Chapter 2

Chlorophyll-a and the Supply Side Ecology: Lessons from the Rocky Shores

Ana Carolina de Azevedo Mazzuco and
Paula Kasten

Additional information is available at the end of the chapter

http://dx.doi.org/10.5772/68044

Abstract

The aims of this study were to summarize and describe the influences of phytoplankton on the larval cycle of rocky shore invertebrates, and to assess the relationship between fluctuations in chlorophyll-a concentration and the rates of larval processes. We carried out a mini review of the published data regarding the theme of the chapter, in which we described the ecological trends for the most common taxa and key species at small and larger spatiotemporal scales. The following topics were addressed: (i) the influence of phytoplankton on larval development, rhythms of larval release, larval quality, larval transport, settlement, and recruitment; (ii) the relationships between variations in chlorophyll-a concentration and the rates of larval processes; (iii) climate change on phytoplankton larva dynamics. The information presented here highlights the role of phytoplankton on rocky shore communities, as well as the importance of chlorophyll-a as a tool for modeling and forecasting the supply side ecology in rocky shore communities.

Keywords: phytoplankton, chlorophyll-a, supply side ecology, marine invertebrates, rocky shores, benthic-pelagic coupling

1. Introduction

Larval supply is the main source of new individuals to the populations of rocky shore invertebrates [1–3]. In these communities, larval success regulates how energy is transferred through the trophic web [4–6]; consequently, variations in the supply of propagules are the basis of trophic interactions at rocky shores [7, 8]. Since phytoplankton is the main food source for planktonic larvae of marine invertebrates [9], variations in phytoplankton biomass and diversity have significant influences on the larval cycle. Larval responses to the variability in phytoplankton abundance and diversity are species-specific. Larval fitness is influenced by environmental conditions experienced by adults and larvae [10, 11]. The effects of phytoplankton on larval dynamics depend on the phase of larval development [12–15] and may be stronger when variations in phytoplankton occur on temporal scales that larvae or breeding adults are able to respond [16]. The direct interaction between phytoplankton and the larval stages have short-term consequences for larval dynamics (e.g., Ref. [14]), and it might have long-term effects as well. Because of that, variations in the rates of the ecological processes of rocky shore invertebrates are commonly correlated with fluctuations in chlorophyll-a concentration in the ocean (e.g., Refs. [17–20]). These numerical relationships are important tools to ecological modeling, and may be used to improve stock management in some extent [21].

2. The role of phytoplankton blooms in reproduction timing and in the rhythms of larval release

In the rocky shore communities, filter feeders depend greatly on phytoplankton as their main source of food and its consumption results in energy for growth and reproduction [22]. It is common to find larger animals with higher fecundity rates at rocky shores located in areas of high primary productivity, as a response to the higher concentrations of phytoplankton, and thus, food availability [19, 23–25]. Different types of phytoplankton present distinct physiological qualities as food particles [26], thereby both the amount of phytoplankton in the water column and their diversity influence the reproductive traits in marine invertebrates.

But not only adults on the rocky shore depend on phytoplankton in order to survive, larvae produced by those organisms also rely on these microorganisms to develop and reach the juvenile phase [27]. As evolution drives maximum reproductive activity to happen when environmental conditions are the best for offspring development, food availability is one of the most important factors regulating reproduction and allowing adults to produce viable offspring. Thus, it is common to observe peaks of larval release by rocky shore invertebrates synchronized with phytoplankton blooms (e.g., Refs. [28, 29]). Some metabolites produced by phytoplankton are signs of favorable environmental conditions for the larval development, trigging the spawning activity of green sea urchins and blue mussels, for instance Ref. [28]. These animals perceive such chemical compounds as an indication of good food abundance, so synchronizing the timing of larval release with high abundance of phytoplankton would promote higher offspring survival. Barnacles, on the other hand, just need a physical contact with phytoplankton cells to trigger their spawning activity, and larger the phytoplankton cell is, the stronger is the response [28].

Therefore, the presence of phytoplankton may overcome other environmental factors in the regulation of reproduction timing and larval release [30]. Spring and summer are the main reproductive periods for rocky shore invertebrates at temperate and upwelling regions [31], as it is during these seasons that phytoplankton blooms occur. Mussels from the Baltic sea, for example, start to develop their gonads when temperature starts to drop in the beginning of winter; but its maturation and ripening processes proceed in a way that the animals are ready to reproduce at the same time that phytoplankton blooms occur in the beginning of spring [32]. Some barnacles are even able to maintain their fully developed nauplii in the mantle cavity until a high abundance of phytoplankton is perceived by the adults and only then, the nauplii will be released, a strategy that enhances the offspring survival due to the higher chance of facing a favorable feeding environment [33].

Similar reproductive timing was registered in the Indian coasts, where phytoplankton blooms occur during the monsoons and barnacles spawn their nauplii short after a break of the monsoon conditions [34]. However, these are not the best conditions for nauplii development, as these breaks stop and unfavorable monsoon conditions for larval development return soon after. Such misleading cue could result in lower recruitment rates for barnacles in this region. In subtropical coasts, peaks of larval production in intertidal barnacles are also preceded by high concentrations of chlorophyll-a in the water column [35]. On the daily scale, phytoplankton diversity might be as important as biomass in the regulation of larval release [36]. The presence of phytoplankton may overcome other environmental factors known to act as synchronization cues for reproduction timing and larval release [30].

3. How do changes in phytoplankton affect larval development from release to competency?

As seen in the previous section, phytoplankton has an important role in the reproductive success of marine invertebrates inhabiting the rocky shores. Part of this reproductive success involves the survival of larvae up to the juvenile stage, and a successful return to the benthic habitat is essential to the maintenance of rocky shore populations [2, 37]. It is straightforward to think that larval development is strictly linked to changes in phytoplankton community, since these cells are the main food items for marine planktotrophic larvae [9]. Because of that, the physiological quality of a larva would be determined in the plankton during its development and influenced directly by the phytoplankton in the water column. However, phytoplankton may change larval physiological quality much before that same larva is produced, through maternal effects, that is, when maternal individuals have the capacity to perceive the environment and manipulate the energy allocated for propagule production [38].

The amount of energetic reserves allocated to each propagule produced depends on the amount of energy the maternal individual can provide to its offspring. This capacity, in turn, is limited by the food available for the mothers, their perception of it, and their competency to gather and assimilate energy [38, 39]. For those marine organisms that produce lecithotrophic larvae, maternal effects are extremely important for shaping larval physiological quality because these larvae depend exclusively on the energetic resources from embryogenesis to survive [40]. If food ration is low, mothers can either preserve the energy acquired for their own metabolism and produce lower quality larvae (a selfish strategy, Ref. [39]) or invest all energy possible into their propagules, enhancing the survival potential of that higher quality larvae (an anticipatory strategy, Ref. [39]). In a scenario where maternal individuals are feeding mainly on phytoplankton, as the majority of filter feeding invertebrates in the rocky shores are, it is possible to understand the effect that oscillations in the quantity and type of phytoplankton available for these animals to feed has on larval quality.

However, most invertebrates that inhabit the rocky shores produce planktotrophic larvae. These larvae are submitted to transport and dispersion; they will feed in the plankton and will probably not experience the same conditions of the maternal environment, hypothetically reducing the necessity of energy transfer from mother to larvae. Thus, one could assume that the food environment experienced by mother would not impact the quality of the larvae produced. Interestingly, few authors have shown that, under stressful temperatures and low phytoplankton concentrations, maternal individuals of a tropical barnacle are able to manipulate the transfer of different types of fatty acids to their nauplii, a possible strategy to guarantee higher survival rates until this same nauplii encounters better food conditions in the water column [41]. Variations in the amount and type of phytoplankton available for planktotrophic larvae during development cycle interfere in the different larval traits, including in the success of metamorphosis into the juvenile stage. Larvae of gastropods [15, 16, 42], bivalves [36, 43, 44], and barnacles [45, 46] vary in size, development rate, and survival to the juvenile stage, in direct association with the quality and amount of phytoplankton offered them during their development.

Larvae must be able to survive from pelagic to benthic conditions and return to the rocky shore communities, in order to reach the adult phase. Settlement success and post-settlement survivorship are also matters of larval history [12, 15, 21], and many more. Contrary of what has been accepted for a long time, settlement of larvae in the benthic environment, and its metamorphose to the juvenile stage do not result in a "new beginning" for those individuals, but the feeding conditions experienced by larvae and its results on their physiological quality can be carried over to the next stage, and those individuals who faced low phytoplankton concentrations during its life in the plankton might become juveniles with lower growth and survival potential, influencing directly on the fate of that population [46–51].

4. Larval transport, settlement, and recruitment

Phytoplankton and larval abundances are sometimes controlled by the same oceanographic processes. Phytoplankton grows and reproduces under very specific environmental conditions, driven mainly by turbulence and nutrient availability [52]. Ocean movements, such as turbulence, vertical mixing, and currents, also affect larval abundance at small (e.g., Ref. [53]) and larger scales (e.g., Ref. [54]). Marine larvae take advantage of meso- and large-scale oceanographic features for transport and dispersion. These larvae have different responses depending on the velocity at that depth, assuming a specific swimming or orientation pattern (e.g., Ref. [55]). Besides, larvae are able to control their position in the water column and move together with the main current at that specific depth [56–58], what in turn might result in variability of larval supply in time and space [59]. Some oceanographic features that accumulate and transport marine invertebrate larvae are responsible for disturbing phytoplankton as well. For example, upwelling currents, which cause phytoplankton blooms by injecting cold nutrient-rich waters in the photic zone, may move larvae of rocky shore invertebrate to shallower waters (e.g., Refs. [60, 61]). Storms are other meteorological-oceanographic phenomena that disturb both chlorophyll-a concentration at the nearshore environments (e.g., Ref. [62]) and the larval abundances close to the rocky shores [63].

Settlement is a function of larval supply [64]. Consequently, successful settlement relies on larvae, which need to find suitable settlement sites and be able to metamorphose. In this phase of the larval cycle, biochemical and physical cues either stimulate or block settlement. The presence of biofilm on the rocks is very important for settling larvae, in particular for the sessile larvae, because biofilm may define if that is a favorable settlement spot. Biofilm characteristics control larval behavior during settlement [65]; as a result, settlement rates and the chlorophyll-a content in the biofilm are correlated [66]. Settlement may also be correlated with fluctuations in chlorophyll-a concentration just as a consequence of the coupling between phytoplankton blooms and larval release [12, 28]. When the latter situation is true, fluctuations in chlorophyll-a concentration and variations in settlement rates are time lagged in several days [35], what may depend on the time that the larva takes to fully develop. On the other hand, if larval supply and phytoplankton dynamics are controlled by the same features, as it was explained in the previous paragraph, peaks in chlorophyll-a concentrations and settlement rates will occur simultaneously (e.g., Ref. [20]).

Recruitment rates are regulated by fluctuations in the pelagic environment affecting larval supply [67]. Recruitment success means that settled larvae survived until they are able to reproduce. In the post-settlement period, phytoplankton availability in the benthos and pelagial can control the survivorship of settlers in rocky shore communities. Although most early recruits of rocky shore invertebrates are filter feeders, they do not have the same diet and they may be very selective [68], choosing determinate phytoplankton species as food items depending on their size. Changes in the phytoplankton community might benefit one or the other species depending on their feeding behavior [68]. Although the relationship between recruitment and chlorophyll-a concentration is influenced by species-specific characteristics, information on this subject is still relatively scarce for rocky shore invertebrates. Small- and large-scale spatial variability in recruitment of rocky shore invertebrates are related to local and regional gradients of chlorophyll-a concentration in the surface waters. Geographic barriers that restrict phytoplankton abundance are also responsible for setting geographical limits for recruitment at the rocky shores. Recruitment rates may vary in several orders of magnitude among regions and sites, potentially due to persistent gradients in phytoplankton availability, and in turn gradients in chlorophyll-a concentration (e.g., Refs. [69, 70]. Even sites within the same bay or just less than 1 km apart may present high contrasts in recruitment rates as a consequence of differences in the phytoplankton dynamics [71].

5. The numerical relationships between chlorophyll-a concentration and larval processes

Phytoplankton is a limiting resource to the survival of marine invertebrate larvae, as it was described throughout the chapter; consequently, chlorophyll-a concentration is a key factor regulating larval dynamics in rocky shore communities. Variations in larval processes and fluctuations in chlorophyll-a concentration tend to be highly correlated (e.g., trends of recruitment rates [69]). These correlations could be incorporated to ecological and numerical models to predict larval processes based on the values of chlorophyll-a concentration in the water (e.g., Ref. [72]). Although there are daily measurements of chlorophyll-a concentration in the ocean surfaces at a global scale, the levels of correlation between chlorophyll-a and larval dynamics are described only for a few species and some coastal areas.

Trends may be divided in groups according to the relationship between larval and phytoplankton dynamics. If the oceanographic processes promoting larval supply and settlement are also responsible for enabling phytoplankton growth and reproduction, variations in larval processes and in chlorophyll-a concentration may be positively correlated. On the other hand, if larval supply and settlement are enabled by less favorable conditions for phytoplankton, the fluctuations in the rates of larval processes may be negatively related to the concentrations of chlorophyll-a. Evidences of both trends were registered for rocky shore invertebrates in several regions [20, 21, 73]. Although the oceanographic and ecological processes that affect community dynamics are similar at the rocky shores, the correlation degrees between phytoplankton abundance and larval processes vary among sites and taxa. Correlations are stronger when reproduction and larval processes are regulated by the same mechanisms controlling phytoplankton blooms. For instance, in upwelling regions, these correlations are expected to be stronger [74], but may not be significant depending on the site (e.g., Ref. [75]). Barnacle and mussel recruits that occupy the same intertidal zone are not necessarily affected by fluctuations in chlorophyll-a concentration in similar ways, even presenting opposite trends in recruitment [21].

6. Climate change on phytoplankton larval dynamics

Climate change has important consequences for benthic-pelagic dynamics. Global warming has already caused alterations in the patterns of sea surface temperature and ocean currents, which in turn directly influenced the trends of phytoplankton abundance. Larvae and recruits of rocky shore invertebrates have to cope with such alterations in food availability concomitant to other climatic changes. The effects of phytoplankton and other climatic factors, such as water temperature, tend to be synergic [76]. Global warming conditions might not be positive for marine invertebrate larvae which, on one hand, survive under a wide range of conditions, but their fitness is highly influenced by changes in food availability. Short- and long-term consequences of climate change on phytoplankton larval dynamics were already detected for rocky shore communities. On the scale of decades, longer events of upwelling in the recent 20 years doubled the recruitment rates in some shores [77]. Results showed that, in small scale conditions, variability in phytoplankton has different effects on larval performance under different levels of climate change (Kasten, personal communication). However, how species will respond to multiple factors under *in situ* oceanic climatic conditions are hard to forecast, since information in larval dynamics are not available for most species and rocky shore systems.

7. Final considerations

Phytoplankton has a high regulatory potential in larval dynamics in the rocky shore communities. Rates of larval processes in rocky shore invertebrates are highly correlated with spatiotemporal fluctuations in chlorophyll-a concentration in the sea surfaces. The role of phytoplankton in larval dynamics at the community levels is not known, because information for most species is incipient. It is important to highlight that scientific improvements are needed to allow that use of variations chlorophyll-a concentration as a tool for modeling and forecasting the supply side ecology in rocky shore communities.

Author details

Ana Carolina de Azevedo Mazzuco[1,2]* and Paula Kasten[2]

*Address all correspondence to: ac.mazzuco@me.com

1 Federal University of Espírito Santo, Dept. of Oceanography, Vitória, ES, Brazil

2 Federal University of São Paulo, Institute of Ocean Sciences, Santos, SP, Brazil

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