Journal of Sea Research 95 (2015) 84–94

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Interaction between stocking density and settlement on population dynamics in suspended mussel culture

Alhambra M. Cubillo [1], Isabel Fuentes-Santos, Uxío Labarta *

CSIC, Instituto de Investigaciones Marinas, Eduardo Cabello, 6, 36208 Vigo, Spain

ARTICLE INFO

Article history:
Received 27 May 2014
Received in revised form 8 August 2014
Accepted 24 September 2014
Available online 6 October 2014

Keywords:
Intercohort competition
Intracohort competition
Mortality
Mussel growth
Population dynamics
Seed settlement

ABSTRACT

Population dynamics on mussels growing on suspended culture depend mainly on the balance of several processes: mortality and/or dislodgements from the ropes, recruitment and growth. The negative effect of overcrowding on mussel growth and survival has been widely studied. Other works have addressed the effect of population size on recruitment on bottom beds. This study aims to provide insight into the processes underlying population dynamics. To this purpose, we analyzed the effect of stocking density on mussel growth, survival and seed settlement, and the post-settlement interaction between adults and recruits in suspended culture. The temporal pattern of the variables involved in population dynamics was fitted by GAM models, which in contrast with parametric models does not assume any prior relationships between variables. Our results show that mussel growth and survival depend on a trade-off between competition for resources at high densities and the risk of great settlements in less crowded adult mussel populations. Intracohort competition increased with stocking density, while seed settlement, which increases the risk of mussel dislodgements and leads to intercohort competition, was higher at moderate stocking densities. Post-settlement competitive pressures were driven by total population density and size composition. Both intracohort competition in adults and asymmetric competition between adults and recruits increase with higher adult–recruit ratios. All these density-dependent processes should be considered in future management strategies and research experimental designs.

1. Introduction

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

Once established, the size of mussel populations can increase through larval settlement and growth of individuals. Most gregarious invertebrates are highly selective in choosing a favorable substrate because after settlement their mobility is reduced or lost (Peteiro et al., 2011). This phenomenon enables us to make assumptions on prevailing circumstances at settlement sites. *Mytilus galloprovincialis* has clear settlement preferences for textured and complex substrates, which offer increased surface area and provide spatial refuges against predation, reducing post-settlement mortality (Carl et al., 2012; Filgueira et al., 2007; Frandsen and Dolmer, 2002; Peteiro et al., 2010; Rilov and Schiel, 2006a, b). Mussel sea beds and culture ropes would then constitute a favorable substrate for the settlement of conspecifics. Dolmer and Stenalt (2010) found positive correlation between the density of recruited and adult populations on mussel bottom beds. Cubillo et al. (2012c) and Irisarri et al. (2013) also reported high settlement abundances on culture ropes. However, larvae that succeed to settle on the ropes will compete for food and space resources with the adult mussels (Dolmer and Stenalt, 2010). Asymmetric competition processes, whereby larger individuals obtain a greater proportion of resources than the smaller ones, have been reported among individuals from the same or different cohorts (Bertness and Grosholz, 1985; Fréchette and Despland, 1999; Fréchette et al., 1992; Lauzon-Guay et al., 2005). Asymmetric competition may lead to declined growth and survival of smaller individuals,

* Corresponding author. Tel.: +34 986 231930x214; fax: +34 986292762.
E-mail address: labarta@iim.csic.es (U. Labarta).
[1] Actual address: IMAR — Institute of Marine Research, Centre for Ecological Modelling, IMAR–DCEA, Faculty of Science and Technology, Qta Torre, 2829-516 Monte de Caparica, Portugal.

http://dx.doi.org/10.1016/j.seares.2014.09.009
1385-1101/

post-settlement mortality and reduced recruitment (Cubillo et al., 2012b; Dolmer and Stenalt, 2010; Frandsen and Dolmer, 2002; Fréchette et al., 2005; Strayer and Malcom, 2006). Therefore, recruitment of conspecifics in adult mussel populations depends on a trade-off between post-settlement predation-refuge and mortality risks by post-settlement intercohort competition (see Fig. 10 in Dolmer and Stenalt, 2010). Although competition in mussel populations is assumed to be mainly asymmetric, settlement can also reduce adult mussel growth (Irisarri et al., 2013) and survival (Fréchette et al., 2010; Irisarri et al., 2013) through resource shortage. Thus, considering intraspecific competition inside each (adult and recruited) cohort and the intercohort competition processes, are key factors to understand the population dynamics of mussels on both natural and culture frameworks.

Several studies have analyzed separately the processes described above. Intracohort competition processes have been widely addressed by self-thinning analysis within adult mussel populations (Alunno-Bruscia et al., 2000; Cubillo et al., 2012a,b; Fréchette and Lefaivre, 1995; Fréchette et al., 1992, 1996; Fuentes-Santos et al., 2014; Guiñez and Castilla, 1999; Lachance-Bernard et al., 2010). Similarly, post-settlement mortality due to self-thinning was detected in mussel seed settled on collector ropes (Peteiro et al., 2007).

The main aim of self-thinning analysis is to determine whether competition is caused by space or food limitations. To this purpose, the dynamics of even-aged mussels growing at different densities are followed over time (see Fig. 1 in Cubillo et al., 2012a), and the limiting factor is estimated by comparison between the exponent of the allometric biomass–density relationship and the theoretical exponents established in the literature (Fréchette and Lefaivre, 1990). However, self-thinning has some drawbacks that should be taken into consideration. The ST model relies on a series of regularity assumptions (Fréchette and Lefaivre, 1990) that not always hold on natural conditions. The proximity between the theoretical exponents hampers the discrimination between space and food limitations (Cubillo et al., 2012a; Fréchette and Lefaivre, 1990; Keeley, 2003; Lachance-Bernard et al., 2010). In addition, competition in sessile animal populations may be caused by the joint effect of space and food limitations (Fréchette et al., 1992, 2010), thus establishing a unique limiting factor is not realistic. Finally, although self-thinning is a dynamic process and is analyzed by sequential samplings, the traditional ST models overlook temporal effects and autocorrelations leading to biased estimates of the ST exponents and to a misspecification of the population dynamics.

Some of these drawbacks have been analyzed and partially overcame by Cubillo et al. (2012a), which fitted the ST model by frontier analysis providing a dynamic interpretation of the ST process through the temporal pattern of site occupancy. Fuentes-Santos et al. (2014) developed a dynamic self-thinning model for multilayered sessile animal populations, which in contrast with the traditional ST model does not rely on any regularity assumptions. This model provides a more realistic description of population dynamics, analyzing the temporal pattern of intraspecific competition, rather than discriminating between limiting factors. This new approach allows the ecological interpretation of any ST exponent, while the traditional model cannot explain any exponent different from the theoretical ones. However, the authors highlight the difficulty of interpreting an intricate process as ST with a single parameter, as the ST exponent and the variables involved in the process should be observed jointly in order to obtain a proper ecological interpretation.

On the other hand, Fréchette et al. (2010) extended ST analysis to populations with more than one cohort. They propose a new model to estimate the B–N curve, i.e. the relationship between biomass and density at a single temporal point, involving both intra- and inter-cohort competition. However, this work overlooks the effect of cohort 2 (2 years old) on the growth of cohort 1 (1 year old) and inherits all the drawbacks of the traditional ST models.

Population density plays an important role on competition processes, which determine both growth and survivorship of mussels, as well as on settlement and post-settlement growth and mortality. Aquaculture practices tend to maximize the density of suspension feeders to achieve a greater commercial yield. In Galicia (NW Spain), where mussels are cultured on ropes suspended from raft systems (Labarta et al., 2004), stocking densities range between 700 and 1200 ind/m depending on mussel size (Cubillo et al., 2012b; Fuentes-Santos et al., 2014; Pérez-Camacho et al., 2013). The negative effect of overcrowding is well known by mussel farmers that conduct one or more reductions (thinning-out) in rope density as mussels grow to achieve more homogeneous and valuable crops. This divides the production cycle, which lasts 16–18 months, into three stages: obtaining and growing the seed, thinning-out the ropes and harvesting the mussels (Labarta et al., 2004; Pérez-Camacho et al., 2013). However, production strategies have overlooked the effects of stocking density on settlement and the post-settlement inter- and intracohort competition, as well as the negative effect of recruitment on the homogeneity of yields.

This study aims to provide a consistent analysis of the effect of stocking density on the population dynamics of mussels (*M. galloprovincialis*) growing on suspended culture. To that end, we monitored the main processes that drive population dynamics: individual growth, mortality/dislodgements and recruitment on three adult mussel density treatments during the upwelling favorable season. We have considered using the dynamic ST approach (Fuentes-Santos et al., 2014) and the multiple cohort model developed by Fréchette et al. (2010) to analyze population dynamics. The former addresses the temporal pattern of intraspecific competition, but is limited to single-cohort populations. The latter involves both intra- and intercohort competition, but is limited to a single temporal point and does not allow a dynamic analysis of competition. Given the limitations of these current parametric models, we applied generalized additive models (GAM) to describe the temporal pattern of the processes that determine population dynamics. These models incorporate the flexibility of nonparametric regression, which does not need to assume any prior relationship between variables on contrast with parametric models, and keep the interpretability of generalized linear models.

2. Material and methods

2.1. Experimental design

The experimental culture was conducted from May to October 2012 in the mussel polygon of Arnela, located in the Mandeo River estuary area close to the 10 m isobaths (Ría de Ares-Betanzos, NW Spain), where rafts with out-growing *M. galloprovincialis* mussels coexist with collector ropes. On 10/05/2012 mussels obtained from seed collector ropes were graded to ensure homogeneous population (mean = 32.3 mm, sd = 7.98) and re-socked on 54 culture ropes at low, medium and high densities (800, 1200 and 1600 ind/m, respectively) to address the effect of density on mussel growth, dislodgement from the ropes, and therefore biomass loss. Experimental ropes were placed in the same (outer) side of the raft to avoid within raft variability in the growth rate of mussels (Fuentes et al., 2000). After grading and socking the ropes, samples of known length (ca. 400 individuals) from nine random ropes (3 per density treatment) were checked for density and homogeneous distribution of mussel sizes. The grading and socking process was the same as that used in commercial culture, which has been proven to succeed in obtaining homogeneous populations and densities along the rope length (the initial size distribution can be observed in Fig. 2 — dashed line).

Along the culture period, thermohaline characteristics and seston availability were weekly monitored at the same mussel polygon. Water temperature and salinity were measured with a multiparameter probe YSI 556, while seston concentration and Chl a availability were measured following the sampling procedure detailed by Filgueira et al. (2009). Furthermore, settlement on empty collector ropes was weekly