Grazer-induced bioluminescence gives dinoflagellates a competitive edge

Prevett, Andrew; Lindström, Jenny; Xu, Jiayi; Karlson, Bengt; Selander, Erik

Published in:
Current Biology

Link to article, DOI:
10.1016/j.cub.2019.05.019

Publication date:
2019

Document Version
Publisher's PDF, also known as Version of record

Link back to DTU Orbit

Citation (APA):
Correspondence

Grazer-induced bioluminescence gives dinoflagellates a competitive edge

Andrew Prevett1,*, Jenny Lindström2, Jiayi Xu1, Bengt Karlson3, and Erik Selander1,*

Bioluminescent dinoflagellates grow at one third the rate of their competitors of equivalent size, such as diatoms [1]. Despite this disadvantage, dinoflagellates successfully persist within phytoplankton communities and even form large blooms during favourable conditions. One explanation for this paradox is that bioluminescence acts as a defence that reduces losses to zooplankton grazers, such as copepods [2,3]. Lindström et al. [4] found that the dinoflagellate Lingulodinium polyedra (F.Stein) J.D.Dodge increase their bioluminescence in response to copepodamides [5], polar lipids exuded by copepod grazers, allowing for a brighter flash when bioluminescent capacity is stimulated. Here, we show that copepodamide-induced bioluminescence in L. polyedra causes a marked shift in the grazing preference of the copepod Acartia tonsa Dana. L. polyedra goes from being the preferred prey when non-bioluminescent to near complete rejection when pre-treated with copepodamides to induce a higher bioluminescent capacity. High-speed and low-light-sensitive videos show how L. polyedra cells flash upon contact with the copepod and are subsequently rejected, seemingly unharmed (Videos S1 and S2). Instead, A. tonsa shows compensatory feeding on the alternative prey.

We established a dose-dependent increase in L. polyedra bioluminescence in response to copepodamides over time (Figure 1A). The bioluminescence capacity of L. polyedra was subsequently manipulated using combinations of light or dark adaption and the presence or absence of copepodamides. Copepod grazers (A. tonsa) were offered mixtures of L. polyedra together with alternative prey (Figure 1B), in which L. polyedra contributed only a small fraction to the phytoplankton composition, simulating a pre-bloom community (see Supplemental Experimental Procedures). We determined the relative proportion of A. tonsa diet from ingestion rate L. polyedra cells were the preferred prey, comprising 76% (non-induced) and 84% (induced) of A. tonsa diet despite L. polyedra contributing only 25% of the available prey biovolume (Figure 1C). This pattern reversed when L. polyedra cells were bioluminescent; the proportion of L. polyedra in the A. tonsa diet was comparable to its fraction in the community (24%) without copepodamide induction and decreased to near complete rejection (2%) when bioluminescence had been induced with copepodamides (Figure 1C). A. tonsa compensated for the reduced ingestion of L. polyedra by increasing ingestion of the alternative prey (Figure 1B). We filmed the rejection of bioluminescent L. polyedra by the copepod Temora longicornis Müller, using both high-speed and low-light-sensitive cameras (Figure 1D, Videos S1 and S2). Bioluminescence was first stimulated upon physical contact between dinoflagellate and copepod. The copepod then rejected the flashing cell followed by forceful beating with its swimming appendages (Figure 1E).

Our results suggest that the copepodamide-induced increase of L. polyedra bioluminescence effectively protects L. polyedra from grazers, which then compensate by increasing ingestion of less defended prey. Consequently, induced L. polyedra are predicted to gain an advantage, allowing them to thrive among faster-growing competitors. The defensive mechanism of dinoflagellate bioluminescence is thought to act as either aposematic colouration, a startle display, or a burglar alarm [2,3]. Our study does not determine which mechanism(s) conveys the defensive benefit. However, the forceful beating of the swimming appendages (Video S1) demonstrates an attempt to leave the flash location, suggesting the copepod is reacting to the flash as a startle display or burglar alarm. Although we cannot discount the influence of unknown induced-toxin production, we consider it unlikely. The L. polyedra strain we used is non-toxic and, moreover, it was still the preferred prey when non-bioluminescent and induced by copepodamides.

The dark environment used throughout the grazing experiment is representative of natural situations, as approximately 90% of copepod grazing occurs during the night due to diurnal vertical migration [6]. The grazing pressure on phytoplankton from microzooplankton is typically more intense than copepod grazing [7]. The combined grazing pressure from mesozooplankton and microzooplankton averages around 80% of the primary production [8]. However, microzooplankton mainly feed on prey smaller than L. polyedra [9]. Therefore, L. polyedra would be almost immune to grazing due to its size and induced-bioluminescence. Thus, we estimate that copepodamide-induced L. polyedra should be able to effectively compete with organisms that divide up to five times more often.

This finding predicts that the proportion of L. polyedra in the phytoplankton community should be contrary to the encounter-rate theory [10] and, instead, positively correlate to copepod biomass in situ. Monitoring data for L. polyedra proportional abundance and copepod biomass from the west coast of Sweden over a 10-year period (2007–2017) supports this prediction; the proportion of L. polyedra in the phytoplankton community is positively correlated to copepod biomass (Figure 1F). Although potentially influenced by other factors such as toxins or seasonal preferences, the positive correlation could also be attributed to copepodamide-induced bioluminescence. Thus, our study infers that instead of reducing L. polyedra populations, the presence of copepods may be key to L. polyedra success. Earlier studies may have underestimated this effect due to the use of grazer-free (non-induced) laboratory cultures. We suggest induced defences may give slow-growing dinoflagellates the edge they need to co-exist with faster-growing phytoplankton competitors.

SUPPLEMENTAL INFORMATION

Supplemental Information includes experimental procedures, references, acknowledgements and two videos and can be found with this article online at https://doi.org/10.1016/j.cub.2019.05.019.

REFERENCES

Figure 1. Grazer-induced bioluminescence reduces grazing losses, improving L. polyedra competitiveness.

(A) Dose response relationship of copepodamide-induced bioluminescence. L. polyedra bioluminescence increases after one hour of copepodamide exposure and reaches 250% increase after 48 hours (p < 0.001). Shaded error bars denote SD, n = 4. (B) A. tonsa ingestion rates (biovolume ingestion *10^6 µm^3 ind^-1 h^-1). Non-bioluminescent L. polyedra (left two bars) are consumed at a higher rate than the alternative prey regardless of copepodamide treatment (CA+, CA-, p < 0.001). A. tonsa exhibit compensatory feeding on the alternative prey when the L. polyedra bioluminescence is copepodamide induced (p = 0.013). Error bars denote SEM, n = 5. (C) Proportion of L. polyedra in diet (%). Increasing bioluminescence in L. polyedra is accompanied by a shift in A. tonsa prey preference. Non-bioluminescent L. polyedra (left two bars) comprise the majority of A. tonsa diet, regardless of copepodamide induction (CA+, CA-, p < 0.001). Bioluminescent L. polyedra are consumed in proportion to their concentration in the prey mixture, but copepodamide-induced bioluminescent L. polyedra are completely rejected by the copepods (p < 0.001). Error bars denote SEM, n = 5. (D) Overlaid frames from Videos S1 and S2. High-speed frames (left) showing the trajectory of an L. polyedra cell trapped in the feeding current of a copepod (T. longicornis) tethered to a human hair. Time between frames is 0.05 seconds and the whole sequence is 0.8 s. Low-light sensitive frames (right) showing corresponding sequence obtained at normal frame rate (30 fps). Time between frames is 0.03 s. (E) A conceptual model based on the results. Copepod prey is drawn in via the feeding current (grey area). Strongly bioluminescent prey is rejected whereas non-bioluminescent prey is consumed. Bioluminescent cells flash upon contact with the copepod and are subsequently rejected. Illustration by J. Heuschele. (F) Copepods and L. polyedra are positively correlated in nature. Copepod biomass (red histogram) and L. polyedra abundance normalized to total chlorophyll (ind total chlorophyll^-1, blue rings) are positively correlated in situ (R^2 adj. = 0.11, p < 0.001).