Stealth Effect of Red Shell Coloration in ~~Laqueus rubelus~~ *Laqueus rubellus* (Brachiopoda, Terebratulida) ~~on~~ at the Sea Bottom: An Evolutionary Insight into ~~the Prey~~ Predator-Prey Interactions

Comment [A1]: Please check the changes made to the title and use the revised version where required.

Abstract

The aim of this study was to examine the possible se~~r~~lective advantage ~~of~~ conferred by red ~~coloration in the~~ shell color of *Laqueus rubellus* (a terebratulid brachiopod) ~~was checked in terms of interactions of prey and~~ in predator-prey interactions. ~~The study was based on comparison of~~ We compared benthic suspension feeders ~~seen~~ found at a depth of about 130 m ~~depth~~ in Suruga Bay, Japan, ~~with peculiar reference to~~ focusing particularly on their visibility under visible and near-infrared light conditions. Our results showed that in visible light, ~~A~~almost all species exhibit~~ed~~ red coloration ~~under visible light~~, ~~while~~ whereas in infrared light, only the shell of *L.~~aqueus~~ rubellus* ~~was~~ is as dark ~~under infrared light, similar to~~ as rocks and bioclasts. ~~Provided t~~The functional eyes of macropredators such as fishes and coleoids~~, which~~ are specialized ~~as~~ for detecting light in the blue-to-green region of the visible spectrum,~~,~~ and predators like malacosteids have ~~even the~~ long-wavelength photoreceptors ~~of malacosteids,;~~- however, because of its unique shell coloration, *L.~~aqueus~~ rubellus* ~~should avoid~~ can possibly escape ~~both visible and infrared~~ detection -by these predators ~~living~~ at ~~in~~ the bottom of the sublittoral ~~bottom~~ zone under both visible and infrared light conditions. This ~~fact~~ suggests that terebratulids have evolved the ability to remain ~~more or less~~ essentially invisible ~~with~~ even as the ~~improvements of optic~~ visual detection abilities of predators have improved.

Comment [A2]: "Red" refers to a frequency of light, whereas "dark" refers to the intensity of light. Therefore, the contrast or comparison between *L. rubellus* and other species is not very clear.

Could this part of the sentence be revised as "only the shell of *L. rubellus* resembles rocks and bioclasts in color?

Comment [A3]: "Sublittoral bottom zone" may sounds slightly non-standard. I have revised this term assuming that you are referring to the sea bottom in the sublittoral zone, here and at subsequent instances.

If, however, you are referring to "the deeper sublittoral zone," please use this phrase instead everywhere.

1. Introduction

Competiti~~ve~~on ~~framework exists in~~ for resources and survival is characteristic ~~in~~ of the natural ~~settings~~ environments of most organisms, and this reciprocal interaction ~~is~~ has been the driving force ~~of~~ in evolutionary arms races ~~in evolution~~ [1]. Predator-prey ~~I~~interactions ~~of predator and prey~~ are ~~interesting for~~ of interest in the research on evolutionary arms races because the corresponding adaptations of prey and predators demonstrate how organisms ~~survive to~~ enhance ~~and/~~or modify their behavioral and functional performances within a biotic community for survival [2]. If either the predator or the prey ~~can't~~ cannot adapt to ~~relevant~~ changes in the other, extinction may occur.

Benthic suspension feeders, such as bivalves, brachiopods, and some echinoderms, have been exposed to predation ~~for~~ by macropredators throughout the Phanerozoic. They have developed several strategies ~~to~~for warding off~~-~~ potential predators. For example, some bivalves ~~exhibit~~ have thickened valves that physically ~~prevent~~ protect them against predator attacks ~~—physically~~ [3–5], while others ~~exhibit~~ have ~~magnified~~ enhanced burrowing or swimming ability [6–8]. Crinoids and ophiuroids have evolved the ability to ~~automize~~ autotomize and regenerate their tentacles ~~that~~ when they are bitten off by predators [9–11]. ~~On the contrary~~In contrast, rhynchonelliformean brachiopods ~~represent~~ are immobile sessile organisms with thin shells [12, 13] ~~in which neither~~ and do not appear to have evolved physical, physiological, ~~nor~~ or behavioral defenses ~~have not evolved~~ against predators.

~~Of~~ Among ~~the~~ rhynchonelliformean brachiopods, terebratulids are known to be the most successful group, having ~~lived~~ survived from the Devonian to the modern era~~s~~. They ~~possess~~ have semi-circular valves and a pedicle for attachment to a hard substratum. ~~As against the~~Unlike ~~simple look of~~ other rhynchonelliformean brachiopods that have a dull appearance, ~~the shells of~~ many living terebratulids have shells ~~exhibit~~ with distinctive ~~colors~~ coloration (pink, orange, red~~-~~, and red-brown ~~pigments~~). ~~It has been taken for granted that the~~ Such characteristic shell colors ~~of living terebratulids~~ have been believed to ~~may exhibit~~ have ~~some~~

a predator~~-~~deterrent effect [14, 15], ~~but antipredator function of colors~~ although no study has clarified how these colors serve this function~~has not been explained~~.

In our previous experiments ~~in our laboratory~~ [16], we ~~have~~ observed that the terebratulid brachiopod *Laqueus rubellus*, which is empire red~~ in color~~, is difficult to ~~be seen by~~ spot using a video-scope under near-infrared illumination. In order to understand how terebratulid brachiopods thrive at the bottom of the sublittoral zone, ~~Based on subsequent observations~~ we ~~using~~ used visible and infrared light~~,~~ ~~we describe~~ to study the optical properties of the shell of ~~this species~~ *L. rubellus* and determine its ecological significance ~~in order to explain why terebratulid brachiopods thrive on the sublittoral sea bottom~~.

2. Materials and methods

2.1 ~~Sample~~ Sampling location

Benthic organisms, including *L.~~aqueus~~ rubellus*, were collected ~~with~~ using a dredge (wideth, 90 cm) at a depth of 130–140 m off Osezaki in ~~the~~ Suruga Bay (Figure 1). Our sampling site was located on the outermost shelf bottom and contained mud and fine-grained sand with abundant debris, such as rounded gravel and bioclasts. The environmental conditions (e.g., water temperature, ~~dissolved oxygen,~~ pH, and the concentrations of chlorophyll a, dissolved oxygen, and nutrients~~ concentrations~~) at the bottom of inner Suruga Bay are ~~same~~ stable over a wide area, but *L.~~aqueus~~ rubellus* ~~is abound~~flourishes only around the sublittoral shelf edge [16, 17].

Comment [A4]: Please check if you need to mention the model and manufacturer details.

Comment [A5]: The width of what are you referring to? The mouth? Please clarify.

Comment [A6]: Please check if you should provide the geographic coordinates of the sampling location.

Comment [A7]: I'm slightly unsure what "outermost" shelf bottom refers to since this is an unconventional term. Please check if this can be revised as "bottom of the outer shelf."

Comment [A8]: This does not appear to be a standard term in this field. Did you instead mean "edge of the outer shelf"?

2.2. Materials

Figure 2 shows the number of living benthic macroorganisms in the recovered dredge sample. ~~Among the suspension feeders,~~ *L.~~aqueus~~ rubellus*, the stalked crinoid *Metacrinus rotundus*, and ophiuroids were the dominant ~~species~~ suspension feeders. In contrast to ~~the~~ free-living

M.~~*etacrinus*~~ *rotundus* and ophiuroids, all living *L*.~~*aqueus*~~ *rubellus* individuals were attached to bioclasts or rock debris ~~using~~ through their attachment organ, the pedicle. Our samples had low numbers of ~~T~~two ~~species of~~ bivalves species, ~~—~~ *Cryptopecten vesiculosus* and *Nemocardium samarangae*, ~~—~~ and scleractinian corals ~~occurred only in low numbers in our samples~~.

2.3. Observation Methods

~~We aimed t~~To examine the differences in the visibility of ~~among~~ the recovered benthic organisms, ~~so they were~~ we photographed them in visible and infrared light while they were resting in a white ~~seawater~~ tray containing seawater. For photographs ~~Under~~ in visible light ~~conditions~~, we used a digital camera (D70, Nikon) and an incandescent lighting system (PRF-500WB, National). ~~To~~ For ~~visualise~~ photographs in infrared ~~illumination~~light, we ~~the organisms were filmed with~~ used a video-scope (DCR-TRV20, SONY) under near-infrared light ~~of around~~ with a ~~800 nm~~ wavelength of around 800 nm ~~(DCR-TRV20, SONY)~~, and ~~the~~ infrared images were captured as video frames. Hereafter, ~~T~~the ~~results~~ visibilities recorded ~~from~~ using these two methods ~~are~~ have been referred to as ~~the~~ natural and infrared visibilities, respectively.

Comment [A9]: Please mention the city and country of all the manufacturing companies mentioned in the Materials and Methods section.

If the manufacturer is US-based, the city and state generally suffice.

2.4. Quantitative Analysis of Grayscale Images

For the quantitative ~~examination~~ determination of visibility ~~for~~ as recorded in infrared images, we obtained ~~the~~ a grayscale histogram ~~of grayscale color~~ using the image~~- analysing~~analysis ~~software~~ program ~~called~~ ImageJ. The image of each animal was taken with a distance of 1 me~~tre~~ ~~distant~~ between the animal and ~~from~~ the video-scope. Animal outlines in the grayscale images were drawn ~~by~~ using the polygon-selection tool ~~of polygon selections~~ in ImageJ, and then the area inside the outline was analy~~s~~zed to obtain a 256~~-~~shade~~s~~ ~~of~~ grayscale histogram.

3. Results

3.1 Natural Visibility ~~(under Visible Light)~~

Figures 3(a), 3(b), and 3(e) show photographs taken under visible light conditions. All organisms observed ~~are~~ were red ~~colored~~ (Figures 3(a) and 3(b)) except ~~the crinoid~~ *M.~~etacrinus~~ rotundus* (Figure 3(e)), which ~~is~~ was white to ivory ~~in color~~. *L.~~aqueus~~ rubellus* ~~has~~ had a thin shell that ~~is~~ was ~~colored~~ orange to empire red and ~~is~~ was transparent enough to ~~see~~ reveal the organism inside (Figures 3(a) and 3(b)). The color of ~~L~~larger shells ~~tend~~ tended to be darker ~~in color~~. The shells of *C.~~ryptopecten~~ vesiculosus* and *N.~~emocardium~~ samarangae* ~~are ornamented with~~ had a ~~mosaics of~~ red~~-~~and~~-~~white ~~colors~~mosaic pattern. The coloration patterns ~~of coloration exhibit~~ showed interspecific variation (Figure 3(a), Figure 3(b). The shell of ~~Cryptopecten~~ *C. vesiculosus* ~~is~~ had a patchy ~~colored by~~ wine~~-~~red ~~pigment in a patchy fashion~~pattern, while that of *N.~~emocardium~~ samarangae* ~~is ornamented with~~ had several radial orange bands. ~~The s~~Scleractinian corals ~~has~~ had reddish soft parts within a white skeleton (Figure 3(a)). The upper sides of all ophiuroids ~~show~~ were red to reddish-brown ~~colors~~, while the lower sides of their bodies ~~are~~ were whitish (Figures 3(a) and 3(b)).

3.2. Infrared Visibility (~~u~~Under Near-Infrared Light)

Figures 3(c), 3(d), and 3(f) show photographs taken in ~~under~~ infrared ~~visibility~~light~~, which are compared with Figures 3(a),3(b), and 3(e), respectively~~. Unlike ~~natural visibility~~the images taken in visible light, infrared images ~~displayed~~ revealed a difference in color intensity among taxa. ~~As was apparent from the infrared images,~~ They showed that the shells of *L.~~aqueus~~ rubellus* were the darkest and ~~were similar in~~ their coloration resembled that of ~~to the attached~~ bioclasts and rock fragments (Figures 3(c) and 3(d)). ~~The s~~Shell darkness tended

Comment [A10]: Since all these figures appear together with those taken in infrared light and obviously allow for visual comparison, this part of the sentence is redundant.

to increase with shell length. ~~Meanwhile~~In contrast, the shells of ophiuroids and ~~the crinoid~~ *M*.~~*etacrinus*~~ *rotundus* were the brightest~~, contrasting sharply with the coloration of *Laqueus*~~ (Figure 3(c): black arrowhead). Molluscan shells were gray in color but somewhat faint compared to *L*.~~*aqueus*~~ *rubellus*. Sediment particles that were trapped in pectinid ribs were dark gray, ~~as were~~ resembling bioclasts and rock fragments (Figures 3(c) and 3(d): white arrowhead).

3.3. Grayscale Image Analysis

Figure 4 shows a 256~~-~~shade~~s~~ ~~of~~ grayscale histogram for selected individuals. Counts of each grayscale plot among the individuals are significantly different (*P* < 0.001, pairwise ANOVA). The ~~M~~mean values ~~in the case of~~ for *L*.~~*aqueus*~~ *rubellus* were around 40, ~~that~~ which ~~was~~ were the lowest (darkest) among the animals. The mean values observed for ~~B~~bivalves, ophiuroids, and scleractinian corals ~~exhibit~~ were similar ~~mean values, the range of which were~~ (around 51–62, 52–77, and 58, respectively), but those of bivalves were slightly lower than those observed for the other two groups. The histograms ~~in the case of~~ obtained for two crinoid *Metacrinus* show a gentle convex shape, with the peak occurring at around 90 ~~in~~ for ~~Metacrinus 1~~ one individual and around 160 ~~in~~ for ~~Metacrinus 2~~ the other.

Discussion

4.1. Optical Evasion from Macropredators

For sessile benthic organisms, ~~Not being~~ remaining undetected by predators is an efficient survival strategy ~~of decreasing the mortality rate of sessile benthic organisms~~. The reddish coloration of the benthic organisms we studied ~~here~~ may help them ~~not be detected~~ avoid detection by macropredators. This phenomenon can be explained by the optical properties of visible light.

Comment [A11]: When you say "faint," do you mean that their color intensity was lower? If yes, please revise this sentence as follows:
"Molluscan shells were gray but had lower color intensity than that observed for *L. rubellus*."

Comment [A12]: This statement is slightly unclear. Could you specify which individuals you are referring to and what you mean by counts of plots?

Comment [A13]: The means of which values are you referring to? Color intensity? Please clarify.

Comment [A14]: This is slightly unclear. Do you mean two individuals belonging to this species? If so, please revise this as "two *M. rotundus* individuals."

Comment [A15]: You have not used these designations (Metacrinus 1 and Metacrinus 2) before. I've revised this sentence to avoid confusing readers. Please confirm that this is indeed what you meant.

~~The reddish appearance of a~~An object appears red ~~means that~~ if the red portion of the visible spectrum is reflected by its surface~~,~~ while other wavelengths ~~of visible light~~ are absorbed. Red light has the longest wavelength~~s~~ in the visible spectrum~~,~~ and ~~its~~ the lowest energy ~~is lower~~ [18]. Such low-energy light is preferentially diffused under water, because of which ~~resulting in a loss of~~ the red ~~optical element~~ component of visible light is lost at the bottom of the sublittoral zone [18, 19]. Benthic organisms that appear reddish under visible light conditions ~~therefore, would~~ will therefore appear black ~~in color~~ at the bottom of the sublittoral ~~bottom~~zone. *L.* ~~*aqueus*~~ *rubellus* and organisms associated with it on the outer shelf of Suruga Bay ~~should~~ must appear dark in color in their natural habitat, making it possible for them to ~~go~~ remain ~~unrecognised~~ undetected by ~~the eyes of~~ macropredators such as fish and squid [20–24].

~~Unlike the natural visibility of benthic organisms, t~~Their contrasting infrared visibility suggests the possibility of another survival strategy against predators. Almost all deep-sea fishes have eyes that are sensitive to light in the blue-to-green visible spectrum because these wavelengths can penetrate deep ~~deeply~~ into the ocean [24]. Malacosteids, however, have retinal pigments that are particularly sensitive to red light, and these fishes have been compared to snipers armed with infrared “snooperscopes” at night [25, 26]. One such predator, the malacosteid *Photostomias guernei*, ~~is reportedly~~ has been reported to be present in the seas around Japan, as well as in Suruga Bay [27, 28]. However, ~~it is unlikely that~~ *L.* ~~*aqueus*~~ *rubellus* is likely to remain undetected ~~affected by~~ even by deep-sea fishes with ~~the~~ long-wavelength sensitivity ~~of deep-sea fishes, as it shows the similarly dark appearance of~~ because it resembles dark rocks and skeletal fragments. The appearance of *L.* ~~*aqueus*~~ *rubellus* shells under infrared light suggests that ~~Laqueus~~ it has evolved a survival strategy in which its shell behaves optically like a nonliving object ~~on~~ at the bottom of the sublittoral ~~bottom~~zone.

Comment [A16]: When you say organisms associated with *L. rubellus*, are you referring to other brachiopods or other organisms found in the sublittoral zone? Please clarify.

4.2. ~~One Likely Possibility for the~~ Possible Evolutionary Arms Race ~~b~~Between Sessile Benthic Organisms and Macropredators

The camouflage strategy of *L.~~aqueus~~ rubellus* ~~to~~ for ~~the~~ evading detection ~~abilities of~~ by macropredators suggests the presence of an intimate and evolutionary interplay or arms race~~.~~, which in turn suggests ~~This leads to~~ several evolutionary scenarios, as discussed below.

L.~~aqueus~~ rubellus and ~~the vision systems of~~ its predators may have experienced selective pressure—the former for developing optical evasion ability and the latter for developing ~~detection ability of the~~ photoreceptor ability to detect long-wavelength light~~, respectively~~. Each enhancement ~~of~~ in one group of organisms ~~one~~ exerts selection pressure for developing a compensating enhancement ~~of~~ in the other. This is a form of coevolution [1, 29]. In addition to this predator-prey interaction, brachiopod survival ~~on~~ at the sea bottom is also affected by competition among benthic organisms, which belong to a similar guild [30–32]. ~~As a consequence~~Consequently, several species of the benthic community are involved, and their abundances are not independent. This corresponds to the concept of "diffuse (or guild) coevolution" [1].

~~In the modern sea, h~~Highly efficient vision systems are ~~evident~~ seen in teleost fishes and coleoid cephalopods, both of which originated in the early Mesozoic and drastically diversified during the Jurassic [33–35]. Spiriferi~~n~~ids, which were one of the most ~~thrived~~ successful brachiopod groups and showed no indications of color [36], became extinct soon after the diversification of ~~the~~ macropredators, even though they had ~~possessed certain morphologies that are considered to be~~ developed ~~exquisite~~ morphological adaptations ~~for~~ of the feeding system that are considered exquisite [37–41]. On the other hand, terebratulids did not become extinct but began to diversify and persisted to the modern era [42]. Considering the improvement over time in the predation abilities of macropredators [43], our results suggest that the red coloration and infrared opacity of terebratulids is an effective adaptation

Comment [A17]: It's not clear what the species of the benthic community are involved in. Did you perhaps mean that this predator-prey coevolution is not restricted to *L. rubellus* but also occurs in other species of the benthic community from the same guild since they are competitors exposed to the same pressures?

Comment [A18]: This section of the sentence is not very clear. Did you mean that their coloration did not evolve over time?

strategy ~~to life~~ for survival at the ~~sublittoral~~ bottom of the sublittoral zone, even though these organisms are immobile and seemingly defenseless.

~~The~~ This possible relationship between ~~the~~ coloration and ~~the apparent evolutionary trend~~ evolution motivated us to consider the etiology of visibility and its evolution. Through biochemical analysis of intracrystalline proteins in the terebratulid shell, Cusack et al. [14] identified the N-terminal amino acid sequence of a 6.5~~-~~kDa protein ~~that may~~ whose function may be to embed a red carotenoprotein in the shell. In this study, the shells of larger ~~Because~~ *L.* ~~*aqueus*~~ *rubellus* individuals ~~shells examined here~~ tended to ~~exhibit~~ have more vivid red coloration ~~in larger individuals,~~; this indicates that the red pigment is ~~probably~~ deposited gradually during the growth of the secondary shell layer. Because the 6.5~~-~~kDa protein has been extracted from different shell layers in each species, it seems to represent a phylogenetic constraint [44].

Comment [A19]: "Etiology" is the study of causes of diseases and does not appear relevant in this context. Please check if you can revise this section as "the evolution of visibility."

~~Enigmatic problems remain in this~~ Our hypothesis is yet to explain some problems, namely, the origin of infrared opacity and its evolution. Further studies will be needed to understand how terebratulids in the marine benthic community have evolved in response to increasing predation pressures.

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Comment [A20]: Please add the volume number.

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Comment [A22]: Please add the year of publication.

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