

1 **INTERACTION BETWEEN STOCKING DENSITY AND SETTLEMENT ON**
2 **POPULATION DYNAMICS IN SUSPENDED MUSSEL CULTURE**

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10

11 **ABSTRACT**

12 Population dynamics on mussels growing on suspended culture depend mainly on the balance
13 of three processes: mortality and/or dislodgements, recruitment and growth. The negative
14 effect of overcrowding on mussels growth and survival has been widely studied. Some studies
15 have also addressed the effect of population size on recruitment on bottom beds. This work
16 analyzes the effect of stocking density on mussel growth, survival and seed settlement, and
17 the post-settlement interaction between adults and recruits in suspended culture. Our results
18 show a trade-off between competition for resources and the risk of great settlements in adult
19 mussel populations. Intracohort competition increases with stocking density, leading to mussel
20 losses and growth declines along culture, while seed settlement, which leads to intercohort
21 competition, is higher at moderate stocking densities. On the other hand, the asymmetric
22 competition for resources between adults and settlers can lead to post-settlement mortality
23 and dislodgments and reduce the growth of recruits.

25 **Keywords**

26 Intercohort competition, intracohort competition, mortality, mussel growth, population
27 dynamics, seed settlement.

29 **1. INTRODUCTION**

30 Mussels, like other sessile marine invertebrates, are gregarious organisms that form
31 highly dense, overcrowded and multilayered matrices on both bottom beds and suspended
32 culture (Capelle et al., 2014; Commito and Rusignuolo, 2000; Cubillo et al., 2012; Guiñez and
33 Castilla, 1999). This gregarious behavior is associated with certain advantages including
34 protection from predators (Bertness and Grosholz, 1985; Lin, 1991; Reimer and Tedengren,
35 1997), reproductive success (Okamura, 1986) and optimization of hydrodynamic regimes
36 leading to a higher flux of seston (Gibbs et al., 1991). However, high population densities may
37 lead to food and space limitations inducing intraspecific competition, which can reduce
38 individual growth and cause density-dependent mortality or dislodgements. This mechanism is
39 known as self-thinning and regulates the size of the population according to the available
40 resources (Filgueira et al., 2008; Fréchette and Lefaire, 1995; Fréchette et al., 1992; Guiñez
41 and Castilla, 1999; Guiñez, 2005).

42 In mussel aquaculture the density of suspension feeders is maximized to achieve a
43 greater commercial yield. In Galicia (NW Spain), where mussels are cultured on ropes
44 suspended from raft systems (Labarta et al., 2004), stocking densities range between 700-1200
45 ind/m depending on mussel size, i.e. around 5 to 7 million individuals per raft (Cubillo et al.,
46 2012b; Fuentes-Santos et al., 2013; Pérez-Camacho et al., 2013). This particular case of
47 extreme aggregation represents an extraordinary framework for the study of intraspecific
48 competition and density-dependent effects on population dynamics (Cubillo et al., 2012a,
49 2012b, 2012c; Fuentes-Santos et al., 2013, 2013; Lauzon-Guay et al., 2005a, 2005b).

51 Once established, mussel populations increase in size through larval settlement and
52 growth of individuals. Most gregarious invertebrates are highly selective in choosing
53 settlement site because after settlement the capability to move is lost or becomes limited
54 (Peteiro et al., 2011). This phenomenon offers a good opportunity to make preliminary
55 assumptions on prevailing circumstances at settlement sites of these animals as they are
56 expected to settle on the most favorable sites available. *M. galloprovincialis* has clear
57 settlement preferences for textured and complex substrates, which offer increased surface
58 area and spatial refuges (Carl et al., 2012; Filgueira et al., 2007; Frandsen and Dolmer, 2002;
59 Peteiro et al., 2010; Rilov and Schiel, 2006a, 2006b). Mussel sea beds and culture ropes would
60 then constitute a favorable substrate for the settlement of conspecifics, providing protection
61 against predation and reducing post-settlement mortality (Carl et al., 2012; Dolmer and
62 Stenalt, 2010; Filgueira et al., 2007; Frandsen and Dolmer, 2002; Peteiro et al., 2010).
63 However, larvae that succeed to settle on the ropes will compete for food and space resources
64 with the adult mussels (Dolmer and Stenalt, 2010). Thus, considering intraspecific competition
65 inside each (adult and recruited) cohort and the intercohort competition processes, are key
66 factors in the analysis of population dynamics on both natural and culture frameworks.

67 Intracohort competition processes have been widely studied within adult mussel
68 populations (Alunno-Bruscia et al., 2000; Cubillo et al., 2012a, 2012b; Fréchette and Lefavre,
69 1995; Fréchette et al., 1996, 1992; Fuentes-Santos et al., 2013; Guiñez and Castilla, 1999;
70 Lachance-Bernard et al., 2010). Similarly, post-settlement mortality due to self-thinning was
71 detected in mussel seed settled on collector ropes ((Peteiro et al., 2007). Some studies have
72 reported a negative effect of settlement and recruitment on adult mussels growth and survival
73 (Fréchette et al., 2010; Irisarri et al., 2013). The effect of adult populations on settlement and
74 recruitment of conspecifics on sea beds have also been analyzed (Chase and Bailey, 1996;
75 Dolmer and Stenalt, 2010; Frandsen and Dolmer, 2002; Strayer and Malcom, 2006). However,
76 the interaction between different cohorts within the same ecosystem (mussel bed or culture
77 rope) needs to be extensively addressed.

78 This study aims to analyze the density-dependent effects caused by intraspecific
79 competition for available resources in the population dynamics of mussels (*Mytilus*
80 *galloprovincialis*) growing on suspended culture. For the first time, we will cover both the
81 effects of intracohort competition among adult mussels and the effects of intercohort
82 competition between adult mussels and recruited seed. To that end, we monitored the three
83 main processes that drive population dynamics: individual growth, mortality/dislodgements
84 and recruitment on three adult mussel density treatments during the upwelling favorable
85 season.

86 87 **2. Material and Methods**

88 ***2.1. Experimental design***

89 The experimental culture was conducted in the mussel polygon of Arnela, located in
90 the Mandeo River estuary area close to the 10 m isobaths (Ría de Ares-Betanzos, NW Spain),
91 where rafts with out-growing *Mytilus galloprovincialis* mussels coexist with collector ropes. On
92 the 10/05/2012 mussels obtained from seed collector ropes were classified to ensure

93 homogeneous populations (mean = 32.3mm, sd = 7.98) and were socked on culture ropes at
94 three different densities (800, 1200 y 1600 ind/m) to address the effect of density on mussel
95 growth, dislodgement from the ropes, and therefore biomass loss. All the process was done
96 following the culture and handling techniques used by the local industry.

97 Along the culture period, thermohaline characteristics and seston availability were
98 monitored weekly at the same mussel polygon. Water temperature and salinity were
99 measured with a multiparameter probe YSI 556, while seston and Chl a availability were
100 measured following the sampling procedure detailed by (Figueira et al., 2009). Furthermore,
101 settlement was weekly monitored on empty collector ropes suspended during 7 days at the
102 same location, following the protocol described in Peteiro et al., (2011).

103 Mussel population on the ropes was followed through monthly samplings until harvest
104 on early October. Each month, a sample of known length was taken from 3 ropes of each
105 density treatment at 4m depth. Settlement of two new cohorts of mussel seed (smaller
106 individuals) on the culture ropes was detected on May-June and August-September. For this
107 reason, growth and population dynamics of the two populations on the ropes, from now on
108 referred as to initial population and settlement, were analyzed independently. Density was
109 calculated as the number of mussels per linear meter of rope (ind/m). Rope weight (kg/m) was
110 estimated from sample weight and total production (kg/m) was expressed as weight of
111 marketable (>50 mm) mussels. Individuals were measured and weighted to establish the
112 frequency distributions of shell length (L; mm), defined as the maximum length of the anterior-
113 posterior axis, and fresh weight (FW, g).

114 **2.2. Statistical analysis**

115 Kernel density estimators with Gaussian kernel and optimal bandwidth selected by
116 Silverman's rule of thumbs (Silverman, 1986) were used to fit mussel length (mm) and fresh
117 weight (g) distributions by stocking density over the culture period.

118 The temporal patterns of density (ind/m) and biomass (kg/m) as well as individual shell
119 length (mm) and fresh weight (g) growth were fitted by generalized additive models (GAM)
120 with interaction factor by curve (Hastie and Tibshirani, 1990) to include the effect of stocking
121 density.

122 GAM models are a generalization of GLM (generalized linear models) that express the
123 relationship between a target response, Y , and a set of continuous explanatory variables,
124 $X=(X_1, \dots, X_p)$, as:

$$125 \quad E[Y|X] = H \left(\alpha + \sum_{j=1}^p f_j(X_j) \right) \quad (1)$$

126 where α is a constant, f_j is the smooth partial function or effect associated with each
127 continuous covariate, X_j , and H is a fixed, known, monotone link function. The principal
128 advantages of using models such as (1) are that they keep the interpretability of GLM, since
129 the additive components simply describe the influence of each covariate, and incorporate the

130 flexibility of the smooth terms f_j . The link function is selected according to the distribution of
131 the response variable: for normal variables (biomass, shell length and fresh weight) we fitted
132 GAM with Gaussian family and “identity” link function, density (ind/m) was fitted by GAM with
133 negative binomial family and “log” link, and variables measuring proportions were fitted by
134 GAM with quasibinomial family and “logit” link.

135 GAM models with interaction factor by curve are a generalization of pure GAM models
136 where the relationship between Y and each of the continuous covariates X_j can vary among
137 subsets defined by levels of a categorical covariate Z with m levels. Thus, model (1) is
138 extended as follows

$$E[Y|X, Z] = H \left(\alpha + \sum_{j=1}^p f_j(X_j) + \sum_{j=1}^p \sum_{l=1}^m g_{j,l}(X_j) I(Z = l) \right) \quad (2)$$

140 where $g_{j,l}$ are smooth partial function depending on X_j . We used the shrinkage variable
141 selection procedure proposed by (Marra and Wood, 2011) to check for interactions between
142 time (X) and stocking density (Z).

143 3. RESULTS AND DISCUSSION

144 3.1 Environmental characteristics and larval abundance

145 The experiment was conducted during the spring-summer season characterized by
146 upwelling favorable conditions (Alvarez et al., 2008; Álvarez-Salgado et al., 2011). Temperature
147 and salinity averaged 16.4 (sd = 1.38) °C and 35.0 (0.71) ‰, respectively, with higher
148 temperatures from June to August. The TPM, POM and PIM averaged 0.99 (0.46), 0.44 (0.08)
149 and 0.54 (0.39) mg/L respectively, with no differences between months, while the mean
150 seston quality (f) was 0.49 (0.13) with higher values from May to July. The mean level of Chl-
151 a along the culture period was 1.24 (0.4) µg/l.

152 We have observed an important settlement on collector ropes in the study area (Fig. 1)
153 with a seasonal pattern characterized by a main peak in April (up to 25000 ind/m) followed by
154 a period (mid-May to early July) with continuous settlement (2000-12000 ind/m), two minor
155 peaks in August and October and absence of settlement from October onwards. This agrees
156 with previous studies where Arnela is characterized by its high larval abundance during the
157 spring-summer season (Peteiro et al., 2011), and with the traditional use of this area as
158 nursery by growers (Filgueira et al., 2007).

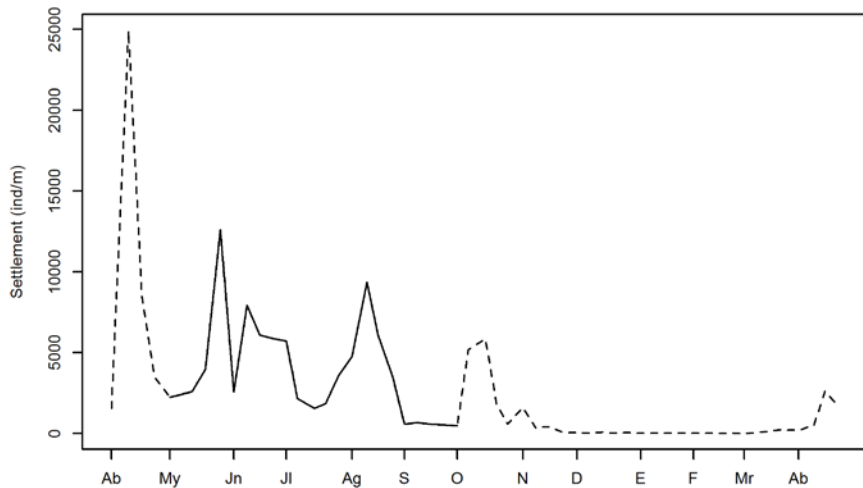


Fig. 1: Larval settlement (0.25-2mm) from April 2012 to April 2013 (dashed line), the solid line shows the experimental period.

3.2. Population dynamics

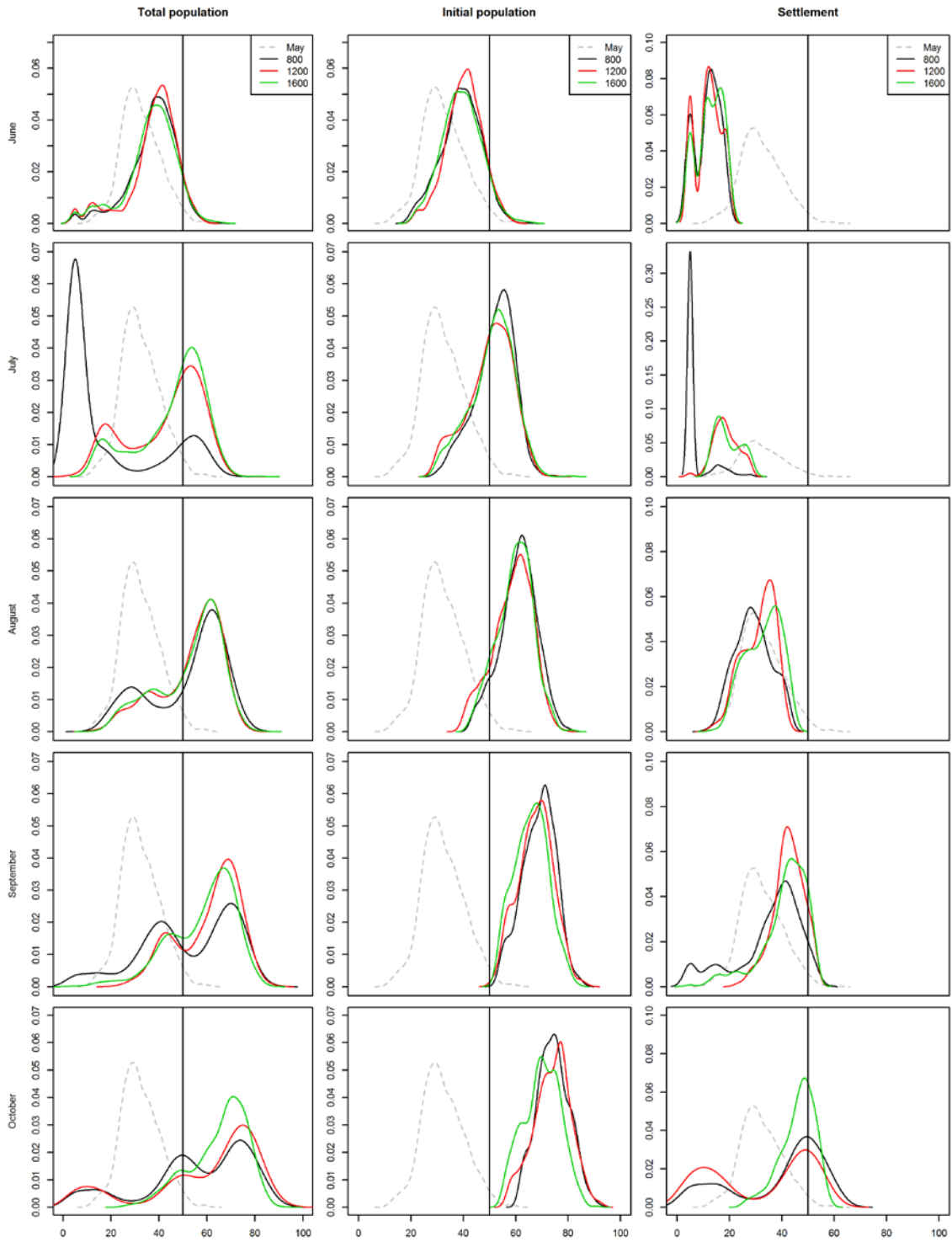
The initial length of mussels followed a unimodal distribution with mean =32.3mm (sd= 7.98). The multimodal size distributions observed from June with individuals smaller than those deployed in early May (Fig. 2, left), indicated settlement of new populations on the ropes. Two settlement episodes were observed along the culture period (May-June and August-September; Fig. 2), common for the three experimental densities but differing in its abundance (Fig. 3, bottom), that affected total density and biomass on the ropes, and thus population dynamics. Settlement was particularly important in the lower density treatment (800 ind/m) during June, where seed density reached 2000 ind/m (Fig. 3), while for the two higher densities was below 400 ind/m. Thus, settlement abundance did not increase with available surface as stated for empty ropes (Filgueira et al., 2007), probably due lower resource availability on high density ropes. These results agree with (André and Rosenberg, 1991) and (Strayer and Malcom, 2006) that found a negative correlation between adult density and recruitment in cockle and mussel populations, respectively. In addition (Dolmer and Stenalt, 2010) showed that when the density of mussels beds and the realized filtration capacity are low, mussel recruitment is controlled by the available substrate, but as the mussel population increases, larval predation increases pre-settling mortality and the food competition reduces the post-settling survival of the mussels.

On the 800 ropes, the June settlement peak caused significant mussel losses, on contrast with the two higher densities, where settlement partially compensated the losses of the initial population (Fig. 3, top). As a consequence of the differential settlement, the proportion of initial mussels for 800ind/m decayed due to June settlement and stabilized thereafter, while the higher densities (p-value < 0.001) showed a similar progressive decrease along the culture period. These different temporal patterns lead to homogeneous densities along treatments at harvest (ANOVA by ranks, p-value = 0.873) as the combined effects of

188 recruitment and intraspecific competition increased density up to 1035 on the 800 ropes
189 ind/m, while on 1200 and 1600 ind/m ropes dropped to 1042 and 1114 ind/m, respectively
190 (Fig. 3, top). However, the proportion of initial population at harvest accounted for 50%, 65%
191 and 80% of total population in 800, 1200 and 1600 ind/m, respectively (Fig. 4).

192 The initial population density underwent a linear decrease through mussel mortality
193 and dislodgements from the ropes in the three treatments (Fig. 3; GLM Adj-R² =0.86). Despite
194 density-dependent survival rates, with higher losses for 1600 ind/m ropes than for 800 ind/m
195 (T-test, p-value= 0.007), initial population densities at harvest increased with stocking density
196 (1600> 1200> 800; ANOVA by ranks, p-value < 0.001). Initial population losses in the 800 ropes
197 can be attributed to the settlement peaks, which caused dislodgements from the ropes mainly
198 during June (Fig. 3). On the other hand, mussel losses in the two higher stocking densities,
199 where minor settlement abundance was observed, can be attributed to intracohort
200 competition due to overstocking, which leads to self-thinning processes (Alunno-Bruscia et al.,
201 2000; Cubillo et al., 2012a; Fréchette and Lefavre, 1995; Fréchette et al., 1996; Fuentes-Santos
202 et al., 2013; Guíñez, 2005; Lachance-Bernard et al., 2010).

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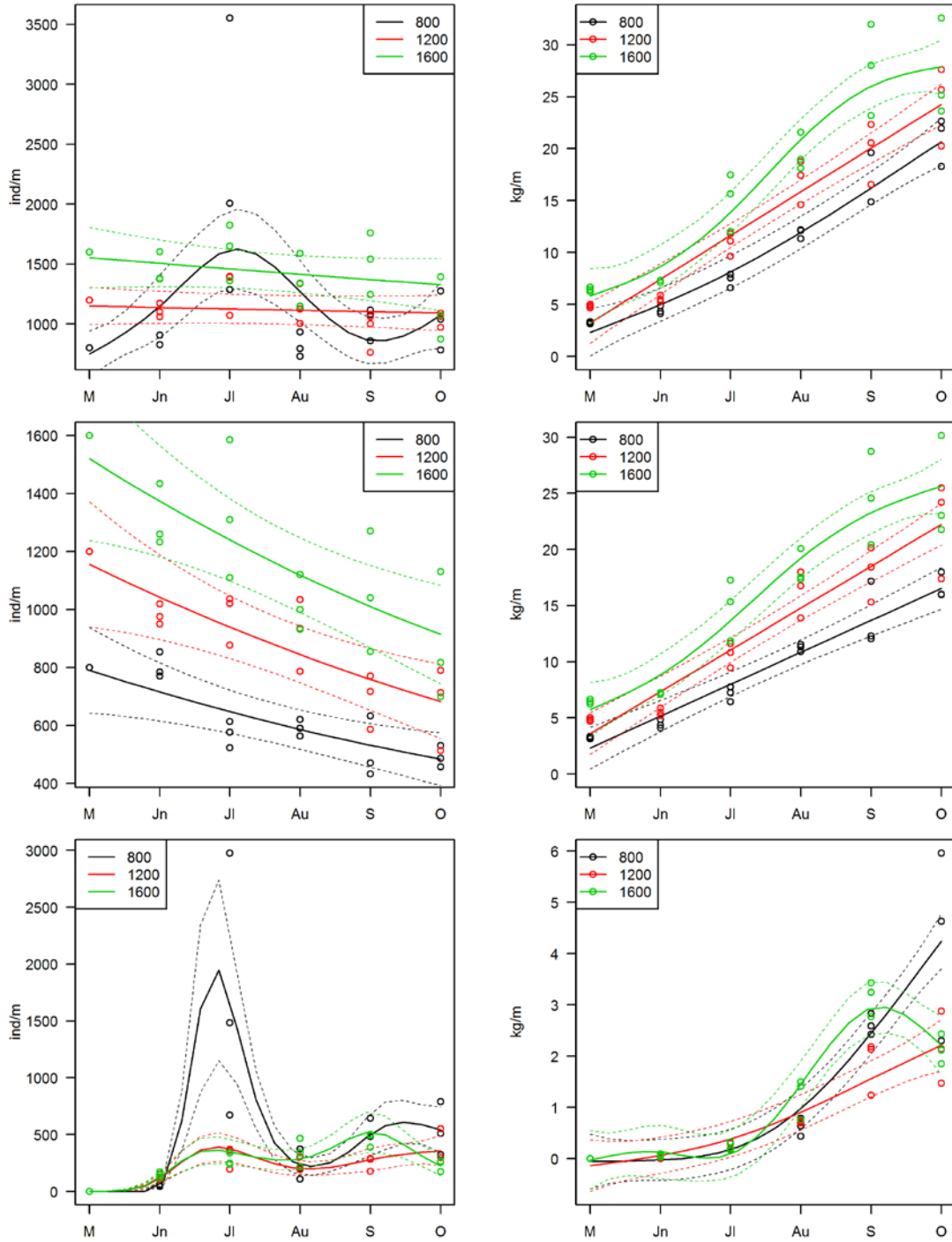
205 **Fig. 2:** Kernel density estimation of shell length by month and stocking density for total population, initial
 206 population and settlement (early and late summer settlement).

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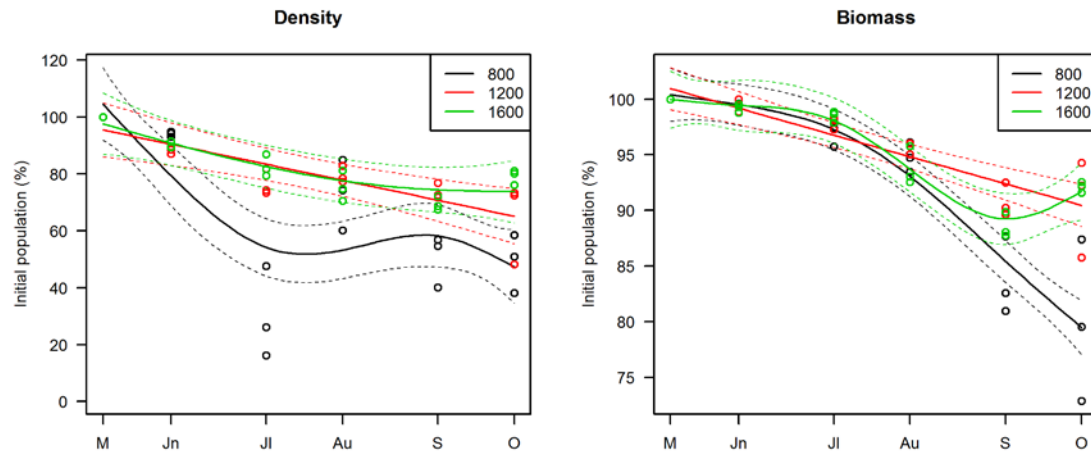
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212 **Fig. 3:** Density (ind/m) and biomass (kg/m) fits by GAM with interaction factor (stocking density) by curve (time).
 213 Top: total population (Density: 72% dev. explained, Biomass: 93.6% dev. explained); centre: initial population
 214 (Density: 87.3% dev. explained, Biomass: 91.4% dev. explained); bottom: settlement (Density: 86% dev. explained,
 215 Biomass: 89,4% dev. explained),

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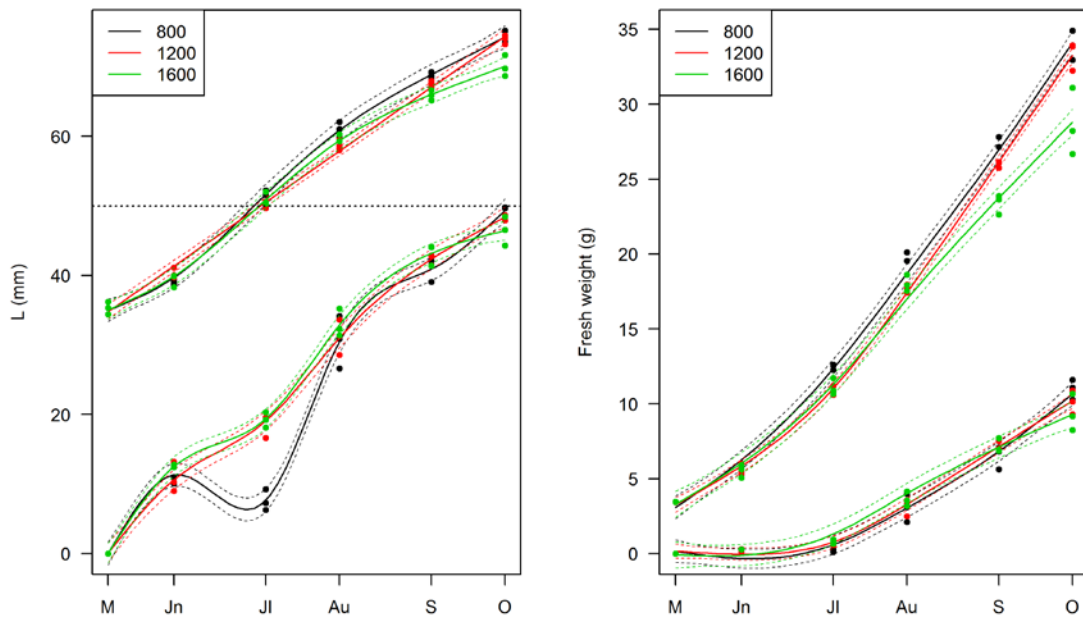
218 **Fig. 4:** GAM fits with interaction factor (stocking density) by curve (time) for percentage of initial population in
 219 terms of density (left, 92.6% dev. explained) and biomass (right, 90.4% dev explained).

220 In a similar study carried out in 2008 at the same time period (May–November) on a
 221 nearby mussel polygon, the 800 ind/m ropes suffered lower mussel losses than those recorded
 222 in this work, while similar density losses were observed for 1200 ind/m ropes in both
 223 experiments (Fuentes-Santos et al., 2013). In 2008 the settlement peak occurred 4 months
 224 after deployment, when individuals were strongly attached to the ropes, while in our
 225 experiment it occurred just after deployment when dislodgment risks are higher due to
 226 reorganization of mussels on the ropes (Capelle et al., 2014). Besides, in this work the greater
 227 settlement peak was registered when the mean length of adult mussels was 40mm, while in
 228 2008 settlement occurred when mussels had reached 65mm. Larger adult mussels can
 229 intensify intercohort competition effects causing post-settlement mortality and reducing
 230 recruitment (Cubillo et al., 2012b; Fr chet te et al., 2005).

231 The initial population showed density-dependent growth in both length (L, mm) and
 232 fresh weight (FW, g) along the culture period (Fig. 5). The 800 ropes registered the lowest
 233 length growth during the first months, which can be attributed to the greater intercohort
 234 competition caused by the big June settlement peak. As pointed out by (Fr chet te et al., 2010),
 235 settlers packed between adult mussels may prevent them from opening properly reducing their
 236 food consumption. (Irisarri et al., 2013) also found a negative effect of recruitment on
 237 individual growth for mussels deployed at the same stocking density in a nearby location in
 238 2011. From August onwards, when density and competitive pressure decreased, the 800 ind/m
 239 ropes registered the greatest individual growth. Mussels at 1200 ind/m showed linear length
 240 growth, while growth at 1600 ind/m ceased on September, when the effects of intracohort
 241 competition among the initial population intensifies as mussel growth and resource
 242 requirements increase (Cubillo et al., 2012; Waite et al., 2005; Xavier et al., 2007). For fresh
 243 weight we only observed a different pattern for mussels at 1600 ind/m, with a slower growth
 244 from August onwards, reflecting again the intensification of competition for resources as
 245 mussels grow.

246 In the settled population, the big amount of small individuals attached to the ropes in
 247 June hid the actual growth pattern during this month, leading to an unrealistic negative

248 growth. A similar situation was observed in early September (Fig. 3). Along the rest of the
 249 culture period the three treatments underwent similar growth patterns, although at harvest
 250 the individuals settled on the 1600 ropes were the smaller and lighter ones, probably due to
 251 intensified competition associated to mussel growth. This agrees with (Chase and Bailey, 1996)
 252 that suggest that recruitment into a population with high adult densities may result in declined
 253 growth of the recruits.



254
 255 **Fig. 5:** GAM fit of growth curves for size (mm) and fresh weight (g). Top: initial population (size: 99.8% deviance
 256 explained; fresh weight: 99.5% deviance explained). Bottom: settlement (size: 95.6% deviance explained; fresh
 257 weight: 99.3% deviance explained). The horizontal dashed line (left) shows commercial length (50 mm).

258 As a consequence of the negative density-dependence effects of overstocking and
 259 seed settlement on mussel growth and survival, the three stocking densities followed different
 260 biomass patterns (Fig. 3, right). In the two lower density treatments, biomass of the initial
 261 population increased linearly along the culture period, with a lower slope for 800ind/m (t-test,
 262 p-value = 0.02) as a consequence of the dislodgements from these ropes caused by the
 263 settlement peaks. In the 1600 ropes, biomass stagnates at the end of culture, reflecting the
 264 negative effect of overstocking on individual growth of the initial population, which intensifies
 265 as mussels grow and consumption increases. However, recruitment hardly increased total
 266 biomass on the ropes due to the lower size of the settled individuals (Fig. 3, right) and initial
 267 population represents 80%, 90% and 91% of the rope biomass at harvest in the 800, 1200 and
 268 1600 ropes, respectively (Fig. 4).

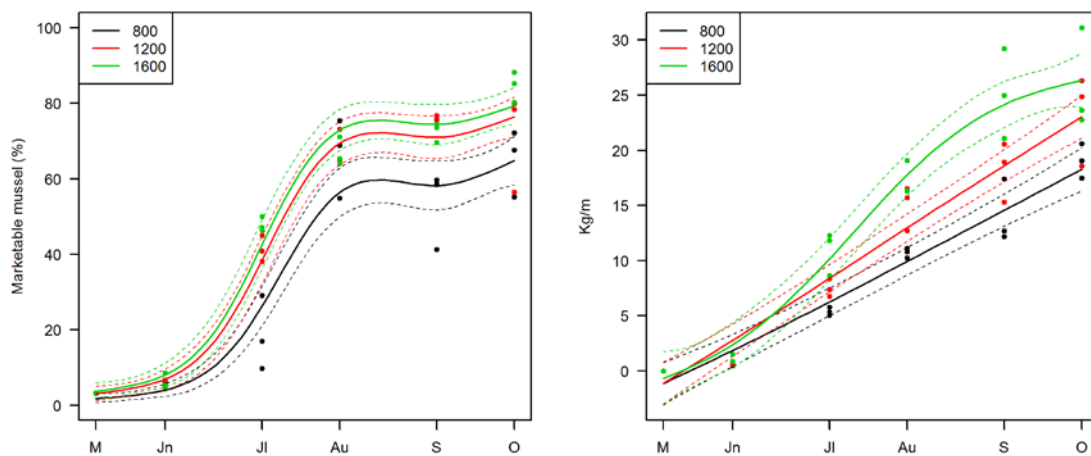
269 **3.3. Mussel production:**

270 In early August >85% of the mussels from the initial population were above the
 271 commercial size (50mm) and in early September they accounted for 100% (Figs. 2 and 5) for
 272 the three density treatments. On the other hand, the proportion of the settled population that

273 reached commercial length at harvest depended on stocking density (45, 35 and 30% for 800,
 274 1200, and 1600 ind/m, respectively; Fig. 2), as intercohort competition intensified with
 275 stocking density. However, as a consequence of the higher recruitment on the 800 ropes, this
 276 treatment provided the lowest proportion of marketable mussels along culture (65% at
 277 harvest), while no differences were observed between the higher stocking densities that
 278 averaged 72 and 85%, respectively (Fig. 6). The high proportion of non-marketable mussels at
 279 harvest could be attached onto new ropes to begin a new culture process.

280 Total production (kg/m) of marketable mussels (Fig. 6) followed a temporal pattern
 281 similar to total biomass (Fig. 3). It increases linearly over time for the two lower densities and
 282 stabilizes in early September for the 1600ind/m treatment as a consequence of the slower
 283 individual growth during the last month (Fig. 4). Despite this stagnation, 1600 ind/m still had a
 284 higher total production than the lower density treatments. But as a consequence of the
 285 density-dependent growth, this treatment provided a lower proportion of highly-priced
 286 mussels (Pérez-Camacho et al., 2013) in September and October than 800 and 1200ind/m.

287 Therefore, from our results the optimal culture density for individuals about 30 mm
 288 would be around 1200 ind/m, i.e. 5 Kg/m of rope. This density was not as low as to suffer the
 289 great settlement peaks that caused growth decline and dislodgments in the 800ind/m ropes
 290 (thus limiting production), nor as high as to show the 1600 ind/m growth limitations through
 291 intraspecific competition.



292
 293 **Fig. 6:** Left: GAM fit of percentage of marketable mussels without interaction factor (stocking density) by curve
 294 (time) (95% deviance explained). Right: GAM fit with interaction factor by curve for total production (95.3%
 295 deviance explained).

296 **4. CONCLUSION**

297 The present work represents a first attempt to address the density-dependent effects
 298 on population dynamics (and marketable production) in a real situation of suspended mussel
 299 culture, through the interaction between stocking density and settlement abundance. We
 300 analyzed the effect of mussel stocking density on settlement and recruitment abundances, as

301 well as on growth and survival of conspecifics, and the post-settlement interaction between
302 the adult and recruited populations, as well as the population dynamics of each cohort.

303 In adult mussel populations, we observed a trade-off between competition for
304 resources and the risk of great settlements. Intracohort competition for space and food
305 resources increases with stocking density, and may lead to mussel dislodgements, especially
306 after deployment, and to growth declines along culture. However, mussel ropes with lower
307 stocking densities represent a more favorable substrate for seed settlement, thus can suffer a
308 more intense intercohort competition that also affects mussel growth and survival. Moreover,
309 big settlement episodes during post-deployment reorganization increase the risk of mussel
310 dislodgments, as mussels have not developed strong byssus threads yet. On the other hand,
311 the asymmetric competition for resources between adult and recruits lead to post-settlement
312 mortality and dislodgments, even at moderated stocking densities, and can reduce the growth
313 of recruits mainly at high adult densities.

314 These density-dependent effects on population dynamics have implications on mussel
315 production. Although population density converged to similar values (ca. 1100 ind/m) in the
316 three treatments, differences in the population composition (% of initial and recruited
317 mussels) and individual growth determined product quality at harvest. The intermediate
318 density (1200 ind/m) found a balance between the negative effects on growth and survival of
319 seed settlement at the lowest density and adult overcrowding at the highest, and yielded the
320 highest benefits during the favorable settlement season.

321 This work shows that seed settlement can alter the population dynamics of mussels
322 growing on culture ropes and limit production. Thus, the spatio-temporal pattern of larval
323 settlement should be taken into consideration by mussel farmers in order to develop culture
324 strategies that minimize these negative effects.

325 **ACKNOWLEDGMENTS**

326 We wish to thank H. Regueiro, M. García, B. González and L. Nieto for laboratory
327 assistance and PROINSA Mussel Farm and their employees for technical assistance during the
328 experimental work. This study was supported by the contract-project PROINSA Mussel Farm,
329 code CSIC 0704101100001 and a CSIC PIE 201030E071 project. A.M. Cubillo enjoys a
330 postdoctoral fellowship program of the Foundation Juana Vega, in the IMAR-DCEA, Portugal.

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FIGURE CAPTIONS

Fig. 1: Larval settlement (0.25-2mm) from April 2012 to April 2013 (dashed line), the solid line shows the experimental period.

Fig. 2: Kernel density estimation of shell length by month and stocking density for total population, initial population and settlement (early and late summer settlement).

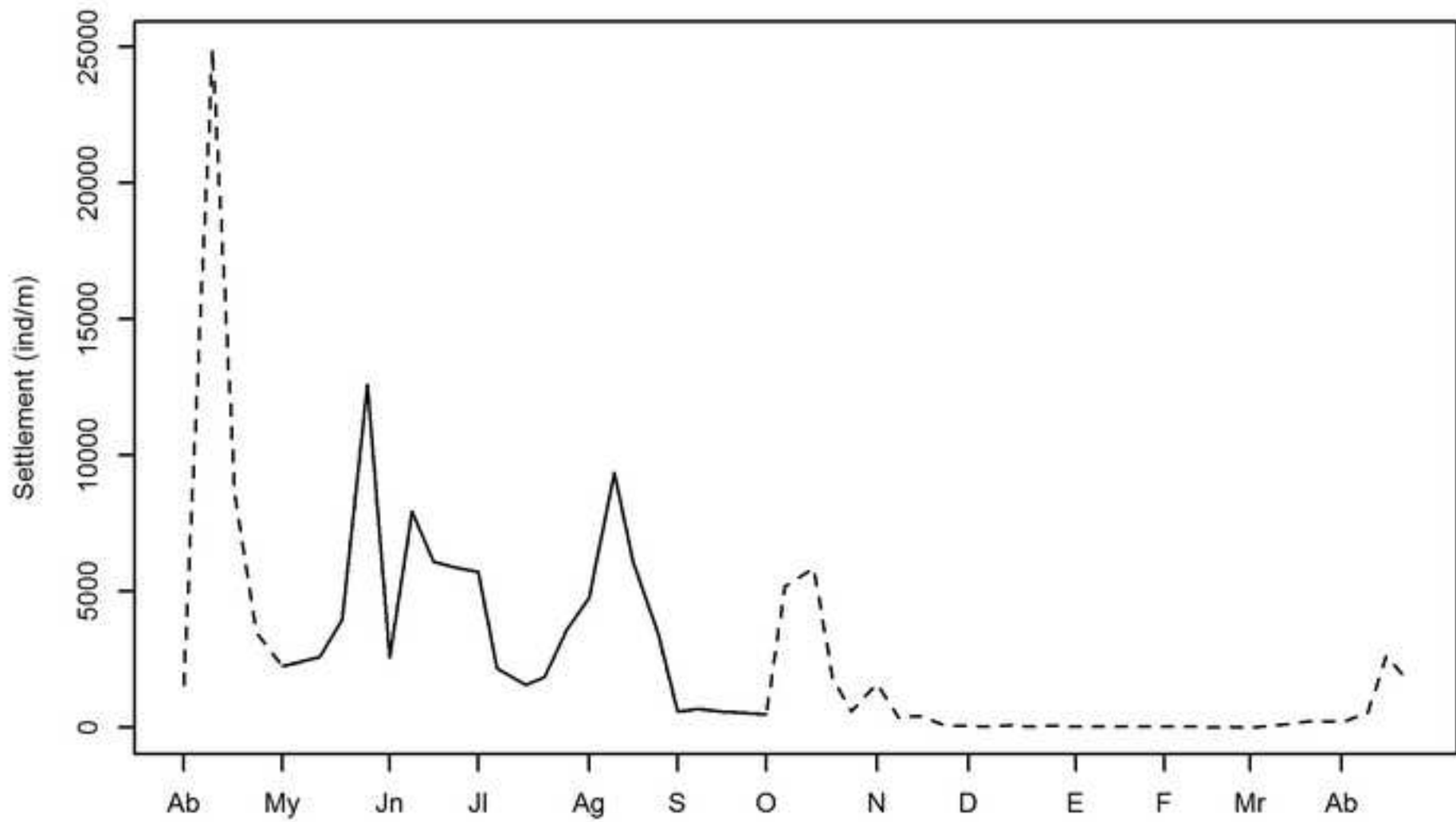
Fig. 3: Density (ind/m) and biomass (kg/m) fits by GAM with interaction factor (stocking density) by curve (time). Top: total population (Density: 72% dev. explained, Biomass: 93.6% dev. explained); centre: initial population (Density: 87.3% dev. explained, Biomass: 91.4% dev. explained); bottom: settlement (Density: 86% dev. explained, Biomass: 89,4% dev. explained),

Fig. 4: GAM fits with interaction factor (stocking density) by curve (time) for percentage of initial population in terms of density (left, 92.6% dev. explained) and biomass (right, 90.4% dev explained).

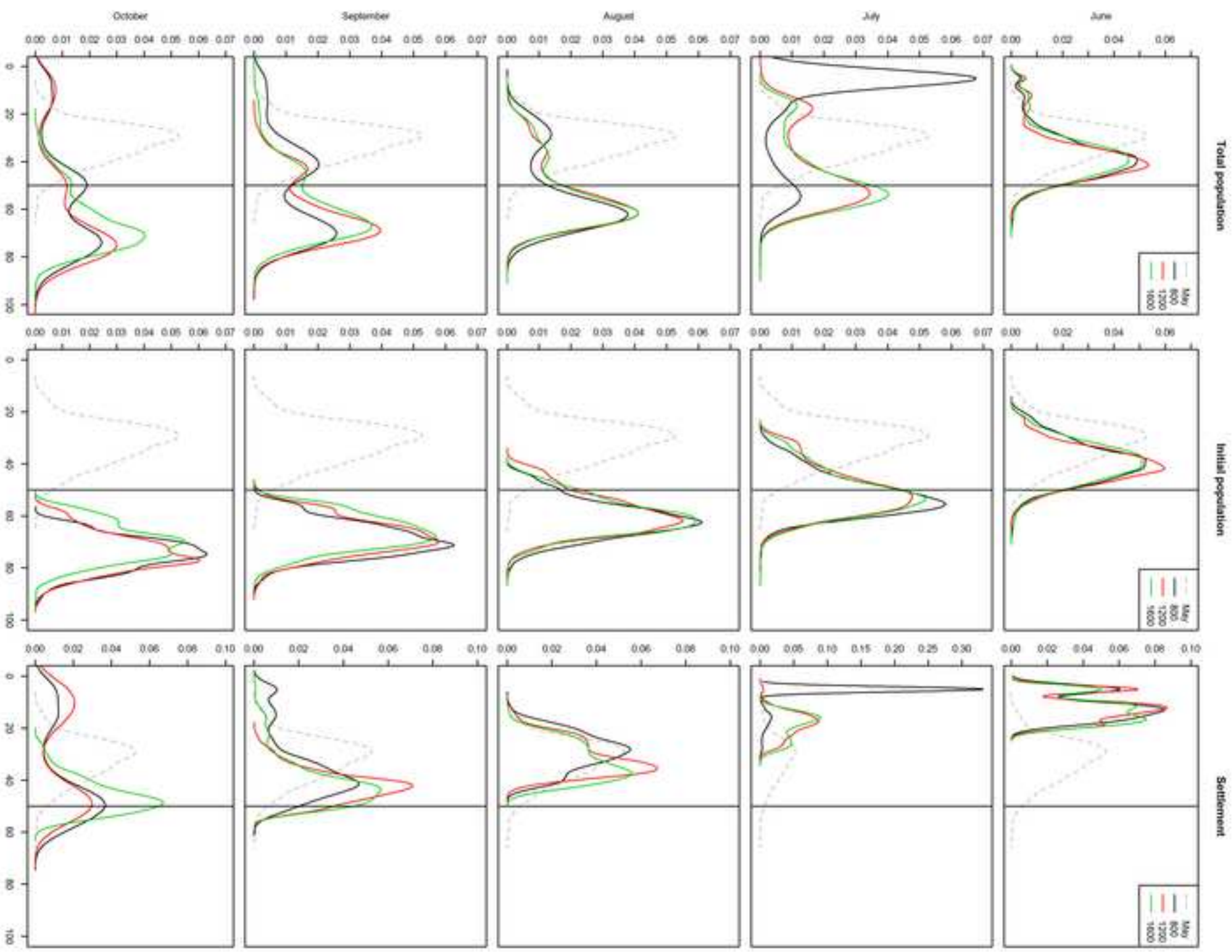
Fig. 5: GAM fit of growth curves for size (mm) and fresh weight (g). Top: initial population (size: 99.8% deviance explained; fresh weight: 99.5% deviance explained). Bottom: settlement (size: 95.6% deviance explained; fresh weight: 99.3% deviance explained). The horizontal dashed line (left) shows commercial length (50 mm).

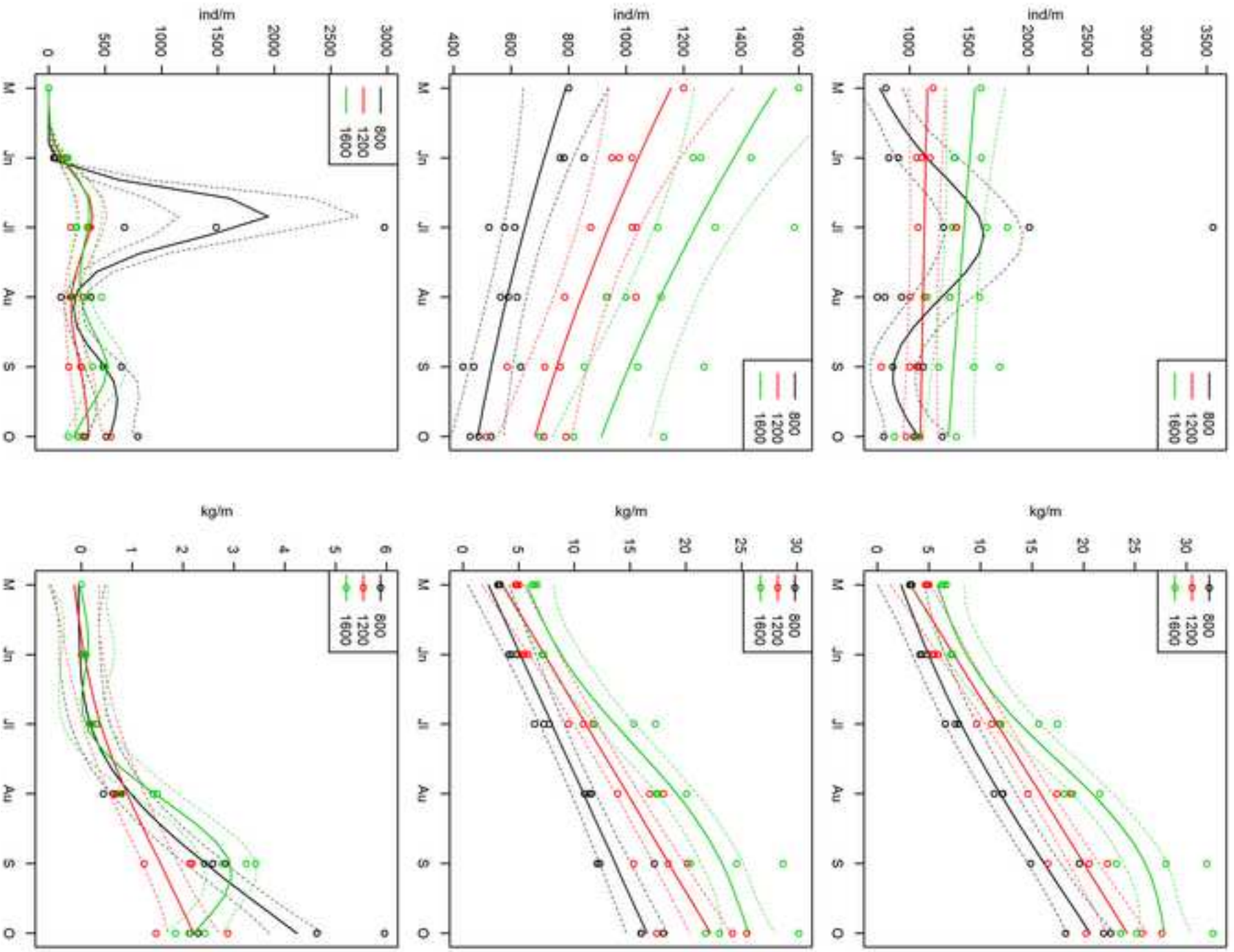
Fig. 6: Left: GAM fit of percentage of marketable mussels without interaction factor (stocking density) by curve (time) (95% deviance explained). Right: GAM fit with interaction factor by curve for total production (95.3% deviance explained).

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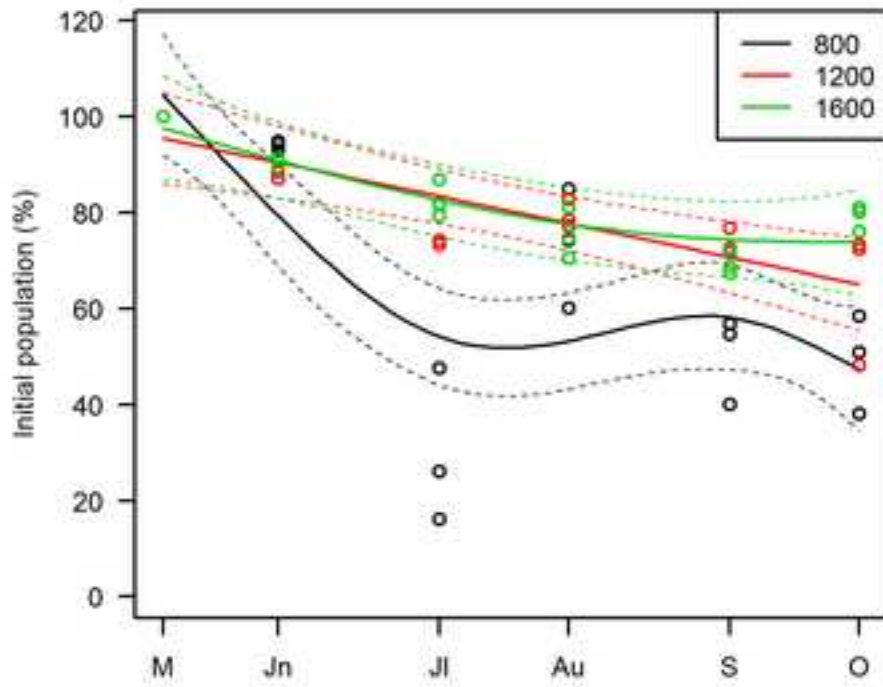
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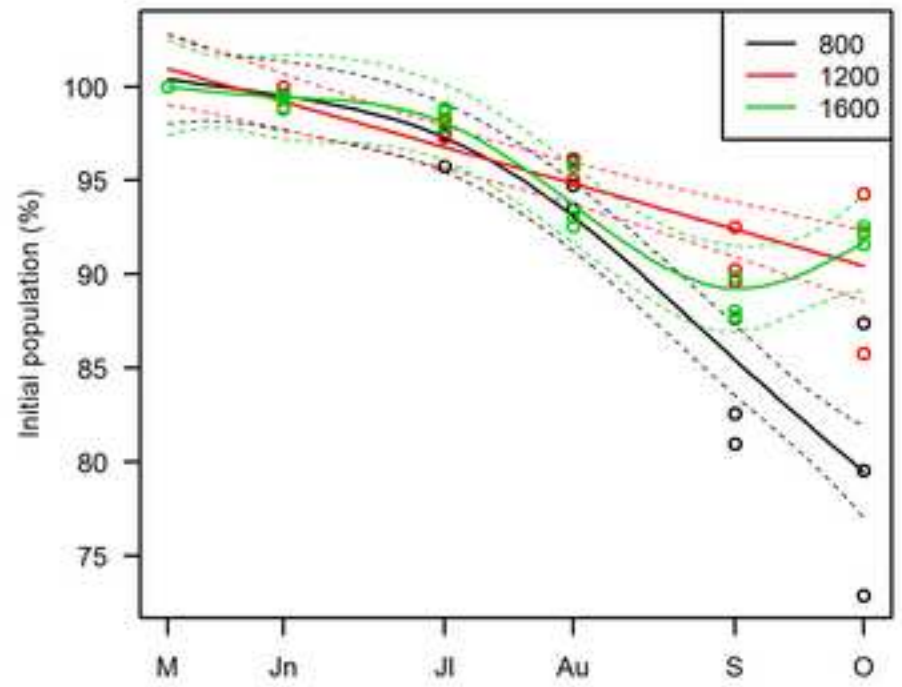


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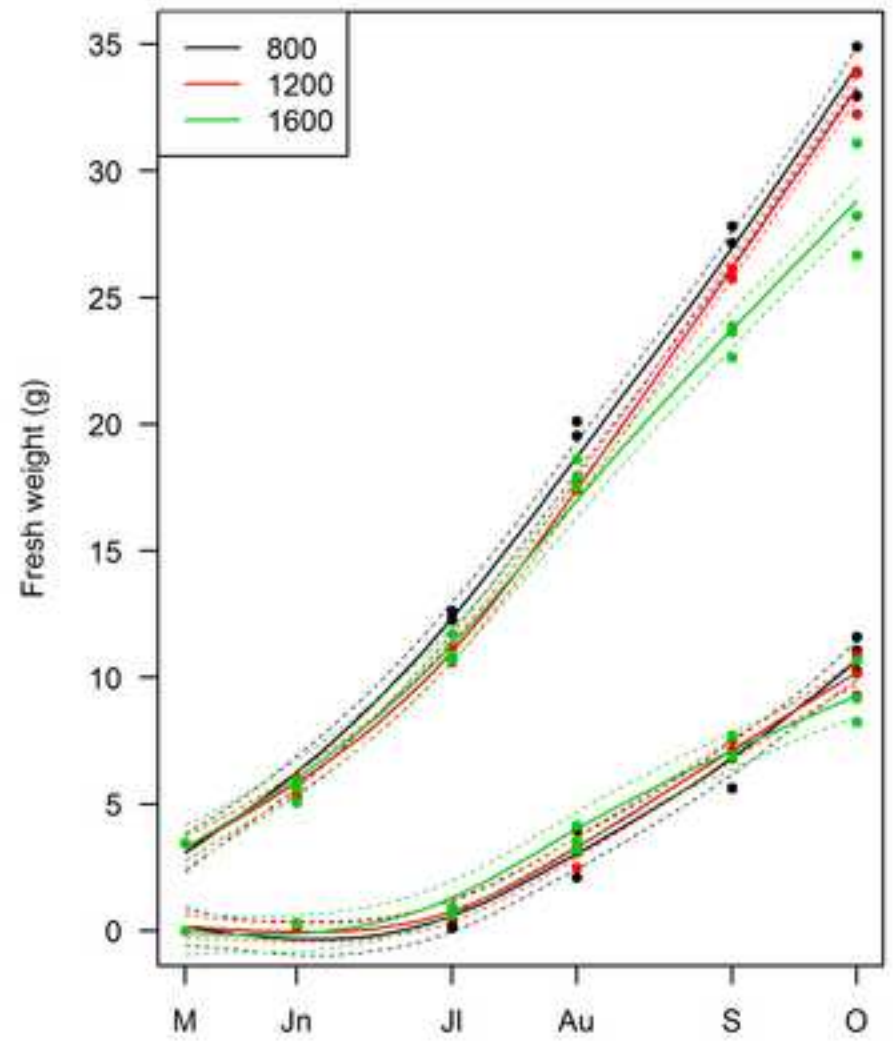
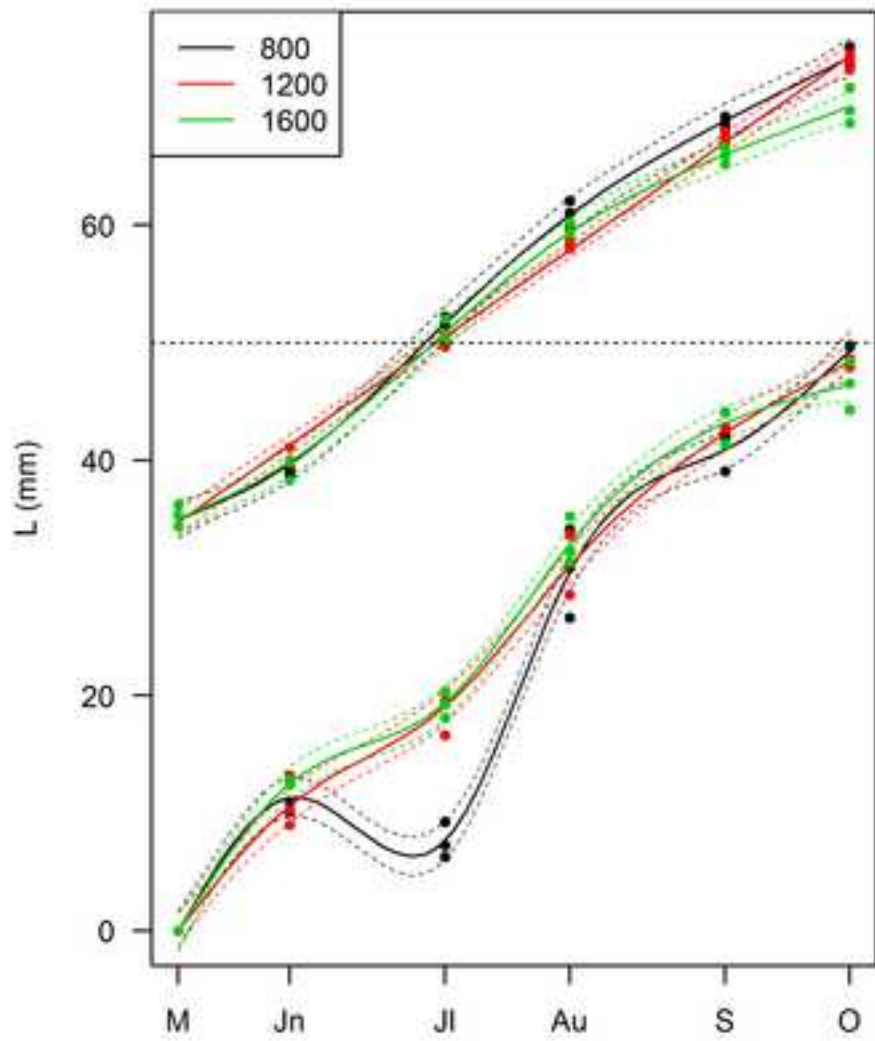
Density



Biomass



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