Parasitism without frontiers: Infection variability of an intermediate host across multiple spatial scales

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Background. Parasites are heterogeneously distributed in intermediate host populations, but how this variability changes between multiple geographic scales remain unclear. Here, we test whether in a complex host-parasite system developing in sandy shores, the high spatiotemporal variability in the physical structure of these habitats will lead to comparatively high variability in parasitosis observed at the local- (i.e. few metres) and meso-scale (i.e. tens of km), relative to the regional scale (several 100s of km).

Methods. Here, we analyse the spatial variability of acanthocephalan parasites infecting decapod molecrabs according to a hierarchical design spanning more than 500 km of the southern-central shore of Chile. We predicted that the local effects could potentially influence the host-parasite interaction by generating a large amount of between-site heterogeneity in parasitosis and thus, to improve our understanding of the development of epidemic and infectious processes.

Results. The analysis of generalized mixed-effect models showed that the spatial variability in parasitosis (i.e. probability of infection, parasite burden, prevalence, mean intensity, and mean abundance) was smallest at the regional scale. On the other hand, the largest amount of spatial variability of most measures of parasitosis was observed at the meso-scale. Prevalence, however, displayed similar (and high) levels of variation at meso- and local-scales.

Conclusions. We suggest that parasite infection could be related with abiotic factors that determine habitat physical stability, such as seasonal morphodynamic of sandy shores. Thus, local environmental filters can have strong and deterministic effects on the regulation of this complex host-parasite system across spatial scales.

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2   **spatial scales**

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16   **Abstract**

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19   whether in a complex host-parasite system developing in sandy shores, the high spatiotemporal

20   variability in the physical structure of these habitats will lead to comparatively high variability in

21   parasitosis observed at the local- (i.e. few metres) and meso-scale (i.e. tens of km), relative to the

22   regional scale (several 100s of km).

23   **Methods.** Here, we analyse the spatial variability of acanthocephalan parasites infecting decapod

24   molecrabs according to a hierarchical design spanning more than 500 km of the southern-central

25   shore of Chile. We predicted that the local effects could potentially influence the host-parasite

26   interaction by generating a large amount of between-site heterogeneity in parasitosis and thus, to

27   improve our understanding of the development of epidemic and infectious processes.

28   **Results.** The analysis of generalized mixed-effect models showed that the spatial variability in

29   parasitosis (i.e. probability of infection, parasite burden, prevalence, mean intensity, and mean

30   abundance) was smallest at the regional scale. On the other hand, the largest amount of spatial

31   variability of most measures of parasitosis was observed at the meso-scale. Prevalence, however,

32   displayed similar (and high) levels of variation at meso- and local-scales.

33   **Conclusions.** We suggest that parasite infection could be related with abiotic factors that

34   determine habitat physical stability, such as seasonal morphodynamic of sandy shores. Thus,

35   local environmental filters can have strong and deterministic effects on the regulation of this

36   complex host-parasite system across spatial scales.

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38   Key words: acanthocephalans, beach morphodynamics, *Emerita analoga*, generalized linear mix-

39   effect models, *Profilicollis altmani*, southeast Pacific

Introduction

41 Parasites are essential components of natural communities over the world. They are

42 generally heterogeneously distributed across space and time (Byers et al., 2008; Johnson &

43 Hoverman, 2014; Byers, Holmes & Blakeslee, 2016), which has important consequences

44 for host mortality and the process of host-parasite regulation (Thieltges & Reise, 2007;

45 Byers et al., 2008; Rodríguez & Valdivia, 2017). In general, parasitological studies have

46 been focused more on temporal than spatial scale (but see Latham & Poulin, 2003; Smith,

47 2007; Powell, Kim & Bushek, 2015; Rodríguez & Valdivia, 2017). Nevertheless, an

48 emergent pattern rising from these studies in that the spatial patterns of parasitosis are

49 scale-dependent; that is to say, patterns observed at a given spatial scale can be absent at

50 other (Smith, 2001; Thieltges et al., 2009; Studer et al., 2013; Thieltges et al., 2013).

51 Spatial scale can be determined in terms of grain size, extent, and the distance between

52 observations (Wiens, 1989; Legendre & Legendre, 1998). In this study, we analyse the

53 differences in parasitosis between host subpopulations separated by few centimetres (local

54 scale), few kilometres (meso-scale), and several hundreds of kilometres (regional scale).

55 Broad-scale infective processes usually develop from infections that occur at local scales in

56 which hosts interact directly, and then propagate toward broader spatial scales (Parietti,

57 Merlo & Etchegoin, 2013; Byers, Holmes & Blakeslee, 2016). Thus, quantifying the

58 variability in parasitosis across spatial scales in determinant to improve our understanding

59 of the development of epidemic and infectious processes.

60   The variation in the spatial distribution of parasites can be important at local scales;

61 e.g within local host populations embedded in a host metapopulation (Smith, 2001; Parietti,

62 Merlo & Etchegoin, 2013). Local factors such as host movement, density, recruitment

63 patterns and host mortality can determine local-scale parasite variability (Blower &

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64 Roughgarden, 1989; Smith, 2001; Johnson & Hoverman, 2014). For example, people

65 movement can explain the fact that the risk of malaria infection is more variable between

66 members of a household (i.e. local scale) than between communities separated by tens to

67 hundreds of kilometres (i.e. meso-scale; Bousema et al., 2011; Carrasco-Escobar et al.,

68 2017). Within host populations in nature, variations in parasite exposure can increase the

69 variability in host's infection probability and infection rate, leading to the usually strong

70 parasite aggregation at the local scale (i.e. spatial variance in parasite load; Anderson &

71 May, 1978). Therefore, factors that affect host' infection rates can generate strong scale-

72 dependent patterns of parasite variability.

73   In natural communities, local factors like physical characteristic of habitat, habitat

74 alteration, and pollution can influence the heterogeneity of infection among sites and

75 generate meso-scale variation in parasitosis (Smith, 2001; Lafferty & Gerber, 2002). For

76 example, Meager, Schlacher & Nielsen (2012) demonstrate that human activities can affect

77 habitat selection of birds (Charadriiformes), which are forced to escape from severely

78 impacted sites. In the case of migratory Charadriiformes that use sandy shores as feeding

79 areas, spatial variability in beach morphodynamics can pose strict restrictions to habitat use,

80 generating significant meso-scale variations in bird abundance (Lafferty, 2001; Meager,

81 Schlacher & Nielsen, 2012; Basso et al., 2017). Since birds are definitive host for many

82 parasites, these alterations of bird abundances can affect the exposure of local intermediate

83 hosts to parasite's dispersive stages and thus increase the between-site heterogeneity in

84 parasitosis (Fredensborg, Mouritsen & Poulin, 2006; Smith, 2007; Byers, Holmes &

85 Blakeslee, 2016; Rodríguez, D'Elía & Valdivia, 2017). Moreover, sandy shores experience

86 broad seasonal variations in terms of sand erosion and accretion, which generates large

87 mortality events of sand-dwelling invertebrates that act as intermediate hosts in complex

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88   host-parasite systems (Bessa et al., 2014; Sepúlveda & Valdivia, 2016). Therefore,

89   alterations of habitats can potentially influence the host-parasite interaction by generating a

90   large amount of between-site heterogeneity in parasitosis (Smith, 2001).

91   Complex host-parasite systems usually include highly mobile definitive hosts,

92   which are able to disperse the parasites over broad spatial scales. For instance, migratory

93   birds can disperse the infective stages of parasites over hundreds and thousands of

94   kilometres (Smith, 2007; Goulding & Cohen, 2014; Gutiérrez et al., 2017). According to

95   metacommunity theory, high dispersal potential can lead to low heterogeneity in terms of

96   species occurrences and abundances across a region (Leybold, 2004). Thus, low variability

97   in parasitosis within a complex host-parasite system can be expected when host populations

98   separated by several hundreds of km—but in the same biogeographic region—are

99   contrasted (i.e. a region-scale spatial comparison). Regarding complex parasite systems

100   developing in sandy shores, regional variation in parasitosis can be expected to be smaller

101   relative to that occurring at local and meso-scales of observation, owing the dynamic nature

102   of the physical structure of these habitats (see previous paragraph). Sandy shores are

103   currently under threat due to urban development and recreational activities worldwide

104   (Defeo et al., 2009; Schlacher et al., 2014; Bessa et al., 2014). In addition, migratory birds

105   face multiple anthropogenic impacts derived from broad- (e.g. global change) and local-

106   scale (e.g. increasing level of human activities) processes (Meager, Schlacher & Nielsen,

107   2012; Navedo & Herrera 2012; Piersma et al., 2016; van Gils et al., 2016). Assessing

108   therefore the scale-dependent variability in complex host-parasite interactions involving

109   sandy-shore coastal ecosystems and migratory birds can be relevant for both applied and

110   fundamental ecology.

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111   In this study we test the hypothesis that, in a complex host-parasite system

112   developing in coastal sandy shores, the high spatiotemporal variability in the physical

113   structure of these habitats will lead to comparatively high variability in parasitosis observed

114   at local- (few metres) and meso-scales (10s of km) relative to the geographic scale (100s of

115   km). In this complex system, the decapod molecrab *Emerita analoga* Stimpson, 1857

116   ingests accidentally the infective stages of the acanthocephalan *Profilicollis altmani* Meyer,

117   1931, which reproduces and completes its life cycle in several seagull species (Goulding &

118   Cohen, 2014; Rodríguez, D'Elía & Valdivia, 2017). Parasitosis was expressed as infection

119   probability, parasite burden, prevalence, intensity, and mean abundance. These estimators

120   were compared between host subpopulations located at increasing distances along the shore

121   of southern-central Chile.

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123

124 **Materials and methods**

125 **Study sites and sampling procedure**

126 This study was conducted across two regions separated by ca. 500 km of distance in

127 southern-central Chile. Both regions belong to the transitional area between the Peruvian

128 and Magellanic biogeographic provinces (Camus, 2001). In each region, four beaches were

129 randomly selected and sampled during April 2014. In the central region (i.e. "Biobío"), the

130 sites were Dichato (36.4ºS – 72.9ºW), Lenga (36.4ºS – 73.1ºW), Playa Blanca (37.0ºS –

131 73.1ºW) and Colcura (37.1ºS – 73.1ºW). In the southern region ("Los Ríos"), the sites were

132 Cheuque (39.3ºS – 73.2ºW), Curiñanco (39.4ºS – 73.2ºW), Calfuco (39.7ºS – 73.3ºW) and

133 Chaihuín (39.9ºS – 73.5ºW; Fig. 1). In each site, we randomly deployed two patches of 10

134 m in alongshore length and separated by 5 m. In each patch, two transects were deployed

135 randomly and perpendicularly to the shoreline—transects were separated from each other

136 by ca. 2 m. In each transect, we placed four sampling stations located ca. 2 m apart from

137 each other from the effluent line (i.e. mid-low intertidal) to the swash line (low intertidal).

138 Plastic corers (0.03 m^{-2}) were buried to a depth of 20 cm (equating a volume of 0.006 m^{-3})

139 and the sand was sieved through a 1-mm mesh sieve. Molecrabs were collected from each

140 corer and transported to the laboratory; cephalothorax length (mm) of each individual was

141 recorded before extracting and counting the *P. altmani* cystacanths (i.e. larval stage) from

142 the haemocoele. The per capita number of parasites (i.e. burden) was estimated for each

143 molecrab. For each transect, beach, and region, we estimated the prevalence (percentage of

144 infected hosts), intensity (mean parasite burden per infected hosts) and mean abundance of

145 parasites (mean number of parasites per host population; Bush et al., 1997).

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147 **Statistical Analyses**

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148   Scale-dependent spatial variability in parasitosis was estimated separately for each indicator

149   (i.e. infection probability, per capita parasite burden, prevalence, intensity, and mean

150   abundance) as variance components of generalized lineal mixed-effects models (GLMM;

151   Pinheiro & Gates, 2000). The regional, meso- (nested in regional), and local (nested in

152   meso) scales were included in the models as random factors. Variance components were

153   calculated according to Pinheiro & Gates (2000) and expressed as standard deviation units.

154   Model parameters were estimated though maximum likelihood. For each GLMM, we

155   estimated two types of pseudo-R^2: the marginal R^2, which represents the variance explained

156   by the fixed factors, and the conditional R^2, which represents the variance explained by

157   both, fixed and random factors (Nakagawa & Schielzeth, 2013; Johnson, 2014). The spatial

158   variance of infection probability and parasite burden were analysed at the per capita level;

159   that of prevalence, intensity, and mean abundance were analysed at the population (i.e.

160   sample) level.

161   In the per capita models, we included molecrab body size as fixed variable due to

162   the strong accumulation of parasites over the ontogeny in this species (see also Rodríguez

163   & Valdivia, 2017). Scale-dependent variance components of per capita infection probability

164   and parasite burden were estimated from a binomial (logit link) and Poisson (log link)

165   GLMM, respectively. In the population-level models, the denominators of the calculations

166   of prevalence, intensity, and mean abundance—i.e. number of hosts, number of infected

167   hosts, and number of hosts, respectively—were included as fixed factors. This was done to

168   account for non-linearity between these measures. Poisson GLMMs were used for all

169   population-level estimations of variance components.

170

171   **Results**

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172   A total of 849 individuals of *E. analoga* were captured in both regions. Molecrab'

173   cephalothorax length varied from 4.8 to 29.5 mm. The size of first infection was 9 mm

174   cephalothorax length. At the per capita level, the probability of infection varied from 0.1 (3

175   mm host) to 0.8 (25 mm host; Fig. 2A) and parasite burden—i.e. the per capita number of

176   parasites—ranged between zero and 12 ind. per molecrab (Fig. 2B). Body size accounted

177   for ca. 14 % of the variability in probability of infection, while the entire model accounted

178   for ca. 25 %. Cephalothorax length explained ca. 17 % of the variability in parasite burden,

179   and the entire ca. 33 %. The variance components suggested that, after controlling for the

180   variation in body size, the meso-scale (i.e. differences between sites) accounted for the

181   largest variation in both probability of infection and parasite burden, followed by the local-

182   and regional-scales (Fig. 2C, and 2D). The regional scale had almost no contribution to the

183   overall variation in infection probability and burden.

184   At the population level, prevalence was high in both regions, reaching values close

185   to 60 % (Fig. 3A). Among sites (i.e. meso-scale), prevalence varied between 40 and 80 %

186   (Fig. 3B). Prevalence was variable at the local-scale (within sites), with maximum values

187   near 90 % in the Biobío region and > 50 % of prevalence in most patches (Fig. 3C). The

188   number of hosts (fixed portion of the GLMM) accounted for ca. 54 % of the variability in

189   prevalence, while the entire model accounted for ca. 76 %.

190   Mean intensity was similar between both regions (Fig. 3D), but it was highly

191   variable at the meso-scale. For example Playa Blanca (Biobío) and Cheuque (Los Ríos)

192   showed the highest values across the entire region (Fig. 3E). The number of infected hosts

193   in the model accounted for ca. 48 % of the variability in intensity, and the entire model

194   accounted for ca. 77 %. Similar patterns of variation showed the mean abundance of

195   parasites (nº of parasite per individual), which was variable at the meso- and local scales

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196   (Fig. 3H, 3I). The fixed model (i.e. number of hosts) explained 28 % of the variability in

197   mean abundance, while the entire model explained ca. 69 %.

198   Prevalence variance component for the local-scale was slightly larger that for the

199   meso-scale, and almost no variability was detected for the regional scale (Fig. 4A). For

200   intensity, on the other side, variance component of the meso-scale was one order of

201   magnitude larger than that of local- and regional-scales (Fig. 4B). Finally, variance

202   component of mean abundance followed a similar pattern, in which the spatial variance

203   assessed at the meso-scale was ca. 3-fold that observed at the local-scale—the regional

204   scale of observation account for ca. zero spatial variability in mean abundance (Fig. 4C).

205

206   **Discussion**

207   This study showed that the spatial heterogeneity of parasitism of molecrabs was in general

208   strongest at the meso-scale. At the per capita level, however, the relationships between

209   parasitosis and spatial scale were rather weak, as the scale of observation accounted for ca.

210   11 % of the variation in probability of infection and 16 % of that of parasite burden. In

211   contrast, we observed that prevalence, intensity of infection, and mean abundance varied

212   strongest at the local and meso-scale. In this host-parasite system, local and meso-scale

213   factors can be determinant predictors of the probability of infection and burden of

214   acanthocephalan parasites, which in turn drive the variation of prevalence, intensity, and

215   mean abundance in the region. Below, we discuss how local filters that influence habitat's

216   physical stability—such as mechanical disturbance and temporal dynamic of sandy

217   shores—can mediate the regulation of this host-parasite system.

218   In our study, most parasitological descriptors were highly variable at the spatial

219   meso-scale. Physical characteristics of sandy shores such as morphodynamics, in addition

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220   to anthropogenic disturbances, could explain these trends (Jaramillo & González, 1991;

221   Jaramillo, Contreras & Quijon, 1996; Dugan & Hubbard, 2006; Meager, Schlacher &

222   Nielsen, 2012). First, in reflective beaches, the drift line is narrow and has less available

223   space for seabirds (Jaramillo, McLachlan & Coetzee, 1993), which release the infective

224   stage of parasites (Byers et al., 2016). In intermediate and dissipative beaches, however, a

225   broader drift line increases the habitat available for seabird (Jaramillo, McLachlan &

226   Coetzee, 1993; Meager, Schlacher & Nielsen, 2012); thereby the source of parasite

227   propagules is larger. In the present work, accordingly, Playa Blanca (Biobío) and Cheuque

228   (Los Ríos) are considered dissipative beaches (Jaramillo, McLachlan & Coetzee, 1993;

229   Jaramillo et al., 2012) and showed highest intensity and mean abundance of parasites.

230   Contrary, Dichato (Biobío) and Chaihuín (Los Ríos) are reflective beaches (Veas et al.,

231   2013) and showed low infection level. Second, anthropogenically impacted beaches are

232   susceptible to decreases in the abundance of seabirds (Lafferty, 2001; Meager, Schlacher &

233   Nielsen, 2012; Navedo & Herrera, 2012), which can also reduce the exposure of molecrabs

234   to the parasitic infective stages. Previous work in this region and elsewhere has shown

235   significant, albeit context-dependent, relationships between seabird (i.e. exposure) and

236   parasite load in intermediate hosts (Latham & Poulin, 2003; Smith, 2007; Zambrano &

237   George-Nascimento, 2010; Byers, Holmes & Blakeslee, 2016; Rodríguez & Valdivia,

238   2017). Therefore, the probability and infection level of *E. analoga* likely varied as

239   functions of local environmental filters that influence parasite exposure.

240   In addition to changes in parasite exposure, natural disturbances such as sand

241   erosion and accretion can cause significant between-site variability in mortality of sandy-

242   shore invertebrate hosts (Jaramillo et al., 2012; Veas et al., 2013; Sepúlveda & Valdivia,

243   2016). These seasonal events remove tons of sand from the lower elevation of intertidal

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244   sandy shores, which leads to massive mortality events of molecrabs and other taxa

245   (Sepúlveda & Valdivia, 2016). In the study regions, seasonal erosion-accretion cycles occur

246   with strongest intensity in Dichato, Curiñanco, and Chaihuín (S. M. Rodríguez, pers. obs.),

247   which can further explain the significant variation in parasitosis at the meso-scale. In fact,

248   our study was carried out during autumn, when erosion can heavily impact mainly

249   reflective beaches (e.g. Sepúlveda & Valdivia, 2016). In these regions, molecrab

250   populations are able to reach between 20 and 30 % of pre-disturbance abundances in two

251   years (Sepúlveda & Valdivia, 2016). This relatively slow recovery rate can disrupt the

252   accumulation of parasites in the molecrabs and further transmission to seagulls (Defeo &

253   McLachlan, 2013; Rodríguez & Valdivia, 2017). Thus, context-dependent disruptions of

254   the host-parasite links, due to decreased molecrab abundance, would affect the transmission

255   and aggregation in the intermediate hosts and lead to high between-site variability in

256   parasitosis.

257   We observed that the second relevant source of variation was the local scale. Smith

258   (2001) and Bousema et al. (2011) indicate that epidemiological processes usually start from

259   local scales. Local biotic factors, such as patchy host mortality, parasite recruitment failure,

260   and host mobility can generate within-site variability in parasitosis (Smith, 2001; Byers et

261   al., 2008; Parietti, Merlo & Etchegoin, 2013). High parasite burden increases the mortality

262   rate in large-sized hosts, producing highly skewed distributions of parasites across the host

263   population (Latham & Poulin, 2002; Rodríguez & Valdivia, 2017). However, temporal

264   variation in molecrab recruitment might decouple the relationship between local variability

265   in parasite exposure and load due to the increase of non-infected hosts (Contreras, Defeo &

266   Jaramillo, 1999; Zambrano & George-Nascimento, 2010). Although these factors can play

267   a major role in generating local-scale parasite aggregation, the results of this study suggest

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268   that their effects would be subordinated to those of factors that operate at broader (i.e.

269   meso) spatial scales.

270

271   **Conclusions**

272   In summary, our results showed that infection variability can be larger when host

273   populations separated by tens of km are compared along the shore. We suggest that parasite

274   infection in this model system could be related with abiotic factors that determine habitat

275   physical stability, such as seasonal morphodynamic of sandy shores. But, how

276   generalizable are these results? Probably, other ecosystems that are subjected to constant

277   environment and physical disturbances, like agricultural lands and wetlands, can show

278   similar patterns of parasitic infection within host populations (Koprivnikar & Redfern,

279   2012; Basso et al., 2017). If anthropogenic impacts negatively affect parasite exposure in

280   sandy shores, then the information on parasite geographical variability would be relevant

281   also for informing conservation strategies (e.g. Lafferty, 1997). Environmental variability

282   can decrease host density and increase parasite mortality, reducing the capacity of the

283   parasite to regulate the host-parasite interaction (Lafferty, 1997; Koprivnikar & Redfern,

284   2012). Therefore, beyond life history traits of hosts, changes in the physical habitat can

285   have strong effects on host-parasite dynamics.

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500   **Figure legend**

501   **Figure 1.** Map depicting the sampling sites across both study regions. Site codes are DICH

502   = Dichato, LENG = Lenga, BLAN = Playa Blanca and COLC = Colcura in the northern

503   region (Biobío), and CHEU = Cheuque, CURI = Curiñanco, CALF = Calfuco, and CHAI =

504   Chaihuín in the southern region (Los Ríos).

505

506   **Figure 2.** Individual-scale parasitosis of *Profilicollis altmani* infecting the intermediate

507   host *Emerita analoga* in southern-central Chile. Probability of infection (A) and parasite

508   burden (i.e. per capita number of parasites; B) were estimated from Generalized Linear

509   Mixed-Effect models as functions of size of molecrabs. The variance components of the

510   probability of infection (C) and parasite burden (D) was estimated for each of three spatial

511   scales of observation: regional, meso-, and local scale.

512

513   **Figure 3.** Population-level parasitosis of *Profilicollis altmani* infecting molecrabs in

514   southern-central Chile. Parasitosis was expressed as prevalence (A, B, C), intensity (D, E,

515   F), and mean abundance (G, H, I) of parasites. These indicators were estimated at the

516   regional (A, D, G), meso- (B, E, H), and local scales (C, F, I) of observation. Values are

517   given as mean and standard error of the mean.

518

519   **Figure 4.** Variance components of prevalence (A), intensity (B) and mean abundance (C)

520   of parasites *Profilicollis altmani*, estimated at regional, meso-, and local scale in the

521   southern-central coast of Chile.

522

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Figure 1(on next page)

Study sites

Map depicting the sampling sites across both study regions. Site codes are DICH = Dichato, LENG = Lenga, BLAN = Playa Blanca and COLC = Colcura in the northern region (Biobío), and CHEU = Cheuque, CURI = Curiñanco, CALF = Calfuco, and CHAI = Chaihuín in the southern region (Los Ríos).
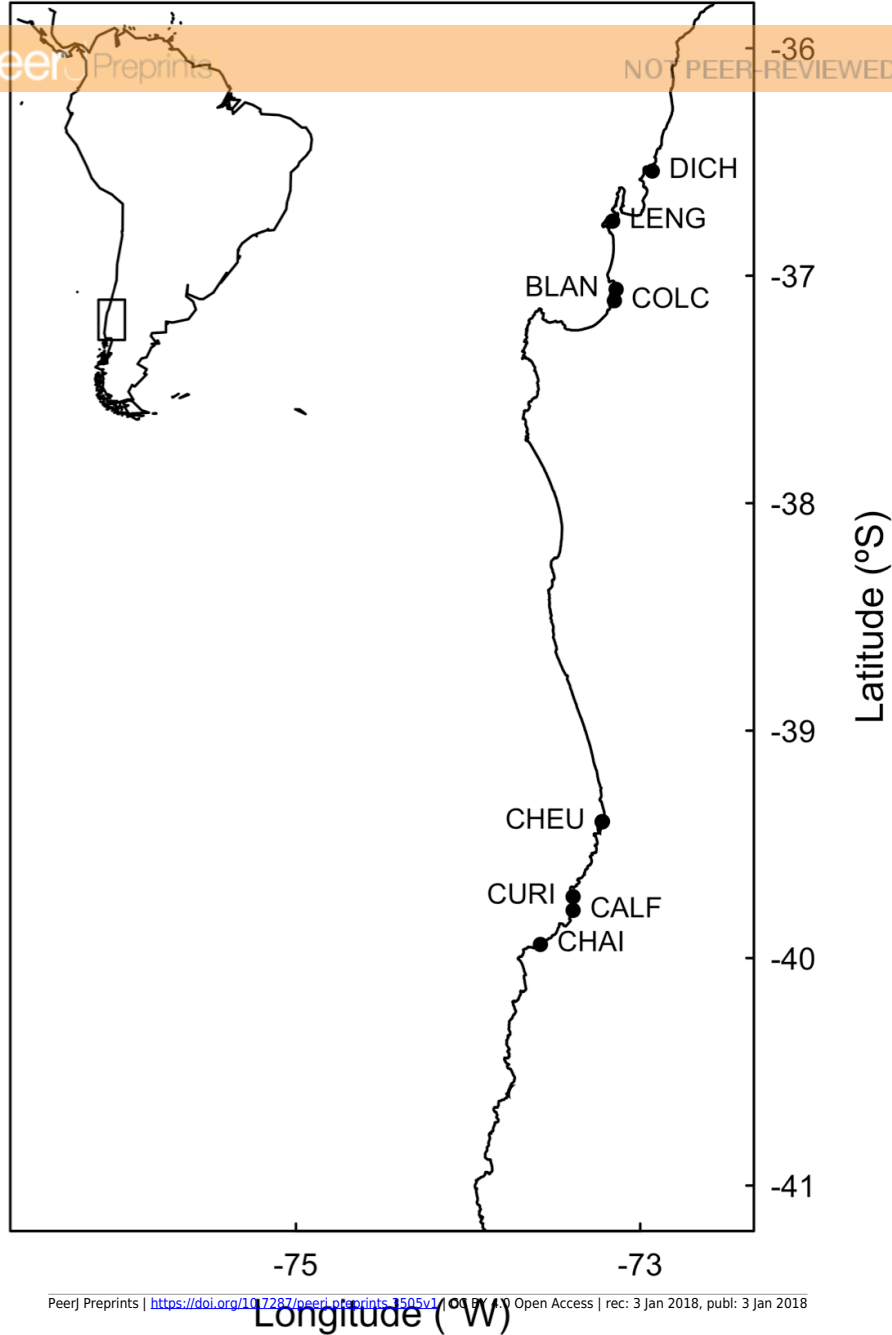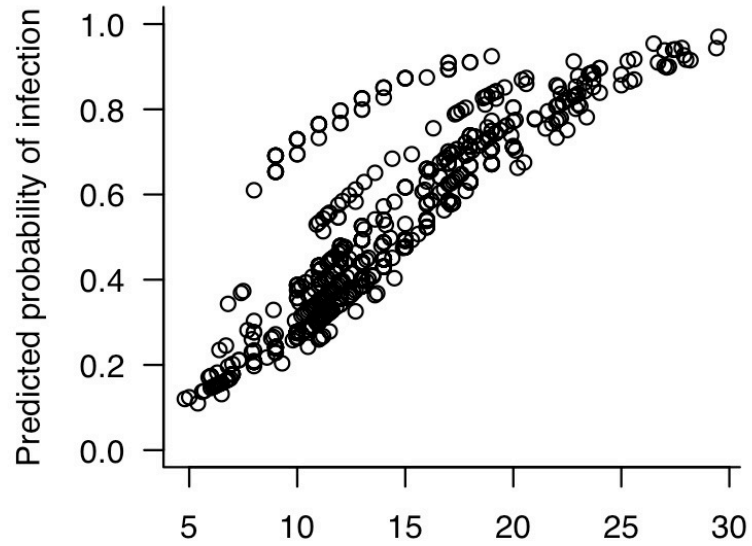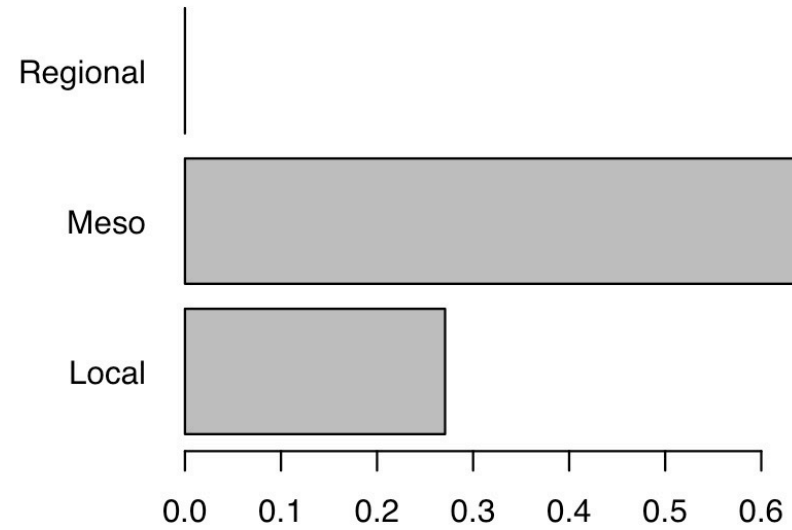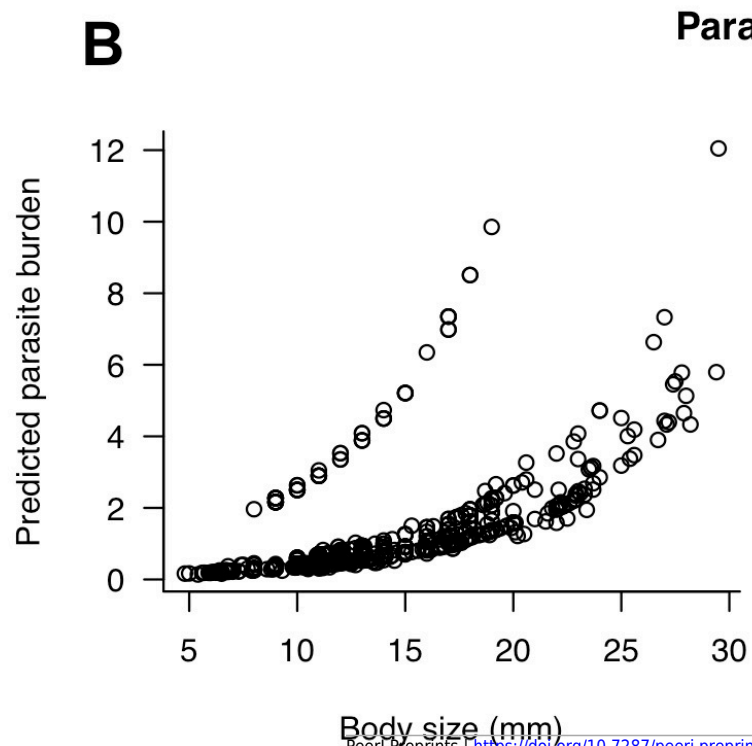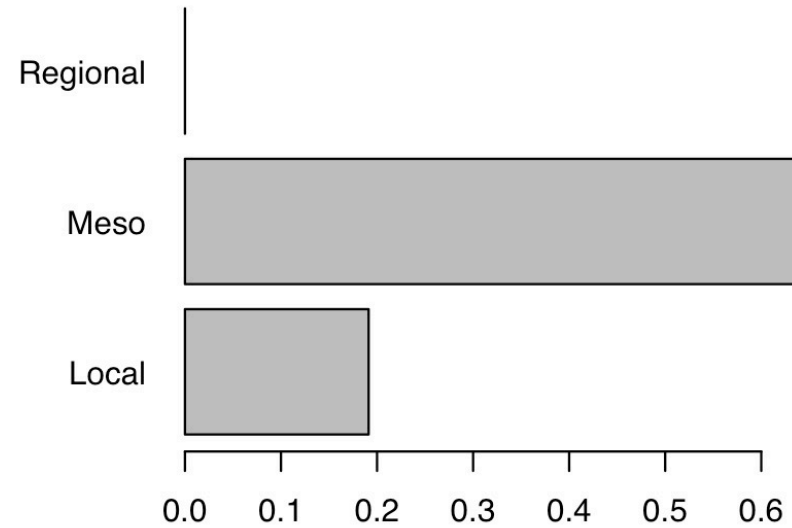
Figure 2 (on next page)

Probability of infection and Parasite Burden in function of body size of mole crabs

Individual-scale parasitosis of *Profilicollis altmani* infecting the intermediate host *Emerita analoga* in southern-central Chile. Probability of infection (A) and parasite burden (i.e. per capita number of parasites; B) were estimated from Generalized Linear Mixed-Effect models as functions of size of molecrabs. The variance components of the probability of infection (C) and parasite burden (D) was estimated for each of three spatial scales of observation: regional, meso-, and local scale.

Figure 3(on next page)

Prevalence, mean intensity and mean abundance of parasites across different spatial scales

Population-level parasitosis of *Profilicollis altmani* infecting molecrabs in southern-central Chile. Parasitosis was expressed as prevalence (A, B, C), intensity (D, E, F), and mean abundance (G, H, I) of parasites. These indicators were estimated at the regional (A, D, G), meso- (B, E, H), and local scales (C, F, I) of observation. Values are given as mean and standard error of the mean.
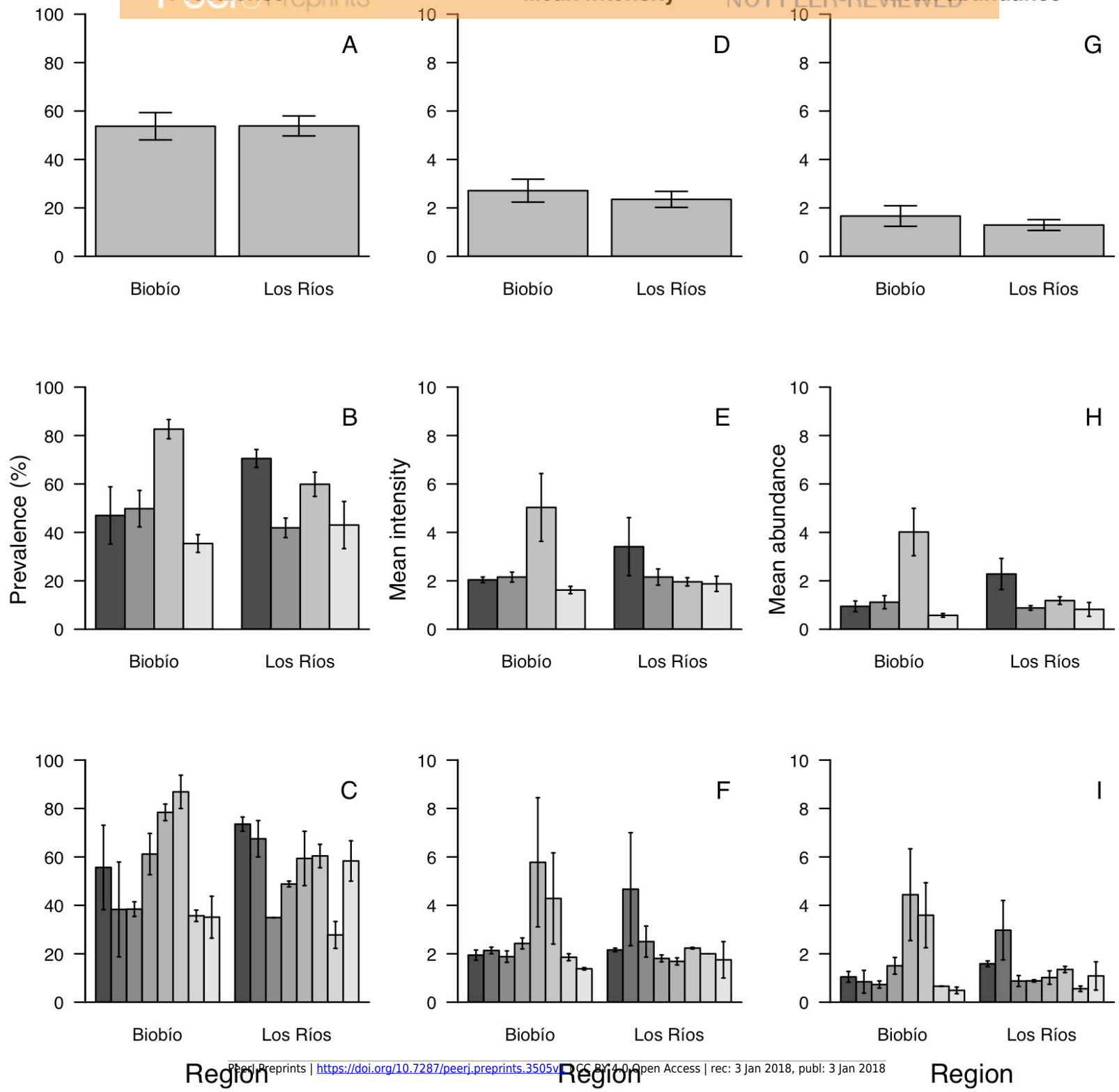
Figure 4(on next page)

Variance components of prevalence, mean intensity and mean abundance of parasites estimated to different spatial scales

Variance components of prevalence (A), intensity (B) and mean abundance (C) of parasites *Profilicollis altmani*, estimated at regional, meso-, and local scale in the southern-central coast of Chile.