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A density dependent *Thalia democratica* population model

Natasha Henschke[1,2,], James A. Smith[1,2], Jason D. Everett[1,2] and Iain M. Suthers[1,2].*
[1]Evolution and Ecology Research Centre, University of New South Wales, Sydney NSW 2052, Australia
[2]Sydney Institute of Marine Science, Building 22, Chowder Bay Road, Mosman NSW 2088, Australia
**Corresponding author. Email: n.henschke@unsw.edu.au. Address: School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney NSW 2052, Australia. Telephone: +61 412 934 014.*

Gelatinous zooplankton such as the small salp, *Thalia democratica*, regularly form dense swarms around the world, however, little is known about the physiological and oceanographic drivers that influence the magnitude and occurrence of these swarms. A discrete-time, size-structured *T. democratica* population model was developed to determine whether food and temperature were sufficient to explain the observed dynamics of salps. The model tracks cohorts of four life stages and incorporates size-dependent reproduction and mortality. Growth is a function of temperature and food (chlorophyll *a* biomass). The model is consistent with general traits of salp population dynamics such as generation times and relative abundances of each stage. A sensitivity analysis revealed that temperature, ingestion rate and doubling time of phytoplankton were the most sensitive parameters driving the observed patterns of salp biomass. A 10-year time-series simulation identified that salp abundances are proportionally higher in winter and spring (up to 90%), consistent with previous observations. This model could reveal areas more likely to promote salp swarms based on satellite oceanographic data and improve the understanding of the impact of salp swarms on food webs in a changing marine environment.

Introduction

Salps are pelagic tunicates that often form large swarms following the upwelling of cool, nutrient rich water which promotes blooms of phytoplankton (Deibel and Paffenhofer 2009). Salps are able to feed efficiently on phytoplankton, consuming particles from <1 μm to 1 mm in size (Vargas and Madin 2004). They then rapidly transfer this energy out of the euphotic zone through fast-sinking carbon-rich faecal pellets (Bruland and Silver 1981) and carcasses (Henschke et al. 2013). When salps occur in large swarms, the carbon flux from salp faecal pellets alone can be 10-fold greater than the average daily flux (Fischer et al. 1988). Despite the ecological importance of salps, there is a lack of data on basic ecological traits such as growth and mortality rates – primarily due to the difficulty in culturing salps in the laboratory (Heron 1972; Harbison et al. 1986; Raskoff et al. 2003). There is strong seasonality to the occurrence of salp swarms by some species (Licandro et al. 2006; Henschke et al. 2014), which suggests that the optimal temperature and chlorophyll *a* conditions driving growth rates would occur during spring when salp abundance is highest (Heron 1972; Licandro et al. 2006; Henschke et al. 2014). At this stage, it is difficult to understand the dynamics of salp populations, or model their distributions, using observational data. One way to enhance and validate the understanding of salp population dynamics is through numerical modelling. In this study two numerical models were used to explore the population dynamics of the ubiquitous small salp, *Thalia democratica.*

Materials and Methods

Two models were used to examine the temporal dynamics within a *Thalia democratica* population. The first was a Lefkovitch (1965) stage class matrix model, which was used to identify which life stage of *T. democratica* has the greatest influence on population growth. The Lefkovitch matrix is a stage-structured model of population growth, and is used to forecast future population states. It assumes that the population will either grow or decline linearly, and that each stage class will grow at the same rate. In a stable environment, the proportion of individuals in each stage class of a population tends toward a steady-state (stable-age) distribution (Lefkovitch 1965). The second model was a discrete-time size-structured population model, following cohorts of each life history stage at an hourly time step. It is size-structured because it uses size-dependent reproduction and mortality, where length (i.e. growth) is dependent on food (chlorophyll *a*) consumption and water temperature. Temperature and chlorophyll *a* concentration (phytoplankton abundance) were used as the external drivers in this model, given their known association with salp abundance (Heron 1972; Licandro et al. 2006; Deibel and Paffenhofer 2009). A 10-year simulation of the size-structured population model was run with a dynamic phytoplankton model to observe basic patterns and cycles within the salp population. To compare model outputs with observational data, and to evaluate predicted seasonal and yearly variation in salp abundance, simulations were also undertaken using a 10-year time-series (2003 - 2012) of satellite derived sea surface temperature (°C) and surface chlorophyll *a* (mg m^{-3}).

Results and Discussion

The size-structured population model in this study is the first *Thalia democratica* population model to incorporate food-based density dependence, and showed that temperature and chlorophyll *a* were appropriate drivers of *T. democratica* population dynamics. Juvenile oozoids were identified as the most influential life history stage to population biomass by both the Lefkovitch matrix and the size-structured population model. Higher population abundances were also associated with shorter generation times (faster growth rates). The sensitivity analysis performed on the size-structured population model suggested that salp abundance was particularly sensitive to the availability of chlorophyll *a* (the proportion of chlorophyll *a* relative to total salp consumption) instead of the overall chlorophyll *a* biomass. This study suggests that for a salp population to develop and sustain itself, higher proportions of juvenile oozoids and faster growth (shorter generation times) are necessary. These population dynamics are driven by changes in temperature and chlorophyll *a* that generally occur during winter and spring. Despite the lack of data available on salp ecological traits, this model is relatively insensitive to many of the unknown parameters. This study confirms the importance of changes in environmental conditions to population-level traits and the relative population biomass of *T. democratica*. This model can be applied to predict conditions that will most likely promote swarms of *T. democratica*. Future experiments should focus on understanding the relationship between salp growth rates and the phytoplankton food type, as well as the offset between phytoplankton blooms and salp swarms.

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