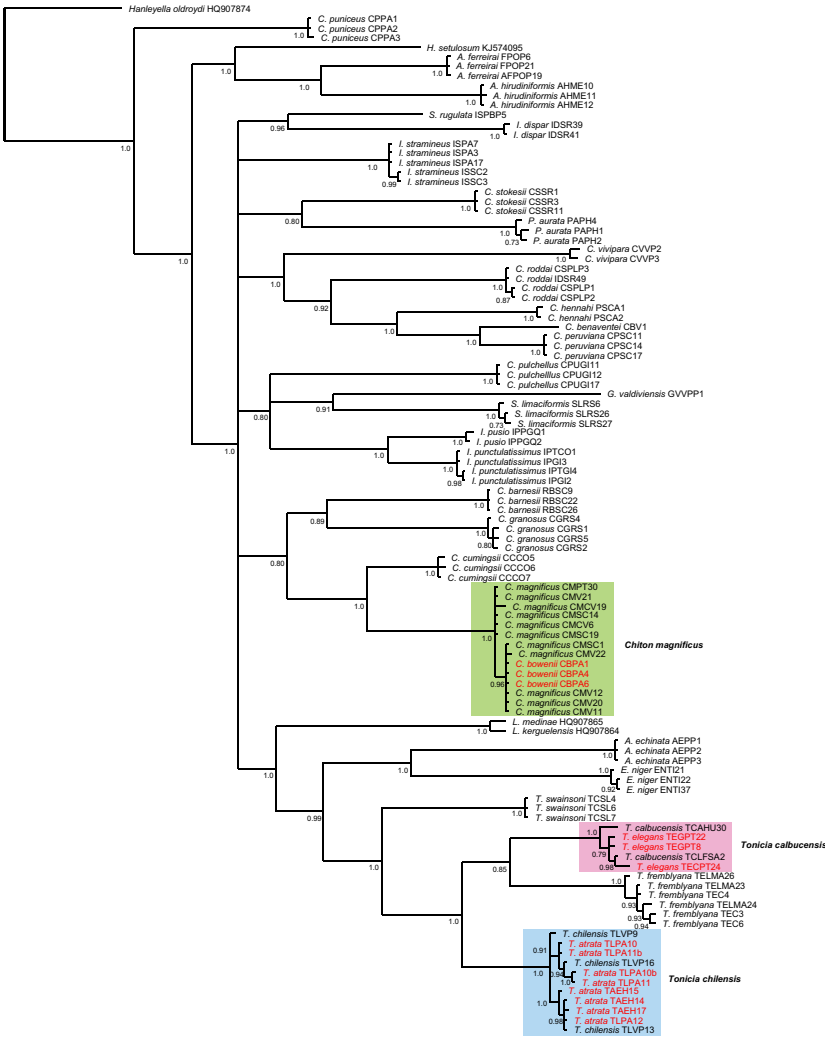
The nMDS ordination by ecoregions showed gradual changes in species composition along the SEP coast (Fig. 5b). Each cluster arranged along the latitudinal gradient constituted an ecoregion, and each biogeographic unit was significantly distinguishable from the others (Table 1). The interaction term of the PERMANOVA analysis (Table 2) reflected changes in composition along the latitudinal gradient, but also reflected uncertainty in species composition given by the exaggerated distribution range of some chiton species (Table 1). Each of the paired comparisons of species composition between LIT and OTUs databases showed significant differences for each ecoregion (Table 2).

Beta diversity was relatively higher among Guayaquil-Central Peru and Central Chile-Araucanian ecoregions (0.27–0.17, respectively), suggesting an important turnover of species among these biogeographic units (Table 2). Beta diversity among Humboldtian-Central Chile, Araucanian-Chiloense and Chiloense-Channels and Fjords ecoregions showed intermediate values (0.012, 0.084, 0.075, respectively), meanwhile beta diversity between the Central Peru-Humboldtian ecoregions was the lowest (0.010), suggesting a low turnover among these biogeographic units (Table 3).

Discussion

Our results highlight the value of exhaustive studies that include multiple sources of evidence for describing the patterns and processes that affect latitudinal gradients in species richness. The re-evaluated diversity of polyplacophoran species along the SEP coast (i.e. OTUs dataset) exhibited a bell-shape pattern with species richness reaching a maximum at intermediate latitudes. Our results are in contrast with previous richness patterns described for polyplacophorans (e.g. Valdovinos et al. 2003; Fernández et al. 2009) as well as for other invertebrate taxa such as sponges, bryozoans, polychaetes, peracarids, and gastropods (Desqueyroux and Moyano 1987;

a COI



b 16S

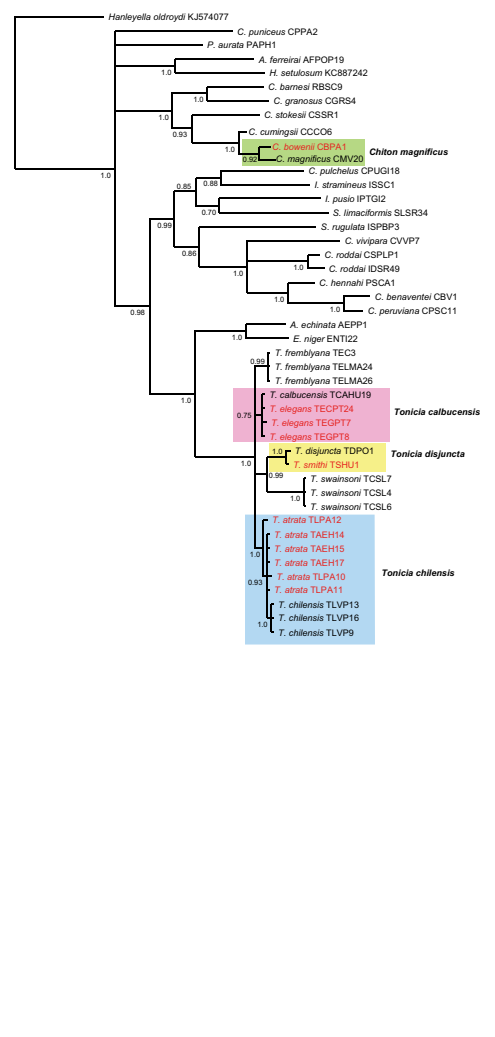
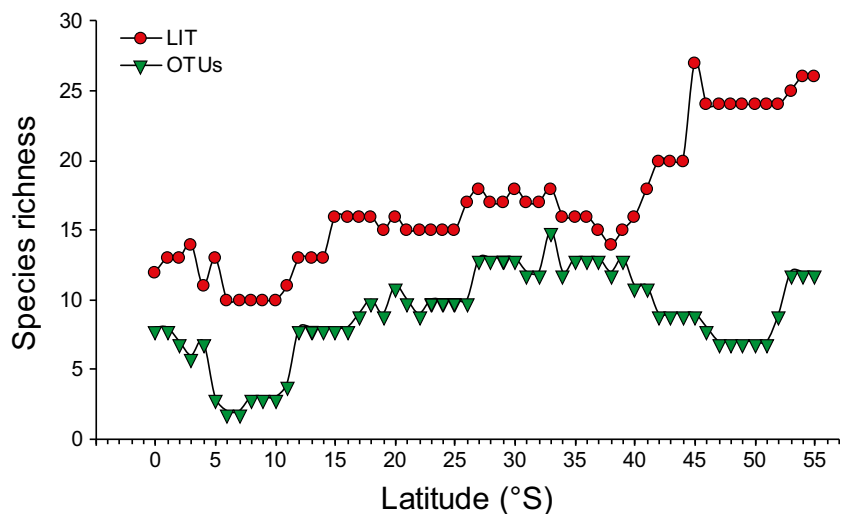


Fig. 3 Bayesian phylogenetic tree of polyplacophorans from the South-eastern Pacific coast. **a** COI sequences; **b** 16S sequences. Node values are posterior probabilities. Coloured boxes indicated species with taxonomic problems

Fig. 4 Latitudinal gradient of polyplacophoran species richness along the South-eastern Pacific coast. Each curve is based on information from two different sources. LIT Literature (red dots); OTUs Operative Taxonomic Units (green triangle)



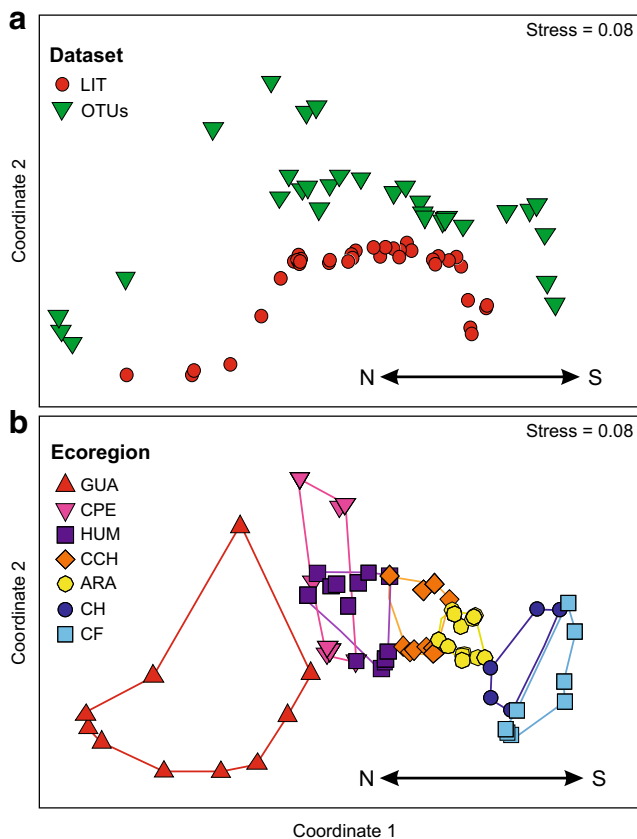


Fig. 5 Non-metric multidimensional scaling plot of polyplacophoran species composition along the South-eastern Pacific coast. Ordination space was built based on Jaccard similarity index. Panel **a** shows the polyplacophoran species composition based on two sources of information. LIT, Literature; OTUs, Operative Taxonomic Units. Panel **b** shows distinctive clusters (ecoregions) ordered along the South-eastern Pacific coast. GUA, Guayaquil; CPE, Central Peru; HUM, Humboldtian; CCH, Central Chile; ARA, Araucanian; CH, Chiloense; CF, Channels and Fjords. Thick black arrow (\rightarrow) indicates latitudinal gradient along the South-eastern Pacific coast

Moyano 1991; Valdovinos et al. 2003; Hernández et al. 2005; Rivadeneira et al. 2011), which describe a steady poleward increase of species richness.

The database created from the literature records provides evidence that the taxonomic richness of polyplacophorans has been greatly overestimated. For instance, 24% (12 out of 50) of the described species include unverified occurrences, and 12% of the occurrences in the literature are synonyms, according to the genetic information provided here. This implies that 46% of all species described in previous studies are invalid (Reid and Osorio 2000; Aldea and Valdovinos 2005; Schwabe et al. 2006; Schwabe 2009; Araya and Araya 2015).

A thorough examination of the literature indicates that inaccuracies in distribution ranges and species richness estimates are mainly due to uneven sampling efforts along the SEP coast. For instance, so far there is only one study describing the composition of polyplacophorans in both the Guayaquil (Ibáñez et al. 2016) and Central Peru (Uribe

Table 2 Results of the PERMANOVA analysis comparing the composition of polyplacophoran species along the South-eastern Pacific coast between datasets (LIT: Literature; OTUs: Operative Taxonomic Units) and ecoregions (after Spalding et al. 2007) based on Jaccard dissimilarity

Source	df	MSq	F	p_{perm}
Dataset (D)	1	35,162	90.32	0.001
Ecoregion (E)	6	29,133	7483	0.001
D \times E	6	8571.8	22.02	0.001
Residuals	111	389.3		

Post hoc following PERMANOVA between LIT and OTUs datasets across different ecoregions

Ecoregions	Latitudinal extent ($^{\circ}$ S)	LIT vs OTUs t value
Guayaquil (GUA)	0–5	2.84*
Central Peru (CPE)	6–12	5.39*
Humboldtian (HUM)	13–25	7.37*
Central Chile (CCH)	26–33	8.78*
Araucanian (ARA)	34–41	5.71*
Chiloense (CH)	42–46	7.78*
Channels and Fjords (CF)	47–55	7.60*

df degrees of freedom, MSq mean square, p_{perm} Monte Carlo permutation significance

* $p < 0.05$

2013) ecoregions. Conversely, the sampling effort in the Chiloense and the Channels and Fjords ecoregions has been high (Reid and Osorio 2000; Aldea and Valdovinos 2005; Schwabe et al. 2006; Sirenko 2006; Rosenfeld et al. 2015), although taxonomic inconsistencies in these regions are still frequent. Overall, inconsistencies could be due to the high intraspecific phenotypic variability associated with habitat heterogeneity and the subsequent assignment of different names to the same phenotypes (e.g. Schwabe 2009). On the other hand, differences in species composition between datasets were low for the Central Chile, Humboldtian and Araucanian ecoregions. This could be due to greater sampling effort, and the occurrence of many research centers in these areas (Camus 2001).

Table 3 Williams' beta diversity results comparing polyplacophoran species turnover of operational taxonomic unit's data (OTUs) along the South-eastern Pacific coast

Ecoregions	Range	Mean	SD
Guayaquil/Central Peru	0.00–0.50	0.27	0.11
Central Peru/Humboldtian	0.00–0.18	0.01	0.04
Humboldtian/Central Chile	0.00–0.25	0.12	0.07
Central Chile/Araucanian	0.00–0.27	0.17	0.05
Araucanian/Chiloense	0.07–0.14	0.08	0.02
Chiloense/Channels and Fjords	0.00–0.20	0.07	0.09

Unravelling biogeographic patterns mainly conducted through a comprehensive review of specimens (i.e. from field sampling and from biological collections) and aided with genetic analysis allowed us to improve taxonomic identifications. With robust estimates of the number of species in a particular area, evolutionary hypotheses related to gradients of species diversity can be thoroughly tested. For example, several studies have used genetic barcoding to verify species diversity and have also found biases associated with either overestimation due to poor identification or underestimation due to cryptic species (Fouquet et al. 2007; Fonseca et al. 2010; Chen et al. 2011; Tedersoo et al. 2014; Leray and Knowlton 2015).

The quantitative results in this study reject the previously reported inverse pattern of latitudinal richness (e.g. Valdovinos et al. 2003; Fernández et al. 2009; Pappalardo and Fernández 2014), mostly due to the previous lack of taxonomic resolution. The improved accuracy achieved in this study, product of 5 years of fieldwork and the re-identification of many specimens deposited during the last century in biological collections (i.e. SSUC, UMIP, MNHNCL, SBMNH and ZISP), has given us some confidence that we have sampled most species present along the SEP coast.

Our genetic results suggest that some genera are in urgent need of taxonomic revision (e.g. *Ischnochiton*, *Chiton* and *Tonicia*). Some taxonomic names of chitons (*Tonicia elegans*, *T. lineolata*) were invalidated by Frembly (1827) because these were used beforehand. Recently, Ibáñez et al. (2019) synonymized *T. elegans* with *T. calbucensis* and clarified the taxonomic position of *T. lineolata* as *T. fremblyana*. Two other *Tonicia* species were synonymized as well, *T. smithi* with *T. disjuncta* and *T. atrata* with *T. chilensis* (Ibáñez et al. 2019), while other species names (e.g. *Chiton granosus*, *C. cumingsii*) are classified as nomen dubium because they were proposed before 1931 (ICZN 1999). In the absence of a taxonomic solution, we used these names provisionally, since they have been frequently used in chiton literature (e.g. Bullock 1988a). Taxonomic problems in marine molluscs related to shell morphology and coloration have been resolved by genetic studies, resulting in the synonymization of species (Knowlton 2000; González-Wevar et al. 2010). Our genetic distance estimates with barcoding allowed a rapid differentiation at species, genus and family level. Similar COI distances have been previously reported for chitons in the USA and China (Kelly et al. 2007; Chen and Sun 2013). This approach is useful to identify species, but for phylogenetic relationships it is necessary to include more mitochondrial and nuclear genes. In our phylogenetic tree, several groups (*Ischnochiton*, *Plaxiphora* and *Stenoplax*) do not result in monophyletic groups (according to taxonomy), probably due to gene saturation. The genus *Ischnochiton*, for example, has resulted to be polyphyletic in other studies with the barcoding approach, even when using more genes (Okusu et al. 2003; Chen and Sun 2013),

suggesting more than one subgroup inside this genus. At the genus level, only four genera (e.g. *Acanthochitona*, *Chaetopleura*, *Callistochiton* and *Tonicia*) represented monophyletic groups. All these taxonomic conflicts, together with the difficulty to identify morphologically several chitons at the species level, have produced a significant bias in the diversity gradient along SEP caused by incorrect geographical distributions.

The geographical bands displaying the highest species richness (often associated with a higher number of genera) of polyplacophorans were located between 20 and 42° S (10–14 species), forming a bell-shaped distribution along the SEP coast, which has also been previously described for organisms such as polychaetes (Hernández et al. 2005), nematodes (Lee and Riveros 2012) and intertidal fishes (Navarrete et al. 2014). This range lies within the Intermediate Area (after Camus 2001), flanked by lower-diversity transitional zones that include mixed components of biota from adjacent provinces. Climatic shifts related to quaternary glacial/tectonic events are expected to have produced biotic shifts in latitude for both the intermediate area and associated transition zones (Camus 2001). In the case of chitons, 11 species, including the monotypic genus *Gallardoia*, are endemic to this region. Similar patterns have been recorded for the northeastern Pacific Ocean, especially as discussed for the California Transition Zone (Briggs and Bowen 2012). Biogeographic transition zones are defined as overlapping geographical areas, with a gradient of substitution and partial segregation between biotic components (sets of taxa sharing a similar geographical distribution as result of a common history) (Ferro and Morrone 2014). In the case of the SEP chitons, the transition zone extends from 20° S to 42° S, since in this range we found the highest diversity and distributional overlap. As evidenced here, nearby localities tended to have similar species, with the exception of the high turnover across the biogeographical break between the Panamian and Peruvian provinces (Guayaquil-Central Peru ecoregions) where species composition varied significantly as the distance between localities increased. The same pattern has been observed by Ibáñez et al. (2016) and by Fenberg and Rivadeneira (2019) suggesting that the type of habitat and environmental influence would be key in explaining differences in composition and diversity. Along the Peruvian and Chilean ecoregions, species replacement did not show a latitudinal pattern since few chitons had small geographical ranges, and the dissimilarity between close localities remained low through the latitudinal gradient with a moderate increment in the Araucanian ecoregion.

Differences in the geographic distribution of chitons revealed by this study are related to errors in the distribution records of some species in the literature (e.g. *Tonicia lebruni*, *T. atrata*, *T. smithi*, *Chiton bowenii*) (Valdovinos 1999; Schwabe 2009; Araya and Araya 2015). For instance, while *Plaxiphora aurata* is reported to inhabit from 34 to 55° S (Schwabe 2009), in this study we propose it would have a

wider distribution, ranging from 23 to 55° S. The opposite was found for *Chiton barnesii*, which in this study was shown to have a much narrower distribution (27–30°S) than that reported in the literature (27° S–45° S: Schwabe 2009).

Our work shows that the exhaustive analysis of specimens for the identification of morphospecies can improve the recorded richness patterns, and where the rapid evolution of the field of molecular biology can help to improve the resolution of conflicting morphospecies. Furthermore, biodiversity should not “have to be just about the number of a species in an ecosystem”, and its study needs a revolution (Cernansky 2017). Not only the variety of sizes, shapes and functional traits of organisms, but also different approaches (e.g. genetic, ecological, physiological) need to be employed to achieve a more comprehensive estimation of biodiversity in all ecosystems.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The research was developed under the ethical guidelines of Universidad Andres Bello, Universidad de Chile and FONDECYT, via the fishing permit # 1554 provided by the Chilean Government.

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Data Availability All data generated or analysed during this study are included in this published article, in its supplementary information file and are available in the Genebank repository <https://www.ncbi.nlm.nih.gov/genbank/>

Author contribution AHN, CMI and JS contributed to the study conception. AHN, CMI, MCP-G and JS contributed to the study design. Data collection was performed by CMI, MCP-G, AHN, JS, BS and DJE. Species identification was conducted by BS, CMI, DE and AHN. Statistical analysis was performed by CMI and AHN. The first draft of the manuscript was written by AHN and all authors commented on

previous versions of the manuscript. All authors read and approved the final manuscript.

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