

Density-dependent condition of juvenile penaeid shrimps in seagrass-dominated aquatic vegetation beds located at different distance from a tidal inlet

Zeferino Blanco-Martínez^{Equal first author, 1}, Roberto Pérez-Castañeda^{Corresp., Equal first author, 1}, Jesús Genaro Sánchez-Martínez¹, Flaviano Benavides-González¹, Jaime Luis Rábago-Castro¹, María de la Luz Vázquez-Sauceda¹, Lorena Garrido-Olvera²

¹ Facultad de Medicina Veterinaria y Zootecnia, Universidad Autónoma de Tamaulipas, Victoria, Tamaulipas, Mexico

² Instituto de Ecología Aplicada, Universidad Autónoma de Tamaulipas, Victoria, Tamaulipas, Mexico

Corresponding Author: Roberto Pérez-Castañeda
Email address: roperez@docentes.uat.edu.mx

Seagrasses are critical habitats for the recruitment and growth of juvenile penaeid shrimps within estuaries and coastal lagoons. The location of a seagrass bed within the lagoon can determine the value of a particular bed for shrimp populations. Consequently, differences in the abundance of shrimp can be found in seagrasses depending on their location. As shrimp density increases, density-dependent effects on biological parameters are more likely to occur. However, knowledge about density-dependent processes on shrimp populations in nursery habitats remains limited. The present investigation was undertaken to examine the effects of population density on shrimp condition in two selected seagrass beds, located at different distance from a tidal inlet, one 25 km away (distant) and the other 1 km away (nearby), in a subtropical coastal lagoon. The study was based on monthly samplings during one year in Laguna Madre (Mexico), performing a total of 36 shrimp trawls (100 m² each one) within each seagrass bed ($n = 3$ trawls per bed per month for 12 months). Shrimp density was related to the proximity to the tidal inlet was (higher density was consistently observed in the nearby seagrass bed), which in turn, adversely affected the condition of both species studied (*Penaeus aztecus* and *P. duorarum*). In this regard, the present study provides the first evidence of density-dependent effects on shrimp condition inhabiting a nursery habitat. Both shrimp species exhibited a negative relationship between condition and shrimp density. However, this pattern differed depending on the proximity to the tidal inlet, suggesting that shrimp populations inhabiting the nearby seagrass bed are exposed to density-dependent effects on condition; whereas, such effects were not detected in the distant seagrass bed. Shrimp density within the distant seagrass bed was probably below carrying capacity, which is suggested by the better shrimp condition observed in that area of the lagoon. Intra and interspecific

competition for food items is surmised to occur, predominantly within seagrass beds near the tidal inlet. However, this hypothesis needs to be tested in future studies.

1

2 **Density-dependent condition of juvenile penaeid**
3 **shrimps in seagrass-dominated aquatic vegetation**
4 **beds located at different distance from a tidal inlet**

5

6

7 Zeferino Blanco-Martínez¹, Roberto Pérez-Castañeda¹, Jesús Genaro Sánchez-Martínez¹,
8 Flaviano Benavides-González¹, Jaime Luis Rábago-Castro¹, María de la Luz Vázquez-Sauceda¹
9 and Lorena Garrido-Olvera²

10

11 ¹ Facultad de Medicina Veterinaria y Zootecnia, Universidad Autónoma de Tamaulipas, Ciudad
12 Victoria, Tamaulipas, Mexico

13 ² Instituto de Ecología Aplicada, Universidad Autónoma de Tamaulipas, Ciudad Victoria,
14 Tamaulipas, Mexico

15

16 Corresponding author:

17 Roberto Pérez-Castañeda

18 Carretera Victoria-Mante km 5, A.P. 263, Ciudad Victoria, Tamaulipas, 87000, Mexico

19 Email address: roperez@docentes.uat.edu.mx

20

21 Equal first author:

22 Zeferino Blanco-Martínez

23 Roberto Pérez-Castañeda

24

25 **Abstract**

26 Seagrasses are critical habitats for the recruitment and growth of juvenile penaeid shrimps within
27 estuaries and coastal lagoons. The location of a seagrass bed within the lagoon can determine the
28 value of a particular bed for shrimp populations. Consequently, differences in the abundance of
29 shrimp can be found in seagrasses depending on their location. As shrimp density increases,
30 density-dependent effects on biological parameters are more likely to occur. However,
31 knowledge about density-dependent processes on shrimp populations in nursery habitats remains
32 limited. The present investigation was undertaken to examine the effects of population density on
33 shrimp condition in two selected seagrass beds, located at different distance from a tidal inlet,
34 one 25 km away (distant) and the other 1 km away (nearby), in a subtropical coastal lagoon. The
35 study was based on monthly samplings during one year in Laguna Madre (Mexico), performing a
36 total of 36 shrimp trawls (100 m² each one) within each seagrass bed ($n = 3$ trawls per bed per
37 month for 12 months). Shrimp density was related to the proximity to the tidal inlet was (higher
38 density was consistently observed in the nearby seagrass bed), which in turn, adversely affected
39 the condition of both species studied (*Penaeus aztecus* and *P. duorarum*). In this regard, the
40 present study provides the first evidence of density-dependent effects on shrimp condition
41 inhabiting a nursery habitat. Both shrimp species exhibited a negative relationship between
42 condition and shrimp density. However, this pattern differed depending on the proximity to the
43 tidal inlet, suggesting that shrimp populations inhabiting the nearby seagrass bed are exposed to
44 density-dependent effects on condition; whereas, such effects were not detected in the distant
45 seagrass bed. Shrimp density within the distant seagrass bed was probably below carrying
46 capacity, which is suggested by the better shrimp condition observed in that area of the lagoon.
47 Intra and interspecific competition for food items is surmised to occur, predominantly within
48 seagrass beds near the tidal inlet. However, this hypothesis needs to be tested in future studies.

49

50 **Introduction**

51 Seagrasses are angiosperms adapted to marine and brackish environments that can be found on
52 the bottom of tropical and temperate coastal ecosystems such as bays, estuaries, or coastal
53 lagoons (Short et al., 2007). Seagrass can form extensive beds that provide structural complexity
54 to the coastal habitats. Its coverage and density have a positive influence on the abundance and
55 diversity of different taxonomic groups of macrofauna (McCloskey & Unsworth, 2015; Junhui et
56 al., 2018; Ruesink et al., 2019). Seagrasses provide refuge and food for the juvenile phase of
57 many species of fish and crustaceans such as penaeid shrimps (Penaeidae family); accordingly,
58 they are recognized as nursery habitats (Jackson et al., 2001).

59 Submerged aquatic vegetation beds can be constituted by seagrasses, macroalgae, or a mixture of
60 both (Haywood, Vance & Loneragan, 1995; Githaiga, 2016). Juvenile penaeid shrimps have a
61 marked preference for these habitats, exhibiting generally greater abundance in sites with high
62 density of submerged aquatic vegetation (Loneragan et al., 1998; Pérez-Castañeda et al., 2010).
63 Additionally, higher levels of aquatic vegetation biomass have been directly related to shrimp

64 growth rates and inversely related to mortality (Loneragan et al., 2001; Pérez-Castañeda &
65 Defeo, 2005).

66 Because aquatic vegetation can support a high abundance of shrimp, this could result in
67 competition for resources (e.g., food and shelter) as shrimp density increases, and resources
68 become limited (Begon, Townsend & Harper, 2006). Evidence of density-dependence in growth
69 and mortality for shrimp in sheltered coastal habitats indicates that the increase in shrimp
70 abundance leads to decreased growth rates and increased mortality (Pérez-Castañeda & Defeo,
71 2005), which may be due to intra and interspecific competition (Dahl, Edwards & Patterson,
72 2019).

73 Condition is a biological parameter involving the body weight at a given length; it is related to
74 the availability and consumption of food, reflecting the uptake and allocation of energy (Lloret,
75 Shulman & Love, 2014). Shrimp condition can be an indicator of the nutritional status of the
76 organisms; however, it may also vary according to the reproductive cycle, where mature shrimp
77 are heavier than immature ones of the same length (Chu et al., 1995). This difference could be
78 due, in part, to the extra weight of the ovaries in mature females, which constitutes up to 13.7%
79 of the total body weight (Peixoto et al., 2003). Shrimps found in coastal lagoons and estuaries are
80 primarily sexually immature juveniles (Dall et al., 1990); therefore, changes in the condition of
81 juvenile shrimps would mainly be associated to their nutritional status, which can be influenced
82 by habitat characteristics.

83 Although there are some studies about the condition in juvenile shrimps (Pérez-Castañeda &
84 Defeo, 2002; Ochwada-Doyle et al., 2011), density-dependence on shrimp condition has been
85 little explored, particularly in nursery areas. While seagrass beds are key habitats for the
86 recruitment of postlarvae and growth of juvenile shrimp, it has been documented that the
87 location of a seagrass bed within the lagoon can determine the value of a particular bed (Bell,
88 Steffe & Westoby, 1988). In some coastal lagoons with minimal tidal currents and limited water
89 circulation, like Laguna Madre (Mexico), the distribution of postlarvae within the lagoon could
90 also be limited. In this coastal lagoon, seagrass meadows nearby a tidal inlet, where the
91 postlarvae enter the lagoon, have a greater abundance of shrimp than distant meadows (Blanco-
92 Martínez & Pérez-Castañeda, 2017). Accordingly, it would be expected that these differences in
93 abundance could result in differences in shrimp condition among seagrass beds. However, this
94 issue has not been assessed. This study aimed to evaluate density-dependence in the condition of
95 two juvenile shrimp species (*Penaeus aztecus* Ives, 1891 and *P. duorarum* Burkenroad, 1939) in
96 seagrass-dominated aquatic vegetation beds located at a different distance from a tidal inlet in a
97 coastal lagoon.

98

99 **Materials & Methods**

100 **Sampling and laboratory analysis**

101 This study was conducted in the central part of the Laguna Madre (Mexico), which is a 200 km-
102 long subtropical coastal lagoon located in the Gulf of Mexico (23°50'–25°30'N, 97°15'–97°45'W)
103 (Fig. 1). The hydrography of Laguna Madre is characterized by a microtidal regime (tidal range

104 < 0.5 m) exhibiting limited circulation and exchange with waters from the Gulf of Mexico waters
105 (Britton & Morton, 1989; Tunnell & Judd, 2002); therefore, minimal tidal currents within the
106 lagoon are generated.

107 The bottom of the lagoon is characterized by the presence of submerged aquatic vegetation in
108 shallow areas along the coast dominated by submerged seagrasses (Arellano-Méndez et al.,
109 2019), which, due to their subtidal nature, are permanently available for aquatic fauna. The last
110 available mapping of seagrasses in Laguna Madre was performed in the 90s using satellite
111 imagery, which displayed seagrass beds distributed at the north-central portion of the lagoon,
112 mostly along the back of the barrier islands (DUMAC, 1996). The selected seagrass beds for the
113 present study were located at the central portion of the lagoon. They were situated within the
114 band of seagrasses previously mapped. Similarly, larger seagrass meadows have also been
115 recently reported for the central portion of Laguna Madre (Arellano-Méndez et al., 2019);
116 however, there are no data on the distribution of seagrasses at different depth strata in the study
117 area.

118 The location of sampling sites is shown in Fig. 1. They were situated in seagrass beds located at
119 a different distance (distant and nearby) from a tidal inlet. The distant bed was 25 km from the
120 inlet, while the nearby bed was only 1 km away. The first seagrass bed was located 1 km from
121 the tidal inlet and was classified as 'nearby'; the second seagrass bed was located 25 km from the
122 tidal inlet and served as the 'distant' seagrass bed. The dominant seagrass species in the shrimp
123 nursery habitat were *Halodule wrightii* (77% of total seagrass biomass) and *Syringodium*
124 *filiforme* (23% of total seagrass biomass) with the presence of some macroalgal species such as
125 *Digenia simplex*, *Penicillus capitatus*, *Jania adherens*, *Laurencia poitei* and *Champia parvula*
126 (Blanco-Martínez & Pérez-Castañeda, 2017).

127 Monthly shrimp samples were collected at night during an annual cycle (January–December
128 2005) in both seagrass beds (nearby and distant) (Permit from CONAPESCA:
129 DGOPA/05675/060505/.-3869). Data were collected as previously described in Blanco-Martínez
130 & Pérez-Castañeda (2017). Specifically, field collection and laboratory analysis of shrimp and
131 seagrass samples, as well as measurements of salinity, temperature, and dissolved oxygen in the
132 coastal lagoon, were performed as previously described in the study mentioned above.

133 Measurement of carapace length (CL, mm), weighing (body weight, g), and the taxonomic
134 identification of shrimp were also carried out as described therein. Individuals under 8.0 mm in
135 carapace length were not identified to species level due to the absence of differentiating
136 morphological characters in those sizes (Pérez-Farfante, 1970).

137 The 2.5 m long beam trawl (1.3 cm mesh size) utilized for shrimp sampling had a 2 m wide and
138 0.6 m high rigid mouth. The sampling gear was hand-hauled parallel to the water's edge
139 (between 1 and 1.5 m depth approximately), covering a swept area of 100 m² per tow. Three
140 replicate samples per seagrass bed were taken each month.

141

142 **Data analysis**

143 For each seagrass bed, a combined length-frequency distribution (grouped by 1 mm CL), was
144 constructed for all shrimp sampled in order to depict the overall size structure of shrimp by
145 seagrass bed. The monthly mean abundance of shrimp (total and by species) was also plotted for
146 both sites.

147 Carapace length-weight (CL-W) relationships for each shrimp species (*P. aztecus* and *P.*
148 *duorarum*) were determined in each seagrass bed. Weight comparison at a given length was
149 utilized as a condition indicator under the assumption that heavier individuals of a given length
150 are in better condition, as considered in previous studies (García-Berthou & Moreno-Amich,
151 1993; Meretsky et al., 2000). In this regard, an analysis of covariance (ANCOVA) was run on
152 differences in weight at a given length (as an indicator of condition in shrimp) between seagrass
153 beds, with log W as the dependent variable and log CL as the covariate (Pérez-Castañeda &
154 Defeo, 2002; Ochwada-Doyle et al., 2011). Data fulfilled the linearity assumption between log
155 CL and log W. The homogeneity of slopes (parallelism test) of the fitted linear functions
156 between seagrass beds was also met, allowing the ANCOVA to be carried out. Subsequently, the
157 predicted mean weights for a covariate value of CL = 11.0 mm (corresponding to the average
158 size) were obtained from the ANCOVA to illustrate differences in shrimp condition between
159 seagrass beds for each species.

160 Additionally, length-weight relationships were obtained by species (*P. aztecus* and *P. duorarum*)
161 fitting the power function $W = a CL^b$ for each month and seagrass bed. Afterward, fitted models
162 were utilized to estimate the predicted weight at a given length as an indicator of shrimp
163 condition (in this case weight at CL = 11 mm). Finally, monthly shrimp condition was plotted
164 against the monthly mean abundance of total shrimp, fitting a linear function to identify density-
165 dependence in shrimp condition by seagrass bed. It is worth noting that this analysis was
166 performed with data from the months when shrimp were most abundant, in order to guarantee a
167 better representation of length/weight data sets for fitting the aforementioned power function. In
168 this regard, the months included in the analysis were January–April and November–December.
169 Data for *P. duorarum* from November–December in the distant seagrass bed were excluded
170 because of low abundance.

171

172 **Results**

173 Within the lagoon, salinity ranged from 31 to 45, temperature from 16.6 to 30.2°C, dissolved
174 oxygen from 2.4 to 6.3 mg/L, seagrass biomass from 10.7 to 1300.7 g/m², macroalgal biomass
175 from 5.6 to 457.1 g/m² and the total seagrass biomass from 47.5 to 1338.3 g/m². Significantly
176 higher mean salinity (40.6 ±4.5) and macroalgal biomass (184.6 ±127.4 g/m²) were registered at
177 the distant seagrass bed. The temperature, dissolved oxygen, seagrass biomass, and the total
178 seagrass biomass were slightly higher at the nearby seagrass bed. However, no significant
179 differences were detected in comparison to the distant bed (Table 1, Supplemental information
180 1).

181 Overall, shrimp size ranged from 2.9 to 23.5 mm CL in the distant seagrass bed and from 1.5 to
182 26.5 mm CL in the nearby seagrass bed. In both vegetation areas, shrimp of 8 to 12 mm CL were

183 the most abundant size classes showing a clear dominance of juveniles (Fig. 2A–B,
184 Supplemental information 2). On the other hand, the abundance of total shrimp and both species
185 were systematically higher in the seagrass bed nearby to the tidal inlet, both annually and in at
186 least ten months throughout the annual cycle (Fig. 2C–H, Supplemental information 2).
187 Shrimp abundance peaked at the beginning and the end of the year, in the case of total shrimp and
188 *P. aztecus*. However, *P. duorarum* abundance only peaked at the beginning of the year (Fig. 2,
189 Supplemental information 2).
190 Length-weight relationships, in logarithmic scale, for both shrimp species from each seagrass
191 bed were successfully fitted by a linear function ($\log W = a + b \log CL$) with r^2 values > 0.9 in
192 all cases (Fig. 3, Supplemental information 3). Both shrimp species showed homogeneity of
193 slopes (parallelism test) among seagrass beds, as indicated by the interaction term between site
194 and $\log CL$ which was not significant ($p = 0.16$ and $p = 0.36$ for *P. aztecus* and *P. duorarum*,
195 respectively; Supplementary information 3). The ANCOVA results indicated significant
196 differences ($p < 0.001$) in weight ($\log W$) at a given length ($\log CL$) between seagrass beds in
197 both shrimp species (Supplemental information 3).
198 The highest predicted mean weight of shrimps (*P. aztecus* = 0.785 g, *P. duorarum* = 0.789 g)
199 utilized as an indicator of body condition, were observed at the seagrass bed with lowest shrimp
200 density (total abundance = 43.72 ind./100 m²). In contrast, the lowest predicted mean weights (*P.*
201 *aztecus* = 0.751 g, *P. duorarum* = 0.759 g) were found at the seagrass bed with highest shrimp
202 density (total abundance = 105.61 ind./100 m²; Fig. 4, Supplemental information 3) indicating
203 that shrimp condition decreased as total shrimp abundance increased.
204 Moreover, when analyzing the data separately by seagrass bed, and merging results from both
205 shrimp species, a negative trend between condition and shrimp abundance was exclusively
206 detected for shrimp inhabiting the aquatic vegetation bed near the tidal inlet (Fig. 5,
207 Supplemental information 4).
208 Although there were significant differences in salinity and biomass of macroalgae between
209 distant and nearby seagrass beds, these variables were not correlated with shrimp abundance and
210 condition (supplemental information 4).

211

212 Discussion

213 Although the size range of shrimp was relatively similar in the distant and nearby seagrass beds,
214 the abundance of shrimp was higher in the seagrass area close to the tidal inlet. This pattern was
215 observed practically all year round, suggesting a possible relationship between shrimp abundance
216 and the proximity to the inlet. The microtidal regime in Laguna Madre generates minimal tidal
217 currents and limited water circulation. This condition might limit the distribution of postlarvae
218 within the lagoon as the distance from the source of postlarvae (tidal inlet) increases. This pattern
219 is consistent with what Bell, Steffe & Westoby (1988) pointed out for recently settled decapods
220 of ocean-spawned species; they hypothesized that the abundance of such species is influenced by
221 their location within the estuary. It has been surmised that the proximity to the tidal inlet could
222 influence the value of seagrass habitats for shrimp recruitment and abundance within the lagoon

223 (Blanco-Martínez & Pérez-Castañeda, 2017); however, further studies should be carried out to
224 validate this hypothesis.

225 Because no recently settled postlarvae or very small juvenile shrimp as indicators of recruitment
226 were sampled, no differences in shrimp recruitment was determined between the two seagrass
227 beds. Our study was focused on mid-aged resident juveniles in both subtidal seagrass beds.

228 According to the life cycle of penaeids, shrimp in our study (mostly 6 to 15 mm CL; Fig. 2A–B)
229 were recruited as postlarvae, approximately at 1–2 mm CL. Afterward, they were probably
230 exposed to predation and competition for several weeks and possible redistribution to
231 microhabitats within the seagrass bed before being sampled as part of this study.

232 The brown shrimp, *P. aztecus*, has also been reported in intertidal salt marsh vegetation from
233 another subtropical coastal habitat (size range: 10–83 mm TL or 2–19 mm CL approximately)
234 (Minello et al., 1989); however, in Laguna Madre salt marsh vegetation is scarce, and therefore,
235 seagrass is the primary habitat with vegetation for penaeid shrimps in this lagoon.

236 The present study provides the first evidence of density-dependent effects on shrimp condition
237 from different seagrass beds vis-à-vis their proximity to a tidal inlet (the site for the entry of
238 postlarvae into the lagoon). The proximity to the tidal inlet was related to the density of shrimp
239 (higher density was consistently observed in the nearby seagrass bed), which in turn, was
240 negatively related to the body condition.

241 Shrimp species (*P. aztecus* and *P. duorarum*) in Laguna Madre were subject to density-
242 dependent effects on body condition, as indicted by the negative relationship between predicted
243 mean weight and shrimp abundance, coinciding with that reported for *P. duorarum* in another
244 coastal lagoon (Pérez-Castañeda & Defeo, 2002); however, this pattern differed according to the
245 proximity to the tidal inlet, since such negative influence of density on shrimp condition was
246 detected in the nearby seagrass bed but not in the distant bed (Fig. 5). This finding suggests, that
247 shrimp populations inhabiting the nearby seagrass bed are exposed to density-dependent effects
248 on the condition, while on the contrary, such effects are not present in shrimp populations from
249 the distant bed. The determining factor for the detection of density-dependent effects on the
250 condition between the two seagrass areas was the contrasting difference in shrimp abundance.

251 As the condition was density-dependent, growth could also be negatively affected by shrimp
252 density, particularly in the nearby seagrass bed. Although density-dependent growth has been
253 demonstrated for juvenile shrimp in seagrass habitats through field samplings (Pérez-Castañeda
254 & Defeo, 2005) and experiments (Loneragan et al., 2001), it has not been assessed whether such
255 density-dependent relationship could be related to distance to the source of postlarvae.

256 Unfortunately, in the present study, it was not possible to carry out the identification and tracking
257 of cohorts over time to estimate shrimp growth, as performed by other authors, because more
258 frequent sampling would have been necessary due to the fast growth of juvenile shrimps before
259 migrating to the sea (Haywood & Staples, 1993; O'Brien, 1994). Therefore, future studies on the
260 possible effect of density on shrimp growth at different distances from the tidal inlet would be
261 necessary.

262 Density-dependent effects may be the result of high depletion rates of food sources caused by
263 increments in shrimp density resulting in intra and interspecific competition, as observed in other
264 marine invertebrates (Gaymer, Himmelman & Johnson, 2002). In this regard, the two closely
265 related shrimp species (*P. aztecus* and *P. duorarum*) analyzed in the study area (Laguna Madre)
266 represent congeneric and sympatric species that co-occur in seagrass beds, exploiting the same
267 resources (space and food). Thus, both penaeid species may be exposed to intra and interspecific
268 competition, especially as shrimp density increases within the seagrass habitat.
269 The body condition of postlarval and juvenile shrimp may be indicative of their health status.
270 This biological parameter may even affect their ability to escape from predators, as suggested for
271 *Penaeus plebejus* in Australian coastal lakes, probably resulting in higher mortality for shrimp
272 with a lower condition, i.e., poorer health (Ochwada-Doyle et al., 2011).
273 According to the above, a better body condition of shrimp in the distant seagrass bed in Laguna
274 Madre could imply an advantage for the survival and persistence of shrimp populations within
275 that bed and its possible contribution to the offshore adult's replenishment population. However,
276 the possible effects of body condition on predation should be evaluated.
277 Although from the site representative point of view, our research was limited (only two sampling
278 beds), it was representative in time (three samples per bed per month for 12 months), observing
279 that differences in shrimp condition between seagrass beds were consistent over the study.
280 Higher data dispersion in the nearby bed could be due to greater shrimp patchiness during the
281 months with peak abundance. However, It would be necessary to evaluate possible differences in
282 shrimp patchiness between seagrass beds in the future, based on a higher number of trawls per
283 bed to differentiate between dispersion due to possible patchiness or low representativeness of
284 the sample size.
285 Shrimp size classes represented in our study inhabiting the seagrass habitats are representative of
286 the interrelation of growth, mortality, and migration, and whose future survival will likely
287 contribute to the offshore adult population. Although shrimp from the seagrass bed near the tidal
288 inlet had a lower condition, exhibiting density-dependent effects, they were much more abundant
289 and located closer to the adult habitat; i.e., the marine habitat. Therefore, the differential
290 contribution of both seagrass beds (distant and nearby to the tidal inlet) to the adults population
291 should be determined evaluating possible differences in shrimp population dynamics between
292 both beds, including the migration of juveniles to adult habitats (Beck et al., 2001). However,
293 such factors have not yet been quantified.

294

295 **Conclusions**

296 Density-dependent effects on body condition were detected in juvenile penaeid shrimps
297 inhabiting seagrass-dominated aquatic vegetation beds. Data indicated that the proximity to the
298 tidal inlet (site where the postlarvae enter the lagoon) was positively related with the abundance
299 of shrimp, which in turn, was negatively correlated with body condition. This fact was evidenced
300 in both penaeid species (*P. aztecus* and *P. duorarum*). In this regard, intra and interspecific

301 competition by food items is hypothesized to occur, predominantly within the seagrass bed near
302 the tidal inlet. However, this hypothesis needs to be tested in future studies.

303

304 **Acknowledgements**

305 We thank Mr. Emeterio Dueñez Resendiz, from Carboneras village, for his help during
306 biological sampling in Laguna Madre. This work is part of the doctoral thesis of the first author
307 (ZBM) at the Instituto de Ecología Aplicada, Universidad Autónoma de Tamaulipas.

308

309 **References**

- 310 **Arellano-Méndez LU, Mora-Olivo A, Zamora-Tovar C, de la Rosa-Manzano E, Torres-**
311 **Castillo JA, Bello-Pineda J. 2019.** Structural complexity of tropical seagrasses meadows in a
312 temperate lagoon in the Gulf of Mexico. A landscape ecology approach. *Journal of Coastal*
313 *Conservation* **23**:969–976 DOI 10.1007/s11852-019-00701-2.
- 314 **Beck MW, Heck KL Jr, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B,**
315 **Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP. 2001.** The
316 identification, conservation and management of estuarine and marine nurseries for fish and
317 invertebrates. *Bioscience* **51**:633–641 DOI 10.1641/0006-
318 3568(2001)051[0633:TICAMO]2.0.CO;2.
- 319 **Begon M, Townsend CR, Harper JL. 2006.** *Ecology: From individuals to ecosystems*. 4th
320 edition. Oxford: Blackwell Publishing.
- 321 **Bell JD, Steffe AS, Westoby M. 1988.** Location of seagrass beds in estuaries: effects on
322 associated fish and decapods. *Journal of Experimental Marine Biology and Ecology* **122**:127–
323 146 DOI 10.1016/0022-0981(88)90180-3.
- 324 **Blanco-Martínez Z, Pérez-Castañeda R. 2017.** Does the relative value of submerged aquatic
325 vegetation for penaeid shrimp vary with proximity to a tidal inlet? *Marine and Freshwater*
326 *Research* **68**:581–591 DOI 10.1071/MF15207.
- 327 **Britton JC, Morton B. 1989.** *Shore ecology of the Gulf of Mexico*. Austin, TX: University of
328 Texas Press.
- 329 **Chu KH, Chen QC, Huang LM, Wong CK. 1995.** Morphometric analysis of commercially
330 important penaeid shrimps from the Zhujiang estuary, China. *Fisheries Research* **23**:83–93
331 DOI 10.1016/0165-7836(94)00342-T.
- 332 **Dahl KA, Edwards MA, Patterson WFIII. 2019.** Density-dependent condition and growth of
333 invasive lionfish in the northern Gulf of Mexico. *Marine Ecology Progress Series* **623**:145–
334 159 DOI 10.3354/meps13028.
- 335 **Dall W, Hill BJ, Rothlisberg PC, Sharples DJ. 1990.** The biology of the Penaeidae. In: Blaxter
336 JHS, Southward AJ, eds. *Advances in Marine Biology Vol. 27*. London: Academic Press, 1–
337 489.
- 338 **DUMAC. 1996.** Vegetación acuática de la Laguna Madre de Tamaulipas (pastos marinos):
339 Informe final de proyecto. Ducks Unlimited de México, A.C. and Instituto de Ecología y
340 Alimentos de la Universidad Autónoma de Tamaulipas. Monterrey, Nuevo León.

- 341 **García-Berthou E, Moreno-Amich R. 1993.** Multivariate analysis of covariance in
342 morphometric studies of the reproductive cycle. *Canadian Journal of Fisheries and Aquatic*
343 *Sciences* **50**:1394–1399 DOI 10.1139/f93-159.
- 344 **Gaymer CF, Himmelman JH, Johnson LE. 2002.** Effect of intra- and interspecific interactions
345 on the feeding behavior of two subtidal sea stars. *Marine Ecology Progress Series* **232**:149–
346 162 DOI 10.3354/meps232149.
- 347 **Githaiga MN, Gilpin L, Kairo JG, Huxham M. 2016.** Biomass and productivity of seagrasses
348 in Africa. *Botanica Marina* **59**:173–186 DOI 10.1515/bot-2015-0075.
- 349 **Haywood MDE, Staples DJ. 1993.** Field estimates of growth and mortality of juvenile banana
350 prawns (*Penaeus merguensis*). *Marine Biology* **116**:407–416 DOI 10.1007/BF00350057.
- 351 **Haywood MDE, Vance DJ, Loneragan NR. 1995.** Seagrass and algal beds as nursery habitats
352 for tiger prawns (*Penaeus semisulcatus* and *P. esculentus*) in a tropical Australian estuary.
353 *Marine Biology* **122**:213–223 DOI 10.1007/BF00348934.
- 354 **Jackson EL, Rowden AA, Attrill MJ, Bossey SJ, Jones MB. 2001.** The importance of seagrass
355 beds as a habitat for fishery species. In: Gibson RN, Barnes M, Atkinson RJA, eds.
356 *Oceanography and Marine Biology. An Annual Review Vol 39*. New York: Taylor & Francis,
357 269–303.
- 358 **Junhui L, Yaqin H, Ucu Yanu A, Heshan L Muhammad Husni A, Jianjun W, Xuebao H,**
359 **Jianfeng M, Kun L, Shuyi Z. 2018.** An ecological survey of the abundance and diversity of
360 benthic macrofauna in Indonesian multispecific seagrass beds. *Acta Oceanologica Sinica*
361 **37**:82–89 DOI 10.1007/s13131-018-1181-9.
- 362 **Lloret J, Shulman G, Love RM. 2014.** *Condition and health indicators of exploited marine*
363 *fishes*. Chichester: Wiley-Blackwell.
- 364 **Loneragan NR, Haywood MDE, Heales DS, Kenyon RA, Pendrey RP, Vance DJ. 2001.**
365 Estimating the influence of prawn stocking density and seagrass type on the growth of
366 juvenile tiger prawns (*Penaeus semisulcatus*): results from field experiments in small
367 enclosures. *Marine Biology* **139**:343–354 DOI 10.1007/S002270100572.
- 368 **Loneragan NR, Kenyon RA, Staples DJ, Poiner IR, Conacher CA. 1998.** The influence of
369 seagrass type on the distribution and abundance of postlarval and juvenile tiger prawns
370 (*Penaeus esculentus* and *P. semisulcatus*) in the western Gulf of Carpentaria, Australia.
371 *Journal of Experimental Marine Biology and Ecology* **228**:175–195 DOI 10.1016/S0022-
372 0981(98)00029-X.
- 373 **McCloskey RM, Unsworth RKF. 2015.** Decreasing seagrass density negatively influences
374 associated fauna. *PeerJ* **3**:e1053 DOI 10.7717/peerj.1053.
- 375 **Meretsky VJ, Valdez RA, Douglas ME, Brouder MJ, Gorman OT, Marsh PC. 2000.**
376 Spatiotemporal variations in length-weight relationships of endangered humpback chub:
377 implications for conservation and management. *Transactions of the American Fisheries*
378 *Society* **129**:419–428 DOI 10.1577/1548-8659(2000)129<0419:SVILWR>2.0.CO;2.

- 379 **Minello TJ, Zimmerman RJ, Martínez EX. 1989.** Mortality of young brown shrimp *Penaeus*
380 *aztecus* in estuarine nurseries. *Transactions of the American Fisheries Society* **118**:693–708
381 DOI 10.1577/1548-8659(1989)118<0693:MOYBSP>2.3.CO;2.
- 382 **O'Brien CJ. 1994.** Population dynamics of juvenile tiger prawns *Penaeus esculentus* in south
383 Queensland, Australia. *Marine Ecology Progress Series* **104**:247–256.
- 384 **Ochwada-Doyle F, Gray CA, Loneragan NR, Taylor MD, Suthers IM. 2011.** Spatial and
385 temporal variability in the condition of postlarval and juvenile *Penaeus plebejus* sampled
386 from a population subjected to pilot releases. *Aquaculture Environment Interactions* **2**:15–25
387 DOI 10.3354/aei00026.
- 388 **Peixoto S, Cavalli RO, D'Incao F, Milach A, Wasielesky W. 2003.** Ovarian maturation of wild
389 *Farfantepenaeus paulensis* in relation to histological and visual changes. *Aquaculture*
390 *Research* **34**:1255–1260 DOI 10.1046/j.1365-2109.2003.00933.x.
- 391 **Pérez-Castañeda R, Blanco-Martínez Z, Sánchez-Martínez JG, Rábago-Castro JL,**
392 **Aguirre-Guzmán G, Vázquez-Sauceda ML. 2010.** Distribution of *Farfantepenaeus aztecus*
393 and *F. duorarum* on submerged aquatic vegetation habitats along a subtropical coastal lagoon
394 (Laguna Madre, Mexico). *Journal of the Marine Biological Association of the United*
395 *Kingdom* **90**:445–452 DOI 10.1017/S0025315409990865.
- 396 **Pérez-Castañeda R, Defeo O. 2002.** Morphometric relationships of penaeid shrimps in a coastal
397 lagoon: spatio-temporal variability and management implications. *Estuaries* **25**:282–287 DOI
398 10.1007/BF02691315.
- 399 **Pérez-Castañeda R, Defeo O. 2005.** Growth and mortality of transient shrimp populations
400 (*Farfantepenaeus* spp.) in a coastal lagoon of Mexico: role of the environment and density-
401 dependence. *ICES Journal of Marine Science* **62**:14–24 DOI
402 10.1016/J.ICESJMS.2004.10.005.
- 403 **Pérez-Farfante I. 1970.** Diagnostic characters of juveniles of the shrimps *Penaeus aztecus*
404 *aztecus*, *P. duorarum duorarum*, and *P. brasiliensis* (Crustacea, Decapoda, Penaeidae). U.S.
405 Fish and Wildlife Service, Special Scientific Report–Fisheries Number 599.
- 406 **Ruesink JL, Gross C, Pruitt C, Trimble AC, Donoghue C. 2019.** Habitat structure influences
407 the seasonality of nekton in seagrass. *Marine Biology* **166**:75 DOI 10.1007/s00227-019-3519-
408 z.
- 409 **Short F, Carruthers T, Dennison W, Waycott M. 2007.** Global seagrass distribution and
410 diversity: A bioregional model. *Journal of Experimental Marine Biology and Ecology* **350**:3–
411 20 DOI 10.1016/j.jembe.2007.06.012.
- 412 **Tunnel JW Jr, Judd FW. 2002.** *The Laguna Madre of Texas and Tamaulipas*. College Station,
413 TX: Texas A&M University Press.
- 414

Table 1 (on next page)

Environmental conditions and submerged aquatic vegetation biomass.

Mean (\pm SD) values of abiotic factors (salinity, temperature and dissolved oxygen) and biomass of seagrass and macroalgae, including total biomass, in two seagrass-dominated aquatic vegetation beds located at different distances (distant and nearby) from a tidal inlet in Laguna Madre (Mexico). Probability values of statistical comparisons (Student's *t* tests) between beds are included.

1 **Table 1:**2 **Environmental conditions and submerged aquatic vegetation biomass.**

3 Mean (\pm SD) values of abiotic factors (salinity, temperature and dissolved oxygen) and
 4 biomass of seagrass and macroalgae, including total biomass, in two seagrass-
 5 dominated aquatic vegetation beds located at different distances (distant and nearby)
 6 from a tidal inlet in Laguna Madre (Mexico). Probability values of statistical comparisons
 7 (Student's *t* tests) between beds are included.

	Distant seagrass bed	Nearby seagrass bed	<i>p</i> -value
Salinity	40.6 \pm 4.5	37.4 \pm 2.6	0.042
Temperature ($^{\circ}$ C)	24.9 \pm 5.0	25.3 \pm 4.4	0.847
Dissolved oxygen (mg/L)	4.2 \pm 1.1	4.6 \pm 0.9	0.345
Seagrass (g/m ²)	310.8 \pm 259.1	433.1 \pm 330.6	0.324
Macroalgae (g/m ²)	184.6 \pm 127.4	84.7 \pm 103.4	0.047
Total biomass (g/m ²)	495.4 \pm 319.1	517.8 \pm 311.2	0.863

9

Figure 1

Study area.

Location of sampling sites in seagrass beds in Laguna Madre (Mexico). The distant (D) and nearby (N) seagrass beds were located at 25 km and 1 km away, respectively, from the tidal inlet (Boca de Catán).

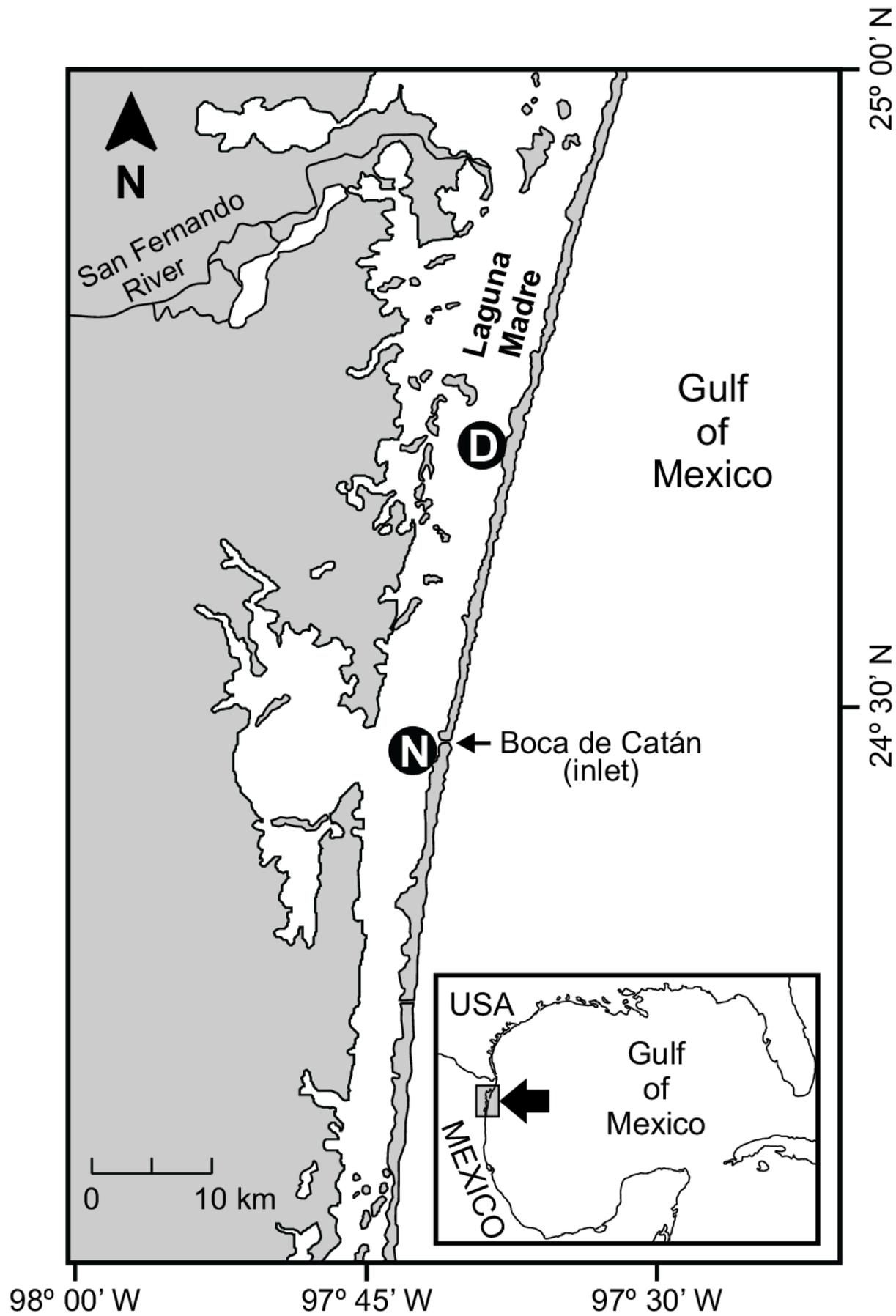


Figure 2

Penaeid shrimps collected in two different seagrass beds in relation to their proximity to a tidal inlet (distant and nearby) in Laguna Madre (Mexico).

(A, B) Length-frequency distributions in carapace length (CL) of all penaeids grouped by 1 mm CL. Monthly abundance (mean \pm SD) of shrimp is displayed as (C, D) total abundance, (E, F) *Penaeus aztecus* and (G, H) *P. duorarum*, respectively.

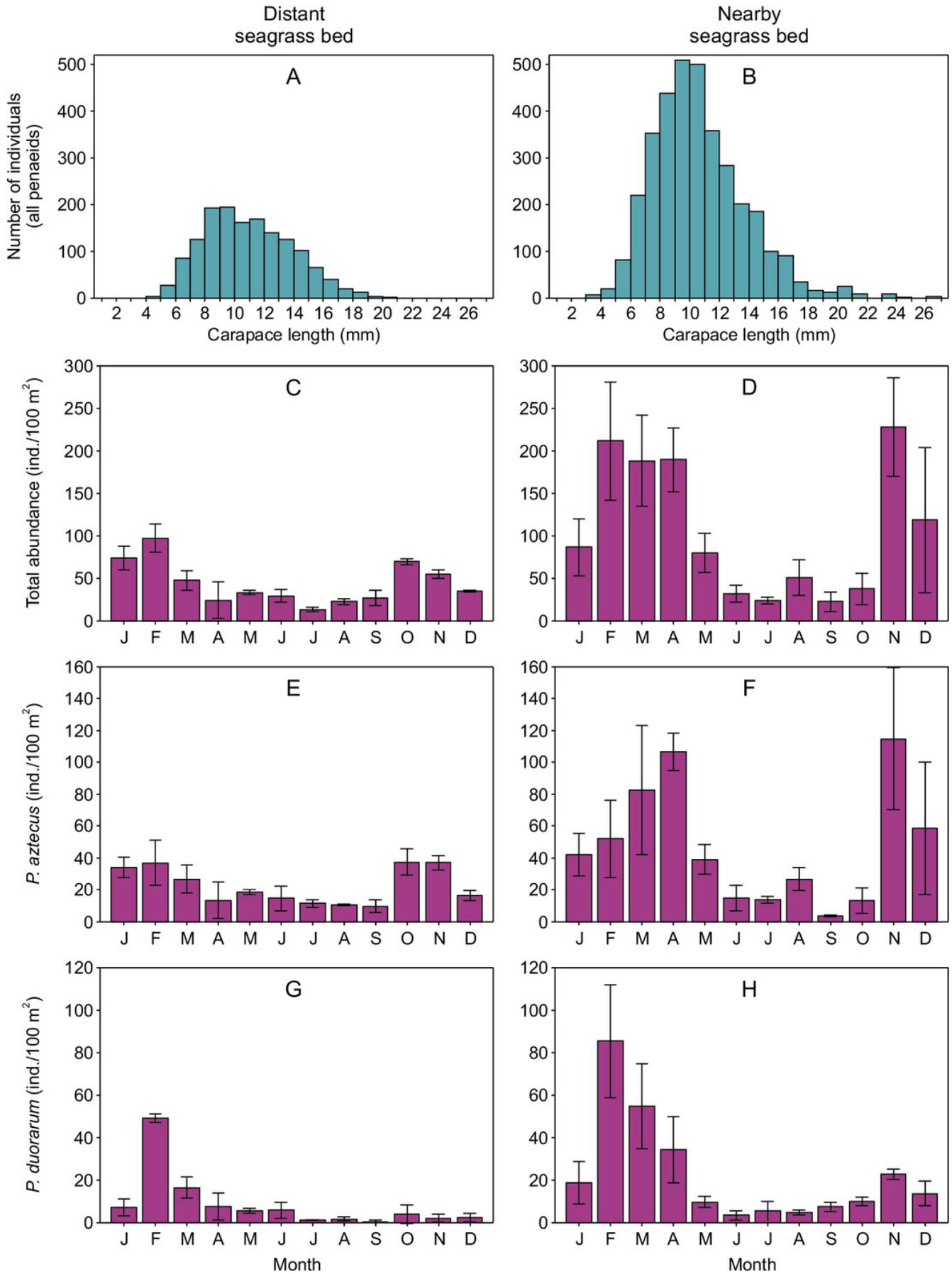


Figure 3

Carapace length-weight relationships (in logarithmic scale) for juvenile *Penaeus* shrimps from two different seagrass beds, distant and nearby to a tidal inlet, in Laguna Madre.

(A) *P. aztecus*: $r^2 = 0.92$, $n = 685$ in the distant bed, and $r^2 = 0.93$, $n = 1426$ in the nearby bed;

(B) *P. duorarum*: $r^2 = 0.95$, $n = 258$ in the distant bed, and $r^2 = 0.93$, $n = 686$ in the nearby bed.

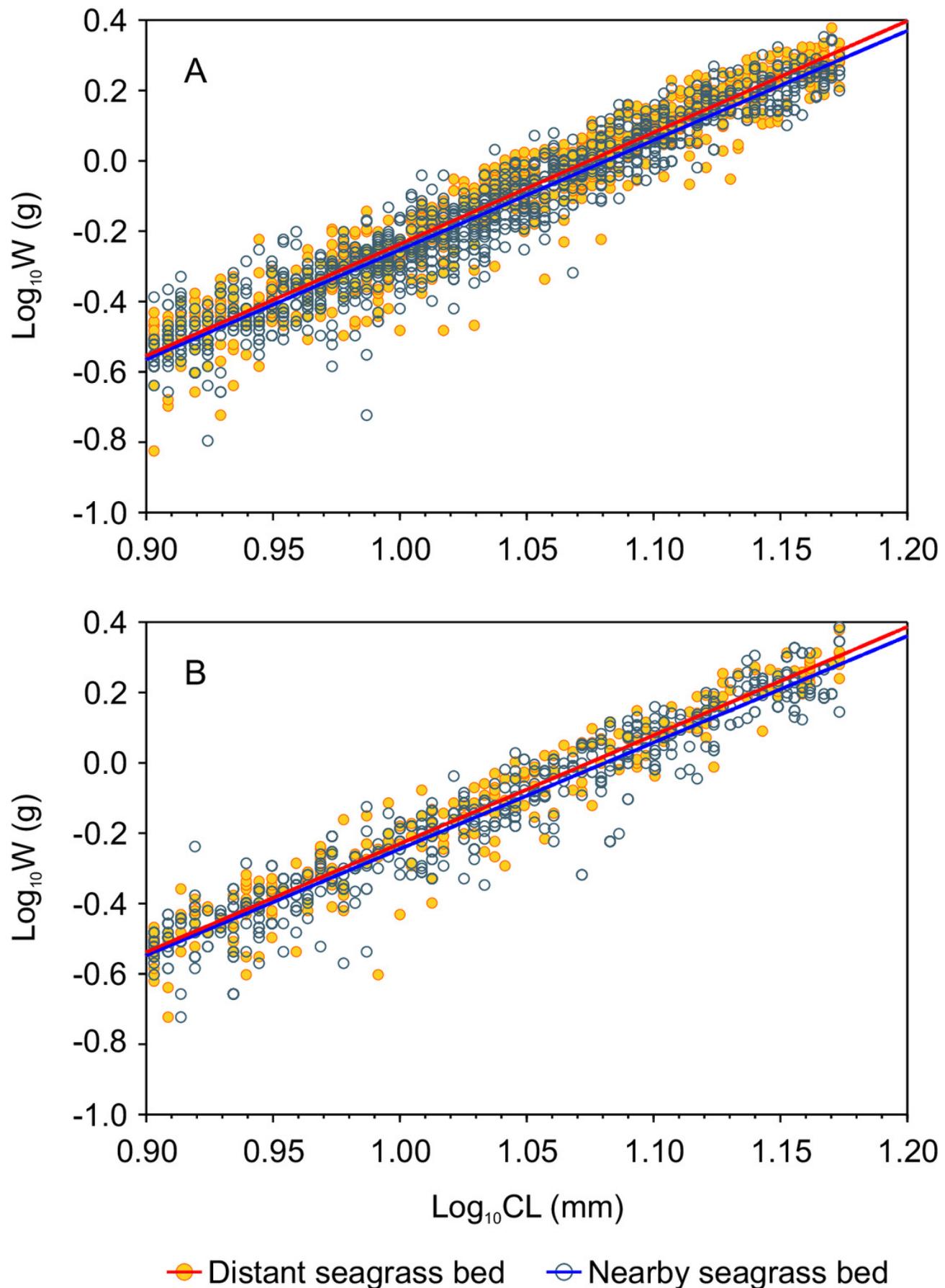


Figure 4

Condition and abundance of *Penaeus* shrimps from two different seagrass beds in relation to their proximity to a tidal inlet (distant and nearby) in a coastal lagoon.

(A) Individual predicted mean weight (\pm SE) at a length of 11 mm CL as an indicator of condition for *P. aztecus* and (B) *P. duorarum*. (C) Mean (\pm SE) total shrimp abundance.

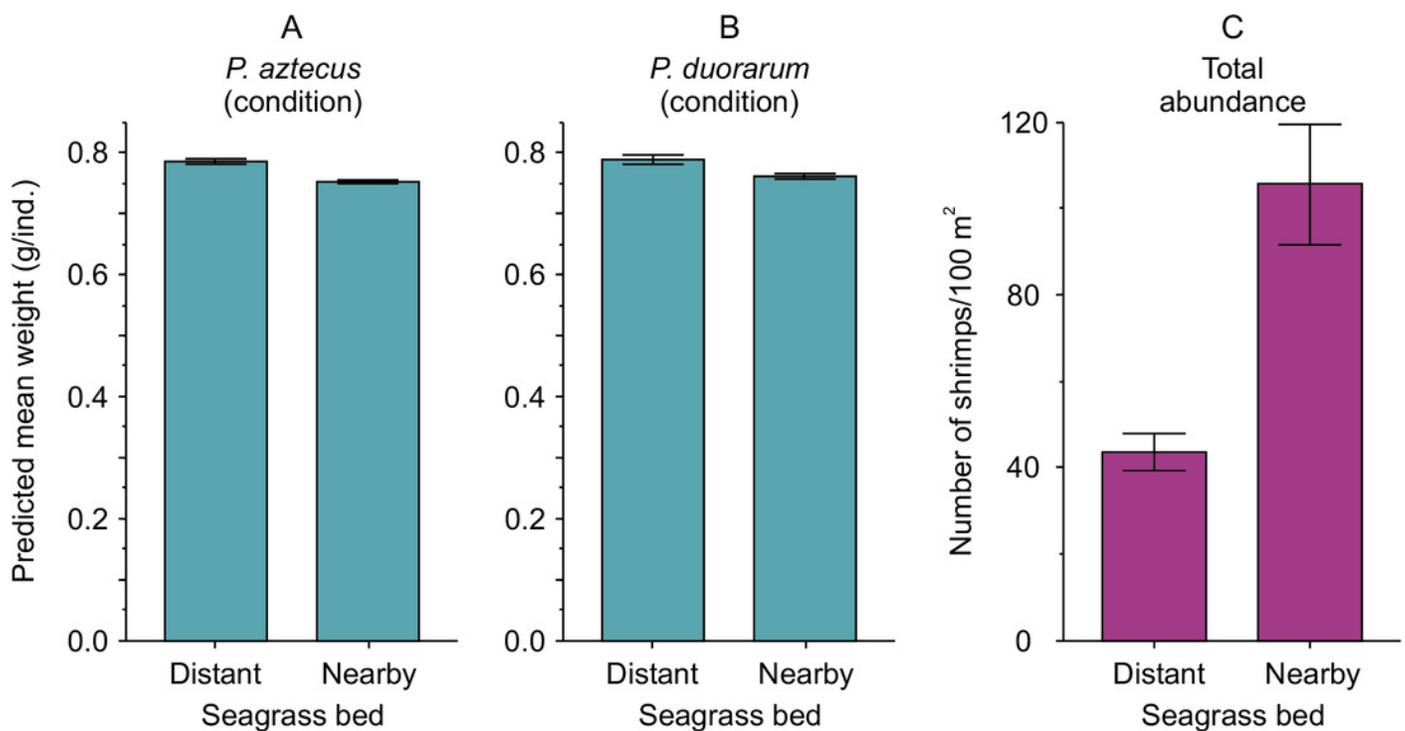
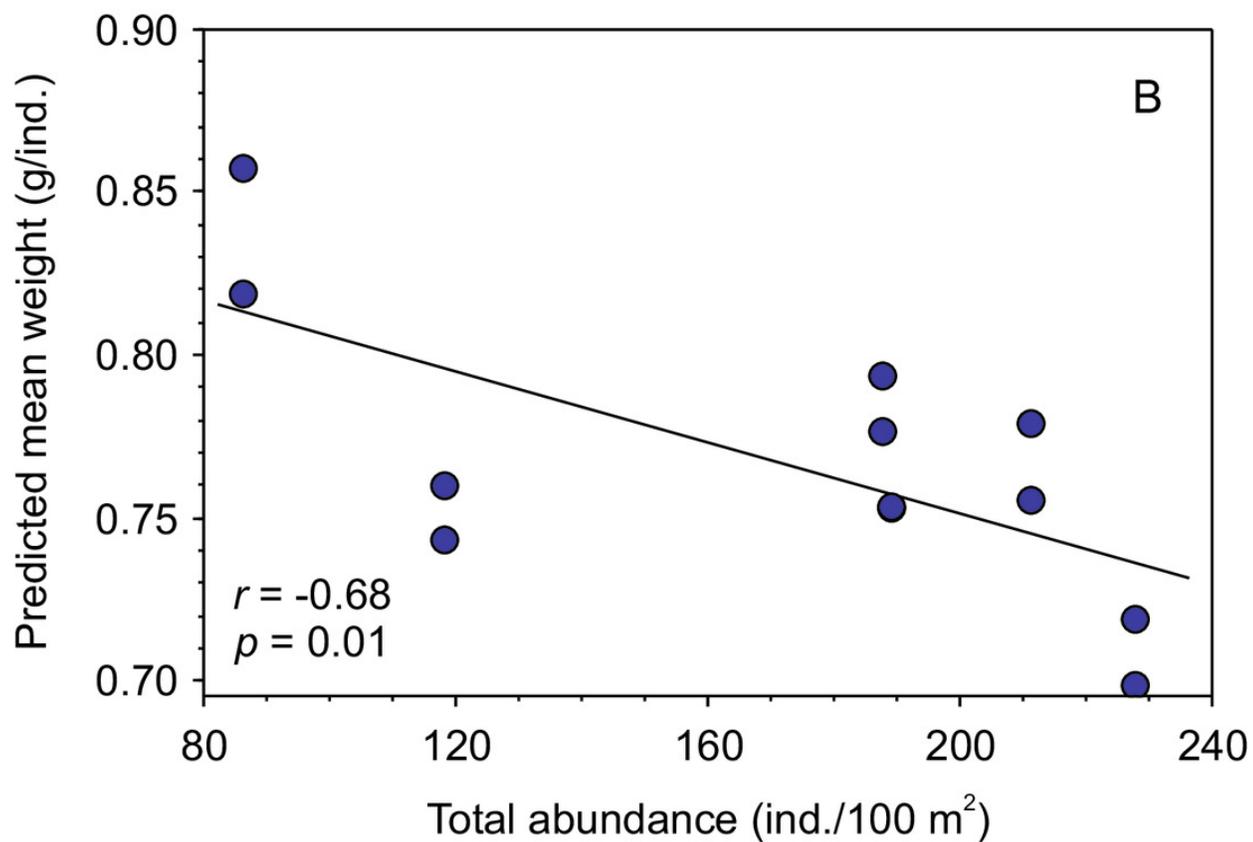
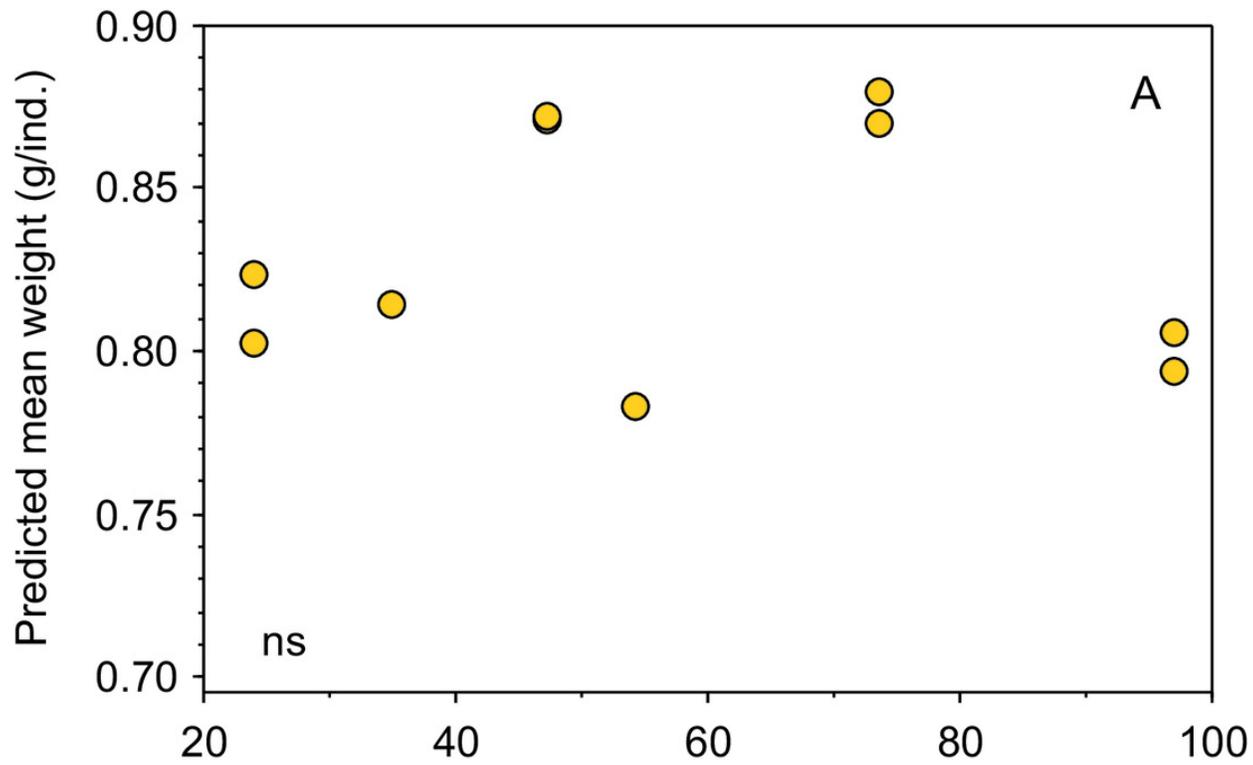


Figure 5

Relationship between body condition (combined data from *Penaeus aztecus* and *P. duorarum*) and total shrimp abundance in two seagrass beds, one distant and one near the tidal inlet in a coastal lagoon.

(A) No significant (ns) relationship was detected in the distant bed, whereas (B) a negative linear function between both variables was observed for shrimp in the nearby seagrass bed. Individual predicted mean weight at length of 11 mm CL was utilized as an indicator of condition.



● Distant seagrass bed ● Nearby seagrass bed