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Incorporating movement and reproductive asynchrony into a simulation model of fertilization success for a marine broadcast spawner

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ABSTRACT

Decline and collapse of populations of harvested marine broadcast spawners has led to broad concern over reproductive Allee effects for these species, acting through spatial challenges to finding a mate. We used an individual-based simulation model to investigate the potential for movement and mate seeking behavior to mitigate spatial challenges. We incorporated asynchrony in spawning spread over a reproductive season rather than the frequently assumed and generally unrealistic scenario of complete synchrony and instantaneous spawning. Movement rules were based on telemetry data for pink abalone (*Haliotis corrugata*), a severely depleted and formerly harvested species, and we used the model to estimate fertilization success for realistic densities and aggregation states in the Point Loma kelp forest (San Diego, CA, USA). Model rules for abalone movement incorporated conspecific attraction and attraction to a home scar, and produced home range areas of realistic size. Initial aggregation state did not affect home range areas as movement overcame distances separating aggregated from random distributions. Movement was capable of compensating for the fertilization drawbacks to asynchronous spawning. However, fertilization success rates based on movement and spawning asynchrony were comparable to success rates assuming no movement and complete synchrony and declined similarly with decreasing population density. When combined with reproductive asynchrony, movement may not mitigate density decline.

1. Introduction

Broadcast spawning, defined as free release of gametes by both males and females into surrounding water for external fertilization, is a common reproductive strategy for many marine taxa. Females are subject to sperm limitation as high densities of sperm are generally required for successful fertilization and because sperm may be rapidly diluted (Baker and Tyler, 2001; Leighton and Lewis, 1982; Levitan and Petersen, 1995). Adaptations for mitigating sperm limitation include individual-level processes that influence fertilization kinetics such as sperm release rate, as well as characteristics of the gametes themselves such as sperm lifespan (Benzie and Dixon, 1994), egg size (Levitan, 1993), sperm packaging (Oliver and Babcock, 1992), and chemical communication between sperm and egg (Riffell et al., 2002). Group-level adaptations for improving fertilization success include ensuring that potential mates are closely spaced at the time of spawning and that spawning is relatively synchronous among individuals (Yund, 2000). Close proximity between mates may be ensured by high population density but is also possible with aggregated spatial distributions, either continuously or at the time of spawning.

Marine invertebrate broadcast spawners are frequently sessile or sedentary, and thus decreases in population density or disruptions to spatial distribution can have lasting consequences for mate proximity and fertilization success. Fishery induced changes in either density or spatial distribution may result in reproductive Allee effects. Reduced reproductive success for individuals results in a component Allee effect that may translate into demographic Allee effects in the form of nonlinear reductions in population growth rate with declining population density (Gascoigne et al., 2009). Linear decline across low densities to zero implies no density dependence in reproductive efficiency. Nonlinear decline, whether exponential or threshold in shape, signals a positive density dependence associated with Allee effects whereby reproductive efficiency is dependent on density. Sedentary species, such as abalone and sea urchins, have the potential for limited movements that can maintain aggregated distributions even in the face of density reduction. Although many of these species constitute highly

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valued fisheries, their movement behaviors have not been quantified, and the potential for movement to influence reproductive success is unknown.

Models of fertilization success for broadcast spawners have shown non-linear, if not threshold, declines in zygote production with decreasing density of reproductively active adults, and moreover, that increasing aggregation level improves fertilization success at low (Claereboudt, 1999; Lundquist and Botsford, 2004, 2011; Zhang, 2008) as well as intermediate (Levitan and Young, 1995) population densities. These models generally assume that organisms are sessile and exhibit synchronized spawning, assumptions that may not apply to abalone, particularly pink abalone, which are highly asynchronous (Tutschulte and Connell, 1981). Some species of broadcast spawning urchins are also known to exhibit asynchrony (Levitan and Sewell, 1998; Pennington, 1985). The effect of asynchrony in spawning on group-level fertilization success should be proportional to a similar decrease in the number of spawners (Claereboudt, 1999; Lundquist and Botsford, 2011). However, the formal equivalence of a density reduction and asynchrony may break down when considering that animals may be mobile while spawning and may exhibit mate seeking behaviors.

In this study, we model pink abalone (*Haliotis corrugata*) movement to investigate the potential for movement and mate seeking behavior to enhance fertilization success in the face of low population density. Pink abalone is a former fisheries species in southern California estimated to be at 0.01% of its peak abundance in the 1950s (Rogers-Bennett, 2002). Little recovery has been observed in population density since the cessation of pink abalone fishing in 1997, and population growth rate estimates are low even assuming high fertilization success (Button, 2008), suggesting that the population is unlikely to recover without intervention. Abalone movement rates are highly variable within and among species, and for some species, extended periods of little movement may be punctuated by long-distance excursions (Ault and Demartini, 1987; Dixon et al., 1998; Officer et al., 2001; Tarr, 1995; Tutschulte, 1975). Although little is known about the factors that motivate abalone movement, conspecific attraction and the potential for mating likely induce movement in some species. For instance, the Australian greenlip abalone *Haliotis laevigata* is aggregated just before the spawning season and randomly distributed during the rest of the year (Shepherd, 1986), and in California, pink abalone and red abalone (*Haliotis rufescens*) both have been found in clustered distributions, even when at low regional density (Button, 2008; Micheli et al., 2008). Acoustic tracking of pink abalone in the Point Loma kelp forest near San Diego, CA, USA demonstrated that most individuals maintain small home ranges by moving frequently around a home crevice or scar (Coates et al., 2013). This type of movement has the potential to bring individuals closer together and improve fertilization success despite low population density or even low aggregation states observed during static survey efforts.

Our study had two major objectives. First, we sought to derive a mechanistic home range model, based on movement rules and habitat distribution. Our individual-based model (IBM) combined a biased random walk routine with attraction to conspecifics. Models incorporating varying degrees of conspecific attraction, site fidelity, and random search behavior were compared with each other and calibrated with actual movement behavior derived from pink abalone acoustic tracking in southern California (Coates et al., 2013) to explore the potential for variation in mechanistic rules to modify space use. Our aim was not to demonstrate that conspecific attraction is a primary mechanism generating movement in the field, but rather that it could be, and to investigate it's potential impacts to fertilization success. Modification to the biased random walk resulting in realistic home ranges have been modeled for territorial taxa, mediated by avoidance of the scent marks made by conspecifics (Lewis and Murray, 1993; Moorcroft and Lewis, 2006; Moorcroft et al., 1999; Potts et al., 2012). This type of conspecific avoidance has been explored in several contexts but the potential for conspecific attraction to shape and potentially constrain home ranges remains unexplored (Borger et al., 2008). Second, we examined the combined effects of movement and spawning asynchrony on the spatial distribution of potential mates and group-level zygote production.

2. Methods

Below we use the overview, design concepts, details (ODD) protocol to describe our model. The protocol is designed to improve repeatability of the model and comparability with other individual or agent-based models (Grimm et al., 2006, 2010).

2.1. Purpose

The primary purpose of the model was to determine how group-level fertilization success changes with change in abalone density under conditions of realistic abalone movement and spawning synchrony. To produce realistic movement, we constructed a mechanistic model based on movement rules and distribution of appropriate rock crevice habitat that replicated home ranges of pink abalone in southern California. Additional goals were to explore conspecific attraction as a movement mechanism and the impacts of conspecific attraction on home range area under varying population density and aggregation states.

2.2. Entities, state variables and scales

Agents represent individual abalone. Abalone are characterized by the state variables identity number, sex, spawning readiness state, position (grid cell), and original grid cell. Spatial units are 1 m × 1 m grid cells that are characterized by the state variables identity number, location, and suitability as abalone habitat. Habitat suitability was categorical (suitable, unsuitable, and crevice). The model space consisted of a 400-m^2 area of suitable habitat cells set within a 10,000-m^2 world (Fig. 1). Abalone were free to move

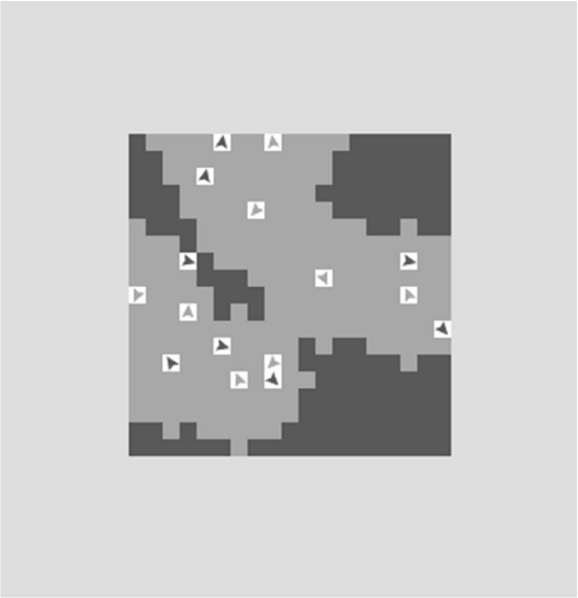

Fig. 1. Model spatial grid. Light gray outer area represents less suitable habitat and was cropped for figure clarity. Dark gray inner box represents suitable habitat. Medium gray in inner box represents areas where crevice grid cells could be placed to produce aggregated distributions. White cells represent crevice grid cells. Triangles represent abalone.