

1 Shell shape as an indicator of phenotypic stocks of Tehuelche scallop (*Aequipecten tehuelchus*) in
2 Northern Patagonia, Argentina

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18 **Abstract**

19 Tehuelche scallop, *Aequipecten tehuelchus*, is a commercially exploited species in
20 Northern Patagonia, Argentina. Without genetic differentiation at the species level, *A. tehuelchus*
21 presents three morphotypes: *tehuelchus*, *madrynensis*, and a non-common variant *felipponei*. The
22 main goal of this study was to analyze the shell shape variation of Tehuelche scallop to
23 differentiate and identify the phenotypic stocks. The shape differences between and within the
24 two main morphotypes (*tehuelchus* and *madrynensis*) were assessed using geometric
25 morphometrics in nine localities. The shell shape presented variability at geographic scale, with
26 the morphologic traits that maximized the differentiation among localities between the *tehuelchus*
27 and *madrynensis* morphotypes. Scallops from *madrynensis* morphotype presented higher and
28 circular shell discs with smaller auricles than those from *tehuelchus* morphotype. Morphometric
29 differentiation was also detected among localities of each morphotype, wherein most of the
30 variability was related to the disc circularity and the symmetry of the auricles. The presence of
31 morphologic variation in San Matías and San José gulfs, wherein a single genetic pool is shared,
32 evidenced the plastic nature of the species. Given the distribution of this resource in distinct
33 provincial jurisdictions, the differentiation of phenotypic stocks has relevance in the context of
34 fishery management, especially if zoning and rotational strategies are implemented.

35

36 Keywords: PHENOTYPIC STOCKS, GEOMETRIC MORPHOMETRICS, LANDMARKS,
37 TEHUELCHES SCALLOP, NORTHERN PATAGONIA, ARTISANAL FISHERY.

38 1. Introduction

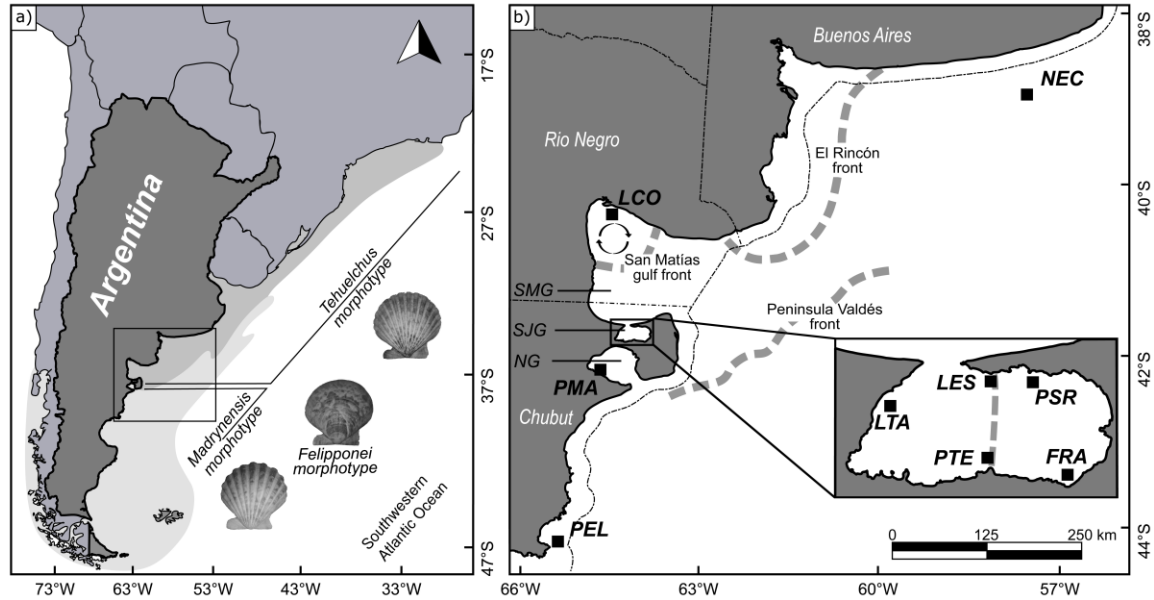
39 Phenotypic plasticity refers to the alternative phenotypes (morphology, physiology,
40 behavior, or other environmental sensitive traits) that a given genotype responds to different
41 ecological conditions (DeWitt and Scheiner, 2004; Nicolaus and Edelaar, 2018; Schlichting and
42 Pigliucci, 1998; Sommer, 2020). This flexible response could be relevant to cope with the
43 environmental heterogeneity, being especially relevant in sessile and sedentary organisms that
44 cannot escape or avoid changes in environmental conditions (Nicolaus and Edelaar, 2018).
45 Particularly, the shell morphology of marine mollusk species is recognized for being susceptible
46 to environmental conditions (Márquez et al., 2017a; Melatunan et al., 2013; Peyer et al., 2010;
47 Scherer et al., 2016; Urdy et al., 2010).

48 In marine shell-bearing invertebrates, shell shape variation is relevant to limit phenotypic
49 stocks (*sensu* Booke, 1981), as were studied for distinct molluscan species with commercial
50 interest (i.e., Márquez et al., 2017b, 2010b; Palmer et al., 2004; Rufino et al., 2013; Trivellini et
51 al., 2021). The use of geometric morphometric techniques has been recognized to help identify
52 phenotypic stocks of marine mollusks (Cadrin, 2020; Márquez et al., 2017b, 2010b; Palmer et al.,
53 2004; Rufino et al., 2013). The identification of stocks is especially relevant for spatially
54 structured populations to define spatial management tools (e.g., no-take zones, zoning, and
55 rotation schemes) or to identify the origin of the landings (Cadrin, 2020; Ibáñez, 2015).

56 Tehuelche scallop, *Aequipecten tehuelchus* (d'Orbigny, 1846) is one of the main coastal
57 shellfish resources that sustain a small-scale fishery in Northern Patagonia, Argentina (Elías et al.,
58 2009; Getino Mamet et al., 2021). The species is found in shallow waters of the Southwestern
59 Atlantic Ocean, between 23° to 45° latitude S, along the Argentine and Magellanic biogeographic
60 provinces (Fig. 1). At the southern end of its distribution range, the presence of oceanographic
61 fronts divides water masses in distinct regions (Acha et al., 2004). Such fronts include El Rincón
62 haline front between 39°S–41°S (Acha et al., 2004), the San Matías Gulf thermal front (Tonini et
63 al., 2013), the Peninsula Valdes tidal front (Pisoni et al., 2015), and the San José Gulf tidal front

64 (Amoroso and Gagliardini, 2010) (Fig. 1). In particular, the San José Gulf tidal front divides the
65 homonym gulf in two hydrographic domains (east and west) that define the local demography of
66 Tehuelche scallop (Amoroso et al., 2011; Amoroso and Gagliardini, 2010).

67 The species present three morphotypes: *tehuelchus*, *madrynensis*, and a non-common
68 variant *felipponei*. The *tehuelchus* and *madrynensis* morphotypes are geographically separated in
69 a distribution that matches the Argentine and the Magellanic Biogeographic provinces,
70 respectively (Castellanos, 1971; Soria et al., 2016) (Fig. 1a); meanwhile, *felipponei* is scarcely
71 found in both biogeographic provinces (Schejter and Bremec, 2007; Trovant et al., 2019). Those
72 have been meristically differentiated by the number of ribs as follows: *tehuelchus* has 14–19 ribs,
73 *madrynensis* has fewer ribs (11–14) but more pronounced, and *felipponei* has no ribs
74 (Castellanos, 1971). Genetic studies using allozymes (Real et al., 2004) and mitochondrial
75 markers (Trovant et al., 2019) indicated an absence of differentiation among morphotypes at the
76 species level. On the other hand, employing more variable microsatellites markers, genetic
77 differentiation at the population level was detected between *tehuelchus* and *madrynensis*
78 morphotypes following the biogeographical distribution of the morphotypes (Getino Mamet et al.,
79 2021). Within the *tehuelchus* morphotype, scallops also present allometric variations (Ciocco,
80 1992; Márquez et al., 2010a). Juvenile scallops present circular shells with symmetrical auricles,
81 while adults present elliptical shells and smaller auricles (Márquez et al., 2010a).



82

83 **Figure 1.** Study area. a) Distribution of *Aequipecten tehuelchus* depicting the *tehuelchus*,

84 *madrynsensis*, and *felipponei* morphotypes. The shaded region indicates the location of the

85 Argentine (northern) and Magellanic (southern) biogeographic provinces. b) Sampling locations:

86 Necochea (NEC), Las Conchillas (LCO), La Esfinge (LES), Punta San Román (PSR), Fracasso

87 (FRA), Punta Tehuelches (PTE), La Tapera (LTA), Puerto Madryn (PMA), and Playa Elola

88 (PEL). The Northern Patagonian gulfs which encompass San Matías, San José, and Nuevo gulfs

89 are indicated (SMG, SJG, NG respectively). Gray dashed lines indicate the location of El Rincón

90 front, San Matías Gulf front and associated cyclonic gyre, San José Gulf tidal front, and Peninsula

91 Valdes front. The dot-dashed lines mark political borders between Buenos Aires, Río Negro, and

92 Chubut provinces, and, to the east, the limit between provincial and federal jurisdictions over the

93 Argentine Sea.

94

95 The Tehuelche scallop fishery of San Matías and San José gulfs take place, respectively, in

96 Río Negro and Chubut provincial jurisdictions that are managed independently. The fishery

97 management in each provincial jurisdiction differs in the fishing method, the access regime, stock

98 assessment, and quota allocation (Orensanz et al., 2007; Orensanz and Seijo, 2013, Getino et al.,

99 2021). However, these scallop demes, belong to a single genetic stock being part of the
100 *tehuechus* morphotype (Getino Mamet et al., 2021). Combining captures from San José and San
101 Matías gulfs, reported landings in 2020 were less than a thousand tons (Getino Mamet et al.,
102 2021). On the other hand, northerly and outside of this regular fishing region, a Tehuelche scallop
103 bed was incidentally detected and exploited in a single fishing pulse near Buenos Aires Province
104 in 2002 by the industrial Patagonian scallop fleet (Lasta and Campodónico, 2003; Soria et al.,
105 2016) without fishing records afterward. The absence of scallop beds in Nuevo Gulf and further
106 south precluded the development of any kind of fishing activity at any scale.

107 In this context, the main goal of this study was to describe the shell shape differences of
108 Tehuelche scallop among nine locations to differentiate and identify the phenotypic stocks
109 throughout the distributional range of the species within the Argentine Sea with particular interest
110 where the fishery takes place. To accomplish this, the shape differences between and within
111 *tehuechus* and *madrynensis* morphotypes were assessed using geometric morphometric
112 techniques (Adams et al., 2004).

113

114 **2. Materials and methods**

115 A total of 307 Tehuelche scallop shells were collected in nine localities: Necochea (NEC),
116 Las Conchillas (LCO), La Esfinge (LES), Punta San Román (PSR), Fracasso (FRA), Punta
117 Tehuelches (PTE), La Tapera (LTA), Puerto Madryn (PMA), and Playa Elola (PEL), (Fig. 1b,
118 Table 1). The outline of the interior size of the right valve of each scallop was digitized using a
119 scanner EPSON Perfection V370 Photo at 600 PPI.

120 The analysis of the shell shape was performed using landmark-based (2D) geometric
121 morphometric techniques, which allow preserving the shape information during the multivariate
122 analyses so results can be graphically displayed (Adams et al., 2004). The shell outline was
123 captured using a configuration with six landmarks (LM) and 23 semi-landmarks (S-LM) (Fig. 2).
124 All specimens were digitized by the same observer using tpsDig2 v.2.17 (TPS series, available at

125 <https://life.bio.sunysb.edu/morph/index.html>). The semi-landmarks were used to capture contours
126 between LM, which were homologated mathematically in an iterative process (sliding) using
127 TpsRelw v.1.53. In this method, the S-LM coordinates are slide along the outline profile of the
128 scallop to minimize the bending energy of the landmark configuration (Gunz et al., 2005).
129 Subsequently, a generalized Procrustes analysis was applied in which landmark configurations
130 were rotated, translated to a common origin, and scaled to a unitary centroid size to obtain the
131 Procrustes aligned coordinates, used as shape data (Bookstein, 1996).

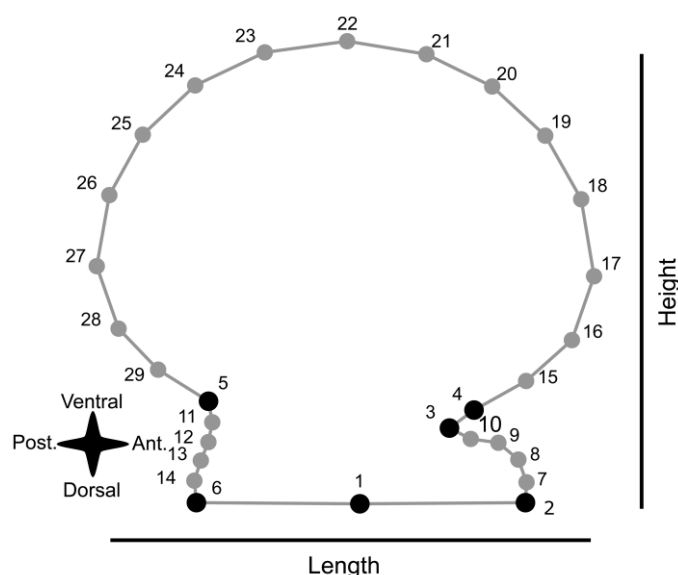
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133 **Table 1.** Sample locations. Sampling locations indicating the code; morphotype; status of the
134 fishery (fishing gear between brackets as following: BT, bottom trawls; AD, artisanal dredge; and
135 HO, hookah-diving); latitude; longitude; sample size (N); and year of collection.

Location	Code	Morphotype	Status of fishery	Latitude	Longitude	N	Year
Necochea	NEC	<i>tehuelchus</i>	Single pulse (BT)	39°30'S	59°30'W	54	2002
Las Conchillas	LCO	<i>tehuelchus</i>	Resumed activity* (AD/HO)	40°53'S	64°45'W	51	2017
La Esfinge	LES	<i>tehuelchus</i>	Regular activity (HO)	42°15'S	64°17'W	30	2012
Punta San Román	PSR	<i>tehuelchus</i>	Regular activity (HO)	42°15'S	64°13'W	33	2012
Fracasso	FRA	<i>tehuelchus</i>	Regular activity (HO)	42°24'S	64°08'W	24	2012
Punta Tehuelche	PTE	<i>tehuelchus</i>	Regular activity (HO)	42°24'S	64°19'W	24	2012
La Tapera	LTA	<i>tehuelchus</i>	Regular activity (HO)	42°18'S	64°32'W	26	2012
Puerto Madryn	PMA	<i>madrynsis</i>	Fishing is absent	42°46'S	65°00'W	37	2017
Playa Elola	PEL	<i>madrynsis</i>	Fishing is absent	44°53'S	65°38'W	28	2016

136 *After fifteen years of absence of the fishery, a new recruitment pulse was recorded in
137 2019-2020 in the NE sector of the San Matías Gulf and a dredge-based fishery is currently active
138 under the Rio Negro Provincial Jurisdiction.

139



140

141 **Figure 2.** Shell shape analysis. Position of six landmarks (black dots) and 23 semi-landmarks
142 (grey dots) used in the geometric morphometric analysis. Numbers refer to each landmark
143 definition: LM 1, the base of hinge; LM 2, end of the anterior auricle; LM 3, posterior end of the
144 byssal notch; LM 4, anterior end of the byssal notch; LM 5, inflection point between the shell
145 disc and posterior auricle; LM 6 end of the posterior auricle; S-LM 7-10, equidistantly between
146 LM 2 and LM 3; S-LM 11-14, equidistantly between LM 5 and LM 6; and S-LM 15-29,
147 equidistantly between LM 4 and LM 5 on the shell disc. Shell orientation (anterior, Ant.; and
148 posterior, Post.) and basic dimension are indicated.

149

150 A multivariate regression was performed in MorphoJ v1.06b (Klingenberg, 2011) in order
151 to account for the shape changes related to the individuals' size and discard this source of
152 variation from the spatial analyses. Therefore, further analyses were made using the residual
153 variation of the multivariate regression as free-size shape variables (Zelditch et al., 2004). The
154 use of such variables can prevent the misinterpretation of among-localities differences if they are
155 correlated to size (Outomuro and Johansson, 2017). The multivariate regression (pooled within
156 localities) was made using the centroid size (CS), defined as the square root of the sum of the
157 squared distances from the LMs to the centroid which they define, as shell size (Zelditch et al.,

158 2004). Procrustes coordinates were used as shape variables. The significance was tested with a
159 permutation test (100.000 rounds).

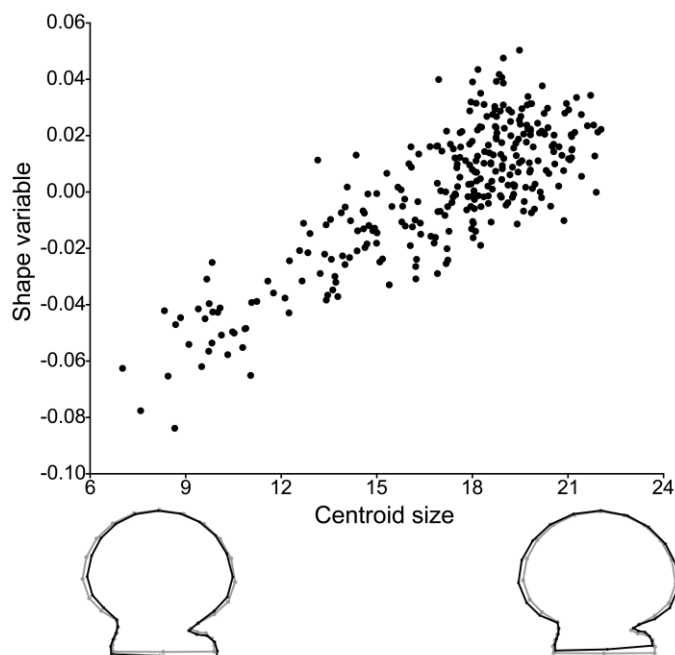
160 To elucidate the shape variation that maximizes the discrimination among localities, a
161 canonical variate analysis (CVA) was performed in MorphoJ. An assignation table for each
162 locality was constructed from the CVA using cross-validation. In the cross-validation, each
163 individual is left out from the analysis and then assigned to one group (a locality in this case)
164 using a function calculated from all other specimens (Kovarovic et al., 2011). This way avoids the
165 biases caused by classifying one specimen using functions that were calculated on samples that
166 included that same specimen (Viscosi and Cardini, 2011).

167 To evaluate the morphologic differentiation between *tehuelchus* and *madrynensis*
168 morphotypes, a discriminant function analysis (DFA) was performed in MorphoJ and the shape
169 differences were tested by the T-square Hotelling test with a permutation test (100.000 rounds).
170 Cross-validation was also performed to check the accuracy of the discriminant function in
171 assigning individuals to each group (morphotypes in this case).

172 Additionally, to summarize shape differences among localities, a hierarchical cluster
173 analysis using an unweighted pair-group method with arithmetic mean (UPGMA) using
174 Mahalanobis distances was performed in InfoStat. To identify the number of groups statistically
175 significant, the UPGMA was coupled to an extension of a multiple comparison method based on
176 cluster analysis (UPGMA-MDGC) (Valdano and Di Rienzo, 2007).

177 **3. Results**

178 The shell shape and CS were allometrically related (multivariate regression analysis,
179 $P < 0.0001$) and accounted for 11.1% of the total shape variation. The allometric component in
180 shape was mainly explained by the shell circularity and the auricles symmetry. Larger individuals
181 were represented by an elliptic shell disc, elongated in relation to the height, and shorter auricles.
182 On the opposite, smaller individuals were represented by a more circular shell disc, and higher
183 auricles (Fig. 3).



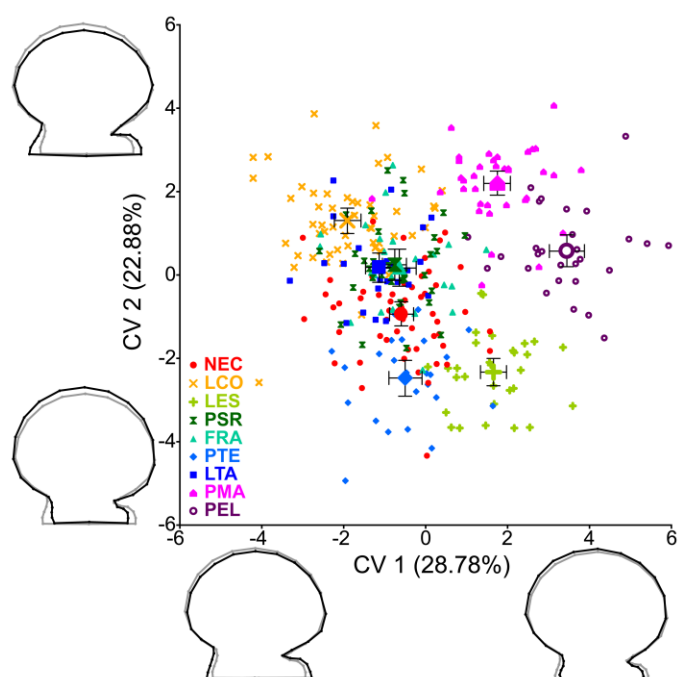
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185 **Figure 3.** Allometric relationship between shape and size. The wireframe diagrams below the
186 scatterplot, indicate the shape change predicted from consensus shape (grey wireframe) to an
187 increment of ± 10 scale factor of centroid size (black wireframe).

188

189 The shape variation that maximizes separation among localities is summarized by the
190 CVA, in which the canonical variables 1 and 2 (CV1 and CV2, respectively) accumulated about
191 51.7% of the variation (Fig. 4). The shape components that differentiate the positive extreme of
192 the CV1 were a higher and more circular shell disc and reduced auricles (Fig. 4). Tehuelche
193 scallops from PEL were the most differentiated individuals, represented by positive values of
194 CV1. Tehuelche scallops from both PMA and LES were also over the positive values of the CV1,
195 although differenced over the CV2. On the other hand, the shell shape associated with the
196 positive values of CV2 has a shorter height in relation to the length that results in an elliptically
197 elongated shell-disc (in the anteroposterior sense) (Fig. 2), and symmetrically expanded auricles
198 (Fig. 4). On the opposite extreme, the negative values of CV2 presented a shape characterized by
199 a more circular and higher shell than the consensus and reduced and asymmetrical auricles.

200 Scallops from LCO and PMA presented positive values of the CV2 while PTE and LES were over
201 the negative extreme of the axis (Fig. 4). Other locations, as PSR, FRA, or LTA, presented near-
202 zero scores in both canonical variables, while NEC was slightly displaced to the negative values
203 of the CV2. The percentages of correct assignment were high in all locations, ranging between
204 82.3% (LCO) and 94.6% (PMA) (Table 2).



205

206 **Figure 4.** Analysis of the maximum variation in shell shape along the first two canonical roots.

207 The expanded symbols indicate each location mean and whiskers are the 95% confidence interval

208 for each mean. The wireframes diagrams show the deformation explained by each canonical

209 variable axis with a scale factor of 10 to improve visualization. Grey color indicates the

210 consensus shape, while black indicates the deformation over each canonical variable. Sampling

211 locations: Necochea (NEC), Las Conchillas (LCO), La Esfinge (LES), Punta San Román (PSR),

212 Fracasso (FRA), Punta Tehuelches (PTE), La Tapera (LTA), Puerto Madryn (PMA), and Playa

213 Elola (PEL).

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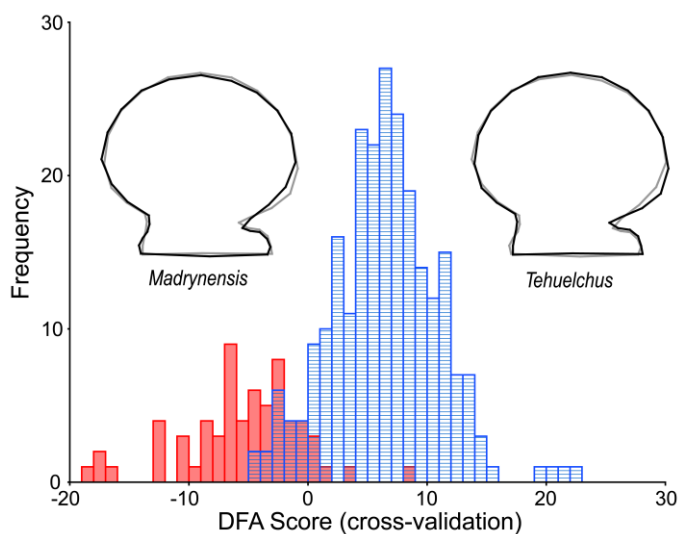
215 **Table 2.** Assignment table for localities and morphotypes resulting from the cross-validation.

216 Rows indicate the true group of origin (locality or morphotype), and columns indicate the groups
 217 in which individuals were allocated.

Location	NEC	LCO	LES	PSR	FRA	PTE	LAT	PMA	PEL	Total	Correct (%)	
NEC	46	3	2	1	1	0	1	0	0	54	85.2	
LCO	0	42	0	2	4	1	1	1	0	51	82.3	
LES	0	0	26	0	2	1	0	0	1	30	86.7	
PSR	0	0	0	31	0	0	2	0	0	33	93.9	
FRA	1	0	0	2	20	0	1	0	0	24	83.3	
PTE	0	0	1	0	0	20	3	0	0	24	83.3	
LAT	0	1	0	1	0	0	24	0	0	26	92.3	
PMA	0	1	0	0	0	0	0	35	1	37	94.6	
PEL	0	0	1	0	0	0	0	1	26	28	92.9	
Total	47	47	30	37	27	22	32	37	28	307	87.9	
Morphotype	<i>tehuelchus</i>					<i>madrynsis</i>						
<i>tehuelchus</i>	224					18					242	92.6
<i>madrynsis</i>	6					59					65	90.8
Total	230					77					307	92.2

218

219 Shell shape between *tehuelchus* and *madrynsis* morphotypes differed significantly (DFA;
 220 $P < 0.0001$). The maximum shell shape deformation that differentiates both morphotypes (Fig. 5)
 221 was similar to the explained by the first canonical variable of the CVA. The *madrynsis*
 222 morphotype presented a more circular shell with symmetric and reduced auricles; oppositely, the
 223 *tehuelchus* morphotype was associated with asymmetric auricles and an elongated shell outline
 224 (Fig. 5). The cross-validation of the discriminant function analysis assigned correctly 92.6% and
 225 90.8% of *tehuelchus* and *madrynsis* samples, respectively (Table 2).

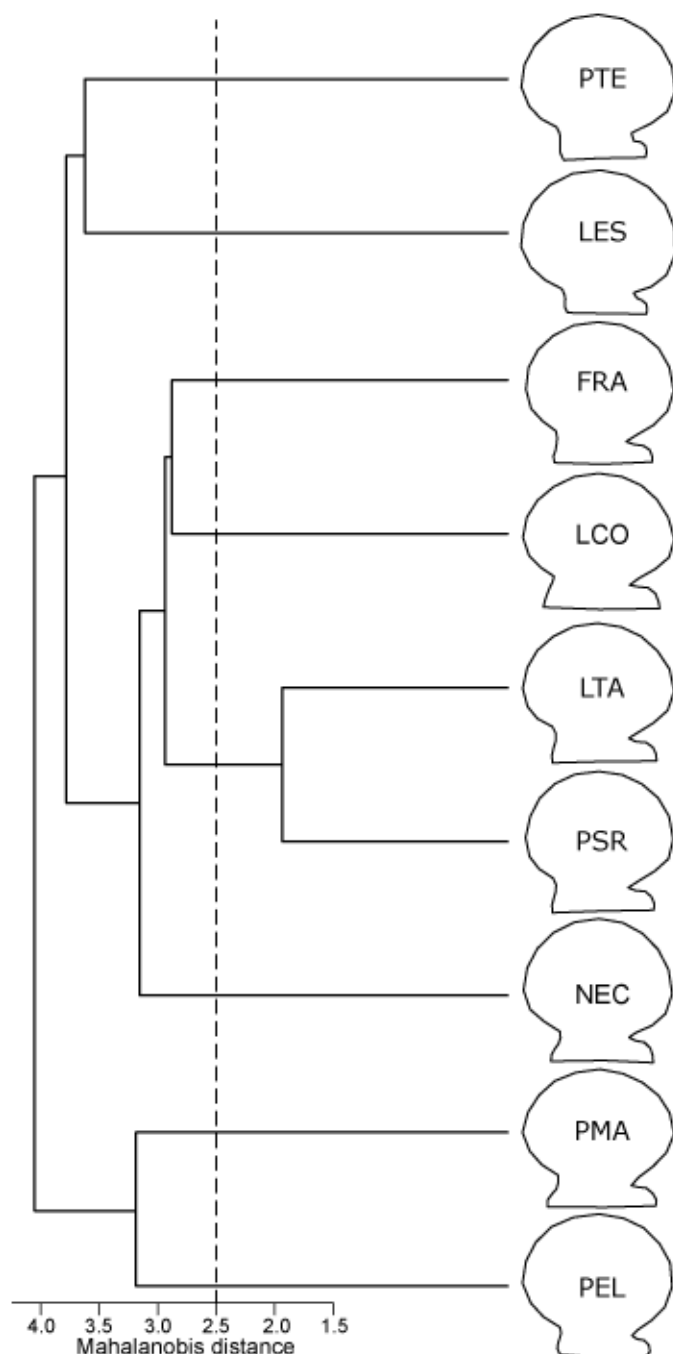


226

227 **Figure 5.** Discriminate function analysis (DFA) indicating the assignment frequency of
228 individuals from each morphotype. The wireframes diagrams show the deformation associated
229 with each morphotype, with a scale factor of 5 to improve visualization. Grey color indicates the
230 consensus shape, while black indicates the deformation of each morphotype.

231

232 The pattern of location similarities (Mahalanobis distances), summarized by the UPGMA-
233 MDGC dendrogram shows the main patterns of differentiation between morphotypes and
234 clarified the similarities within *tehuelchus* locations. The most divergent group was compounded
235 by PEL and PMA localities (*madrynsis* morphotype) (Fig. 6). Within the *tehuelchus* group, the
236 most divergent shell shape was at PTE and LES. The remaining location formed an inner group
237 wherein NEC was differenced from LCO, PSR, LTA, and FRA localities. Except for LTA and
238 PSR which lack differentiation, the remaining locations present statistically differenced shapes.



239

240 **Figure 6.** Dendrogram of the unweighted pair-group method with arithmetic mean (UPGMA)

241 based on Mahalanobis distances. Branches indicate the patterns of shape similitude among

242 locations. The vertical dashed line indicates the cut-off criterion for statistically distinct groups

243 identified by the MDGC test ($p=0.05$). Shape diagrams represent the average shape for each

244 location; deformation was exaggerated three times to improve the visualization. Sampling

245 locations: Necochea (NEC), Las Conchillas (LCO), La Esfinge (LES), Punta San Román (PSR),
246 Fracasso (FRA), Punta Tehuelches (PTE), La Tapera (LTA), Puerto Madryn (PMA), and Playa
247 Elola (PEL).

248

249 **4. Discussion**

250 One of the most remarkable features of scallops is the swimming capability; such
251 characteristic defines the main patterns of shell shape variation of these species (Stanley, 1988;
252 Tremblay and Guderley, 2016). Additionally, the local environmental conditions prevailing
253 where scallops live might be among the forces that drive the shell outline. In this context,
254 Tehuelche scallop from northern Patagonia, Argentina, presents polyphenism wherein the shell
255 shape variability of adults has been driven by oceanographic heterogeneity.

256 The principal variability of the scallops shell shape was detected between the *tehuclchus*
257 and *madrynensis* morphotypes. The *madrynensis* morphotype presents higher and circular shell
258 discs with reduced auricles than those from the *tehuclchus* morphotype. Also, significant
259 differences were detected at PMA, with an elliptically elongated shell-disc (in the anteroposterior
260 sense) and symmetrically expanded auricles. These findings complement the morphotype
261 characterization defined solely based on the number of ribs (Castellanos, 1971; Real et al., 2004).
262 The geographic limit between both morphotypes matches the boundary between the Argentine
263 and the Magellanic Biogeographic provinces (Balech and Ehrlich, 2008; Cousseau et al., 2020).
264 While the *tehuclchus* morphotype is found in the warm-temperate waters from the Argentine
265 Biogeographic province, the *madrynensis* morphotype inhabits the cold-temperate Magellanic
266 province (Real et al., 2004; Trovant et al., 2019). The presence of the Peninsula Valdés tidal front
267 in this region (Pisoni et al., 2015) seems to act as a physical barrier that partially constrains larval
268 dispersal (Alfaya et al., 2020; Getino Mamet et al., 2021). The isolation resulting from such
269 barrier might be strong enough to produce both the morphologic and genetic differentiation
270 between morphotypes (Getino Mamet et al., 2021). The findings of both genetic and morphologic

271 differentiation within the species according to the oceanographic differentiation between
272 biogeographic provinces could be indicative of the presence of two ecotypes.

273 On the other hand, high shell variability was found among locations of the northern
274 *tehuelchus* morphotype. Most of the variability is related to the symmetry of the auricles and the
275 shell disc circularity, the last one referred to as height/length proportion in other studies using a
276 classical morphometric approach (Ciocco, 1992; Gould, 1971; Orensanz, 1986). Both continuous
277 characters have been related to the swimming capability of scallops (Gould, 1971; Stanley, 1972,
278 1988). While an elliptically elongated shell-disc (in the anteroposterior sense, with smaller
279 height/length proportion; Fig. 2) is better to balance forces during the swimming making it easier,
280 a more circular shell-disc shape (larger height/length proportion) has the opposite effect and can
281 be associated with more sedentary habits (Gould, 1971). On the other hand, auricle symmetry is a
282 feature associated with swimming activity, while an asymmetrically elongated anterior auricle
283 may prevent the overturning of byssally attached individuals (Stanley, 1988, 1972). Under such
284 theoretical frame, the symmetric auricles and the elliptically elongated shell-disc shape of
285 scallops from LCO in San Matías Gulf suggest a more active swimming behavior than scallops
286 from the San José Gulf and NEC location. This finding agrees with Orensanz (1986), who found
287 a smaller height/length proportion in San Matías Gulf than in San José Gulf. Such shape was
288 attributed to the high predation pressure in San Matías Gulf that may favor swimming escape
289 responses. Instead, in San José Gulf, the wind-induced beach stranding exposure may be
290 responsible of favoring a more sedentary shell shape (Orensanz, 1986). The fact that the
291 morphologic differences between San Matías and San José gulfs in 1974-1976 (Orensanz, 1986)
292 are similar to the finding in the present study suggest that the morphologic differentiation may
293 have long-term stability. Further efforts should be directed to include more locations and distinct
294 cohorts to test the temporal stability of the phenotypic trends (Cadrin, 2020).

295 Within San José Gulf, LES and PTE constituted a separated cluster (Figs 4, 6) with the
296 most sedentary phenotypes (i.e., more circular shell-disc shape and asymmetrically small

297 auricles). This morphologic differentiation is coincident with the presence of the San Jose front,
298 as LES and PTE are located on each extreme of the front (Fig. 1). Larger morphologic
299 differentiation at these places was previously noticed for the striped clam, *Ameghinomya antiqua*
300 (Márquez et al., 2010b). The morphology of these locations might be reflecting how local strong
301 tidal currents at these places drive the shell outline. The coastal geomorphology in conjunction
302 with the tidal regimes (Tonini and Palma, 2017) produces strong tidal currents at LES and PTE
303 (Picallo, 1980; Tonini and Palma, 2009), which are less stronger in other locations as Bengoa
304 beach (eastward PSR) that respond mainly to the wind-stress (Moreira et al., 2009).

305 The morphometric differences founded along San Matías and San José gulfs may be the
306 result of phenotypic plasticity driven by environmental conditions. In this geographical region,
307 the lack of genetic differentiation indicates a plausible scenario of a common pool of larvae
308 seeding the San Matías and San José gulfs (Getino Mamet et al., 2021). In this sense, given the
309 shared larval pool genetically homogeneous, the morphological differentiation could be related to
310 the local environmental conditions (e.g., currents) in which each cohort develops.

311 Finally, at the Buenos Aires shelf waters, although NEC presents a shape similar to the
312 consensus, samples were correctly identified (Table 2) indicating that NEC can be differenced
313 from the remaining locations inhabiting both gulfs. Such results are relevant considering the
314 opportunistic nature of the fishery in this region. For example, during the fishing pulse of 2002, in
315 the Buenos Aires shelf region, around 20,000 tonnes were fished in only three months before
316 being wiped out by the bottom-trawl-based industrial Patagonian scallop fleet (Lasta and
317 Campodónico, 2003; Soria et al., 2016). To give an idea of its importance, such captures
318 represent more than the sum of fifty years of landings from San José Gulf, since the beginning of
319 the activity. Currently, those beds lack fishing interest and it is uncertain if they have recovered
320 after the 2002 fishing pulse. If such fishery reactivates, the morphometric differentiation will be
321 useful information to properly distinguish captures from Buenos Aires.

322 The plasticity of the shell shape variation detected in this work has relevance in the context

323 of fishery management. The scallop fishery from San José Gulf is managed as a single stock
324 under a Total Allowable Catch system (Cinti et al., 2011; Orensanz and Seijo, 2013; Soria et al.,
325 2016). However, the recruitment locations and depths in the gulf are rather heterogeneous, and
326 therefore, fishers often propose a rotational/zoning scheme to focalize the fishing pressure in
327 concordance with the stock assessment information (Fiorda and Parma, 2015; Soria et al., 2017).
328 Additionally, phenotypic traits can be used as natural tags to the identification of the geographic
329 origin of landings during the initial steps of the commercial process (Ibáñez, 2015, 2014; Shepard
330 et al., 2010). The identification of the origin gives traceability to the capture, which is relevant to
331 aid in law enforcement under a spatially structured management (Ortea and Gallardo, 2015). For
332 example, the morphometric characterization of each bed could be relevant to control the origin of
333 the scallops when some areas of the gulf are temporally closed due to a red tide event, which is a
334 frequent phenomenon in the northern Patagonian gulfs (Sastre et al., 2018).

335

336 **5. Conclusion**

337 The findings of this study have relevance not only for the understanding of ecological
338 adaptation to distinct environments of Tehuelche scallop but also for its fishery management. The
339 shape differences between morphotypes complement the main distinction solely by the number of
340 ribs and, together with the genetic differentiation, reinforce the idea of the presence of two
341 ecotypes. Within the northern *tehuelchus* morphotype, the shell shape variation might be
342 associated with environmental conditions indicating the plasticity of the shape outline. Further
343 work is needed to understand the temporal stability of the phenotypic plasticity. Likewise, other
344 biologic variables that may affect the swimming behavior (as predators, epibionts loads, bottom
345 current, growth rate, dense-dependence) need to be studied. The findings of the present study
346 have relevance for phenotypic stock identification that could be useful to know the origin of
347 captures during the initial steps of the fishing process if zoning and rotational fishing schemes are
348 implemented.

349

350 **CRedit authorship contribution statement**

351 **Getino Mamet Leandro Nicolás:** Conceptualization, Methodology, Formal analysis,
352 Investigation, Visualization, Writing - Original Draft; **Gaspar Soria:** Conceptualization,
353 Resources, Methodology, Formal analysis, Investigation, Funding acquisition, Project
354 administration, Supervision, Writing - Review & Editing; **Laura Schejter:** Resources, Writing -
355 Review & Editing; **Federico Márquez:** Resources, Methodology, Formal analysis, Writing -
356 Review & Editing.

357

358 **Declarations of competing interest**

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

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376

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