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Sea Urchin Covering Behavior: A Comparative Review

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<http://dx.doi.org/10.5772/intechopen.68469>

Abstract

Covering behavior in sea urchins is an important aspect of many species' ecology and has a variety of perceived benefits including food source, mechanical defense, shielding from sunlight, and predator protection. The goal of this study was to determine whether an urchin genus's main benefit from this form of crypsis is correlated with either phylogenetic relationships or environmental factors (ocean depth and climate). To evaluate this hypothesis, a literature review was conducted on 15 urchin genera that use the covering reaction. The function of this behavior for the aforementioned genera was both mapped onto a phylogeny and evaluated, based on the climate and depth of the genera's habitats to determine whether the patterns exist. The results suggest that phylogenetic relationships provide a more functional predictive tool for determining the purpose of covering in an urchin genus than its environment. This conclusion is useful for understanding the biology of sea urchins as well as how the covering reaction relates to the many other cryptic behaviors used by animal species.

Keywords: crypsis, ecology, protective behavior, phylogenetics

1. Introduction

The crucial roles that sea urchins play in aquaculture and coral reef ecosystems warrant the study of their ecology and behavior [1, 2]. Many species exhibit a special form of crypsis called covering behavior [3–5], also known as “dressing” or “heaping” [6] (**Figure 1**), which involves securing algae, rocks, and other items in their environment to their tests using a combination of spines and tube feet [7]. While the mechanics of this reaction are well understood, the reasons for it remain nebulous.

Two conflicting hypotheses exist with respect to this form of crypsis: the “reflexive” hypothesis, which proposes that the covering reaction is automatic, and the “functional” hypothesis, which suggests that heaping is used for specific purposes. The reflexive hypothesis has been supported

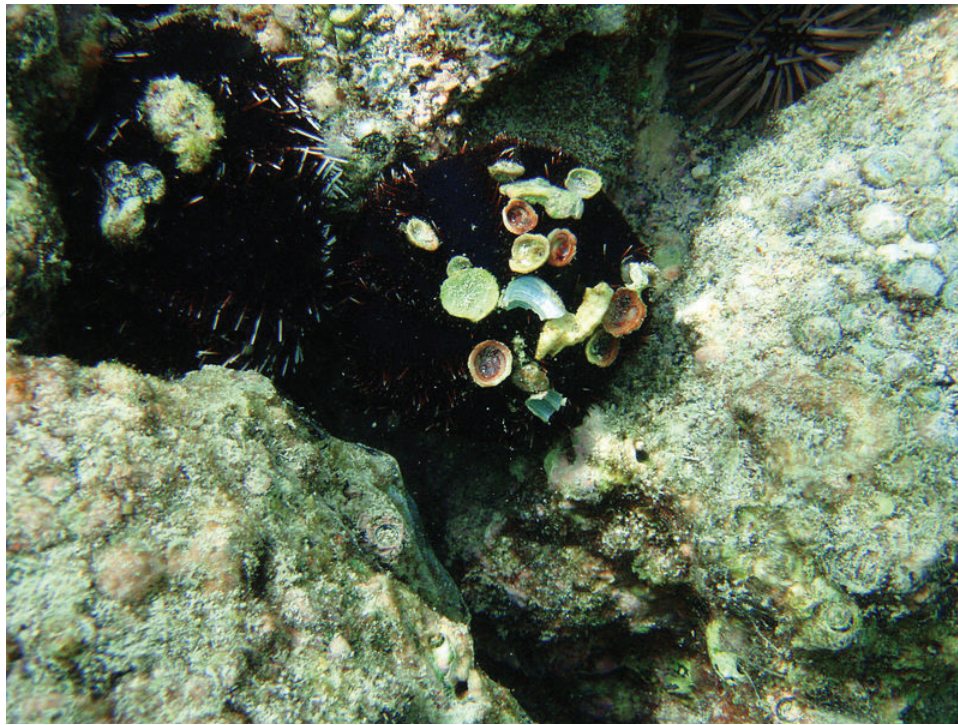


Figure 1. A covered sea urchin. An example of the covering behavior of the sea urchin *Tripneustes gratilla* in Hawaii, USA.

by several studies. One such study examined the covering behavior of *Strongylocentrotus* urchins and concluded that the reaction is innate because it is not affected by inbreeding or urchin age [8], suggesting that covering might not be decision based. It has also been noted that the stimuli often seemed to promote more activity in the animal [9]. Another study argued that the movements involved in moving covering material from one part of the test to another were indistinguishable from the urchin's movement when righting itself if flipped over, which is reflexive [10]. Based on these results, these studies concluded that covering is merely a by-product of additional movement.

In contrast, the functional hypothesis theorizes that covering behavior is a conscious decision by sea urchins. Many species have been shown to choose when to cover and to what extent, based on a variety of environmental stimuli [4, 5, 7, 11–13]. One study noted the differences between both species and individuals in the amount of covering even in similar environmental conditions, which suggest that this crypsis is a decision, as otherwise all urchins would cover themselves to an equal extent [14]. Additional research has found that urchins choose objects of particular sizes with which to cover themselves [15], a result that would not be expected were the action reflexive. While both hypotheses have convincing evidence, the functional hypothesis has been assumed for the current study based on the variety of species-specific reactions to environmental stimuli, in addition to the fact that not all urchin species use heaping behavior.

Covering can provide sea urchins with protection from predators [16], mechanical damage (wave surge or floating debris) [11, 17], overexposure to light [7], or can act as a food source [18]. However, no prior studies have considered a relationship between sea urchin biology and the reaction. Such a relationship would provide both a framework to understand why such a variety of applications for covering have been observed and a tool for predicting what function crypsis serves in an unstudied species of urchin.

One source for such a framework might be environmental considerations. The reason for crypsis and the extent to which it is seen differs widely between species [14]. However, the behavior is also affected by size and mobility [19] as well as the energetic cost of covering [20]. It is possible, then, that the differences in the covering reaction between species are due to variations in animal size and mobility as well as energetic costs, rather than genetics. In this case, the reason for covering might be deduced not by a species' evolutionary relationships, but rather by the climate and ocean depth at which it is found.

It has been shown, though, that differences in the heaping reaction persist even for species such as *Strongylocentrotus purpuratus* and *Paracentrotus lividus* that share very similar environments [21]. This points to the possibility that covering, and perhaps, a particular genera's reason for using the behavior, has an evolutionary basis. The covering behavior of some sea urchin genera has been previously mapped onto a phylogeny of sea urchin species which demonstrated that it likely evolved once and was subsequently lost from the genera *Glyptocyphus* and in the *Colobocentrotus-Heliocidaris* clade [5] (**Figure 2**). The finding that species exhibiting heaping are closely related suggests that some genetic basis does exist.

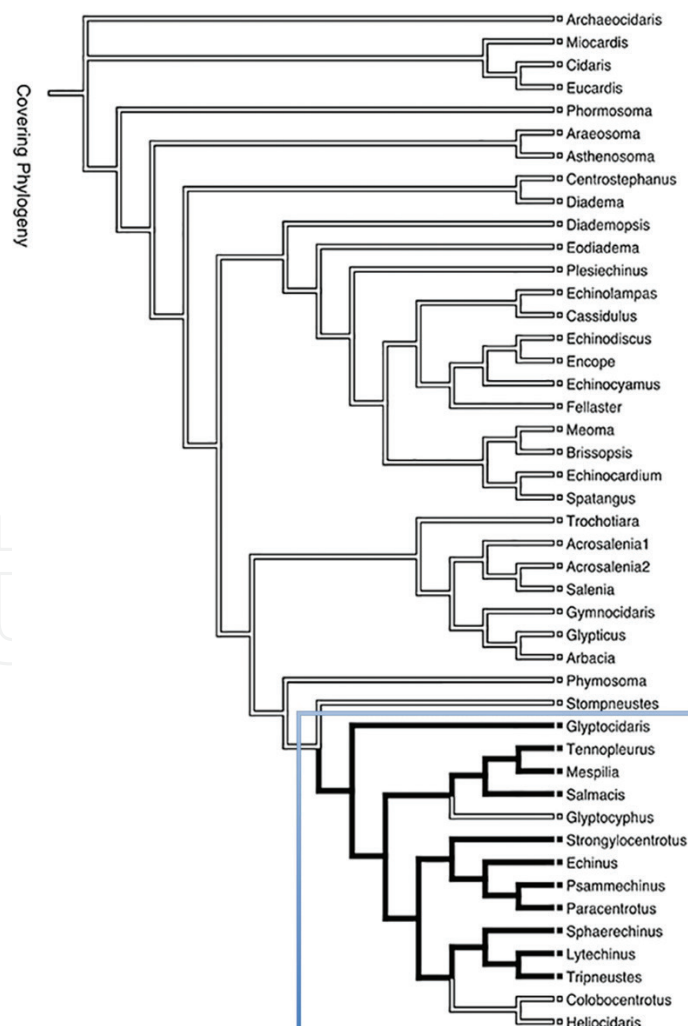


Figure 2. Sea urchin phylogeny. A phylogeny of urchin genera courtesy of Ziegenhorn (2016). The species that cover are noted in dark lines within the box.

The purpose of this study was to review all existing studies of cryptic sea urchins to determine whether covering behavior can be predicted from either (1) the depth and climate within which an urchin resides (the species' environment), or (2) the species' relationship to other cryptic sea urchins.

2. Methods

Studies of 15 urchin genera were researched to determine the reason for their cryptic behavior, chosen based on a previous paper that researched which species of sea urchins use covering [5]. The genera considered were *Glyptocidaris*, *Temnopleurus*, *Mespilia*, *Salmacis*, *Strongylocentrotus*, *Echinus*, *Psammechinus*, *Paracentrotus*, *Sphaerechinus*, *Lytechinus*, *Tripneustes*, *Pseudoboletia*, *Toxopneustes*, *Pseudechinus*, and *Genocidaris*.

Four main reasons for covering were considered: predator defense, protection from mechanical damage (wave surge/floating debris), use as a food source, and protection from bright light (sunlight/UV). When it was possible, this list was narrowed down to one main use for crypsis, though in some cases, two uses had equal evidence and were both noted as main covering reasons. For some genera (*Pseudoboletia*, *Genocidaris*, *Psammechinus*, *Mespilia*, and *Temnopleurus*), it was impossible to determine the reason for covering behavior. In this case, the explanation was considered unknown.

2.1. Phylogenetic methods

To determine whether evolutionary relationships provide a solid framework for urchin's covering motivation, the use of heaping by eleven of the 15 urchin genera was mapped onto an existing phylogeny [5] (**Figure 2**). The genera included in the phylogeny were *Glyptocidaris*, *Temnopleurus*, *Mespilia*, *Salmacis*, *Strongylocentrotus*, *Echinus*, *Psammechinus*, *Paracentrotus*, *Sphaerechinus*, *Lytechinus*, and *Tripneustes*.

2.2. Environmental condition methods

To consider whether the environmental conditions are the best indicator of covering purposes, an additional four urchin genera for which the reaction has been noted (*Pseudoboletia*, *Toxopneustes*, *Pseudechinus*, and *Genocidaris*) were reviewed. A most likely reason for crypsis in these four genera was assigned and information on the depth and area of the world in which all fifteen genera have been found was determined from a previous study [22]. Because of its wide range of climates and ocean depths, the genus *Strongylocentrotus* was divided into three species (*S. purpuratus*, *Strongylocentrotus intermedius*, and *Strongylocentrotus drobachiensis*) that each had different climate and depth ranges. These data, combined with the most likely explanation for covering behavior, were used to create two tables: one for ocean depth and one for ocean climate. Ocean depth ranges were divided into five categories: 0–50, 0–100, 0–250, 0–1000, and 0–1200 meters. Ocean climate ranges were divided into four categories: tropical, tropical/temperate, temperate, and temperate/polar. Two additional maps were created to

illustrate the range of each species with regard to various sea surface temperatures (SST), and this map was modified to show the different uses of heaping in regards to SST.

3. Results

3.1. Covering as sunlight/UV protection

Protection from sunlight was the most common reason for using the behavior in the urchin genera considered, with six of the total fifteen genera covering primarily for this reason. *Lytechinus* urchins tested in the lab react to UV light and direct sunlight, but discard covering in darkness, exhibiting a diurnal pattern of crypsis [15, 23–25]. Because urchins discard covering in darkness, but tropical urchins are often nocturnal, it was concluded that covering was likely not a source of shelter from predation [25]. This study also found that urchins covered in response to wave surge regardless of the light condition [25]. However, other studies of *Lytechinus* support the hypothesis that their cryptic behavior is primarily light-based as it is affected by light in the absence of wave surge action [15, 25]. In addition to this, one study noted that covering might even be a mechanical disadvantage, as it makes it more difficult for the urchin to right itself, and there is no evidence that heaping provides additional mechanical defense [25].

For *Tripneustes* urchins, it has been found that albino urchins cover more than pigmented specimens and that both albino and pigmented *Tripneustes* urchins heap more in response to sunlight in lab settings [5, 26, 27]. In the field, *Tripneustes* urchins cover more when exposed to light [27] and show no preference for being under rocks that might better protect them from predators and wave surge [5]. Additionally, *Tripneustes* urchins do not prefer either algal or coral materials, which suggest that cover is not an important food source and is not used to weigh urchins down [5].

Several other urchin genera also likely cover to shelter themselves from overexposure to sunlight. *Salmacis* urchins have been found to heap significantly more in response to light, particularly UV-C [12]. Light protection also remains the dominant explanation for the *Paracentrotus* heaping reaction, and lab studies of covering have shown that *Paracentrotus* urchins avoid bright light if possible [4, 28]. It has also been suggested that the behavior has little to do with predators, as *Paracentrotus* urchins have been observed to cover most in the summer when their predators are least active [4, 28]. Some studies have considered floating debris and food source as factors that affect the covering reaction [3, 11], but in both studies, the effect of light was not considered. For *Sphaerechinus* urchins, an ability to cover and a sensitivity to UV light have been noted, which makes it likely that light is the reason for their cryptic behavior [29, 30]. For *Strongylocentrotus* urchins, UV light seems to be one of two main reasons for the reaction along with using covering materials as a food source. Previous studies of this genera have suggested that the urchins in the lab heap more in response to UV-A and UV-B rays [7], and that males in particular show a strong response when exposed to higher intensities of sunlight [31].

3.2. Covering as mechanical protection

Of the urchin genera considered, two were found to cover primarily for mechanical protection (*Glyptocidaris* and *Toxopneustes*). *Glyptocidaris* urchins show increased cryptic behavior in the lab when sand is poured into their environment, which suggests that these urchins cover themselves to shield from floating debris [13]. Another study noted that starved *Glyptocidaris* urchins continue to cover themselves, which suggests that the behavior is important for survival, as it persists even when the energetic cost of maintaining it is fairly high [32]. *Toxopneustes* urchins have been observed in the field covering themselves to differing extents in relation to their body size, as if to achieve a certain heft that keeps them secure on rocks [33]. This same study also noted that urchins in areas of highest current have a higher covering to body weight ratio and concluded from these observations that these urchins use the reaction to defend themselves from wave surge [33].

3.3. Covering as a food source

Two urchin genera, *Echinus* and *Strongylocentrotus*, use covering as a food source. *Echinus* sea urchins have been observed using primarily algae species that are a part of their diet as cryptic material, and from this, it has been concluded that heaping is likely a way of capturing food, as these urchins are deep enough in the ocean (up to 1200 meters) that visible light or hydro-dynamics seem less likely explanations for the reaction [34, 35]. *S. purpuratus* urchins do not show a diurnal pattern of covering, and, though they seem to cover in areas with more wave surge, their behavior is most likely linked to food capture as their hold on the rocks is strong enough to defend them from strong currents [18, 36].

3.4. Covering as predator protection

For *Pseudechinus* urchins, cryptic behavior seems to be an effective method of predator defense in the field [16]. One study of *Strongylocentrotus* urchins found that covering can protect urchins in the lab setting from predation by crabs for short periods of time, up to 2 hours [1]. However, a more recent experimental study of these urchins found no correlation between amount of covering and presence of predators, suggesting that protection of this type is coincidental rather than a functional reason for heaping in this genera [37].

3.5. Covering for unknown reasons

While both *Pseudoboletia* and *Genocidaris* urchins have shown crypsis [38, 39], no information was found regarding the reasons for this behavior in either genera. For *Psammechinus*, *Mespilia*, and *Temnopleurus* urchins, phototaxis has been noted but the covering reaction has not been experimentally studied [6, 7, 40–42].

3.6. Covering by evolutionary relationship

The various reasons for urchin heaping were mapped on to the existing phylogenetic tree (Figure 3). As previously noted, *Lytechinus*, *Tripneustes*, and *Sphaerechinus* urchins all cover to

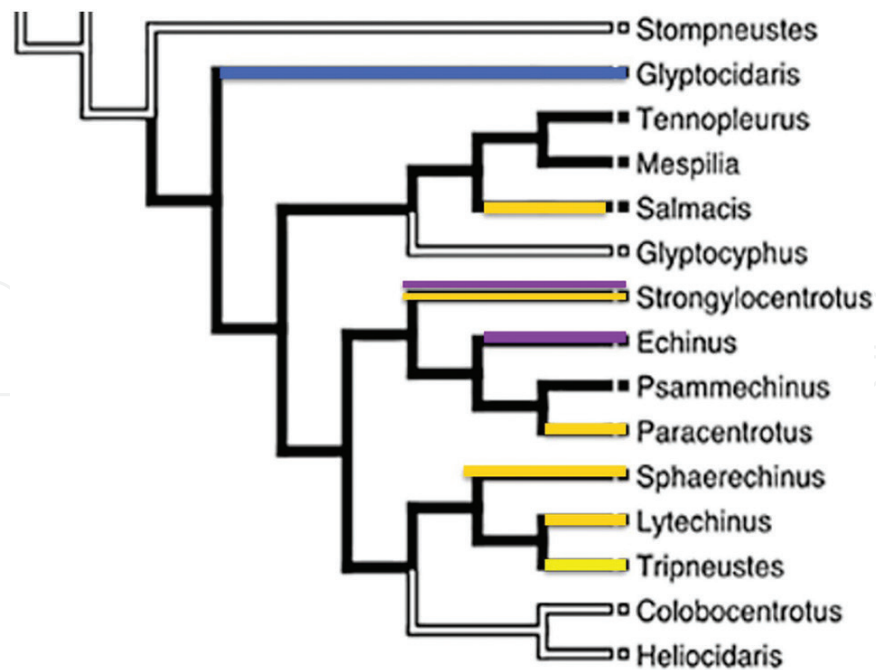


Figure 3. Covering behavior and evolutionary relationships. The uses of heaping by eleven urchin genera, mapped onto a phylogeny of urchin covering species courtesy of Ziegenhorn (2016). The colors represent different reasons for covering behavior.

shield themselves from light, and these urchins are closely related. *Strongylocentrotus* urchins, which use cover as a food source as well as protection from sunlight, are most closely related to *Echinus* urchins and *Paracentrotus* urchins, which use the reaction for the same reasons, as well as *Psammechinus* urchins, whose reason for crypsis is unknown.

In the *Salmacis*-*Mespilia*-*Tennopleurus* clade, relationships are less clear between genera as only *Salmacis* urchins' covering behavior has been explicitly studied (**Figure 3**). However, based on the phototactic ability of both *Mespilia* and *Tennopleurus* urchins, it would be reasonable to conclude that these urchins also cover themselves for UV protection [6, 41]. *Glyptocidaris* is the only urchin genera in the phylogeny that heaps primarily for mechanical defense (**Figure 3**).

3.7. Covering by ocean depth

No relationship was found between the depth at which an urchin was found and its use for covering behavior (**Table 1**). For both 0–50 and 0–250 meter range of depths, UV protection was the most common reason for covering (**Table 1**). However, most urchins found in the range 0–100 meters had unknown reasons for heaping, and for the deeper ranging urchins (0–1000 and 0–1200 meters), light, mechanical damage, and predator protection were all reasons for covering (**Table 1**). These results suggest that there is no correlation between ocean depth of the urchin's environment and the function of their cryptic behavior.

Depth (meters)	Genera	Climate(s)	Climate(s)
0–50	<i>Paracentrotus</i>	Temperate	L
	<i>Strongylocentrotus intermedius</i>	Temperate/polar	L
	<i>Toxopneustes</i>	Tropical	M
0–100	<i>Psammechinus</i>	Polar	U
	<i>Temnopleurus</i>	Temperate	U
	<i>Sphaerechinus</i>	Temperate	L
	<i>Strongylocentrotus purpuratus</i>	Temperate	F
	<i>Tripneuste</i>	Tropical	L
	<i>Pseudoboletia</i>	Tropical	U
	<i>Mespilia</i>	Tropical/temperate	U
0–250	<i>Salmacis</i>	Temperate	L
	<i>Glyptocidaris</i>	Temperate	M
	<i>Lytechinus</i>	Tropical/temperate	L
0–1000	<i>Pseudechinus</i>	Temperate	P
	<i>Genocidaris</i>	Tropical/temperate	U
0–1200	<i>Echinus</i>	Temperate	F
	<i>Strongylocentrotus drobachiensis</i>	Temperate	L/M

NOTE: U stands for unknown, L stands for sunlight/UV protection, M stands for mechanical defense, and P stands for predator defense.

Table 1. Urchin covering by ocean depth: List of the 15 urchin genera and their use of covering behavior, organized by the depth ranges in which they are found.

3.8. Covering by climate

Though urchins who cover to protect themselves from light tend to be found in warmer oceans, this rule does not apply for all genera (**Figure 4a, b**). Some urchins within tropical regions cover for mechanical reasons (**Table 2; Figure 4b**). Additionally, some urchins use the behavior to shield themselves from light are also found in temperate and polar waters (**Table 2**). Based on the studies reviewed, no clear trend was found between urchin crypsis and ocean climate.

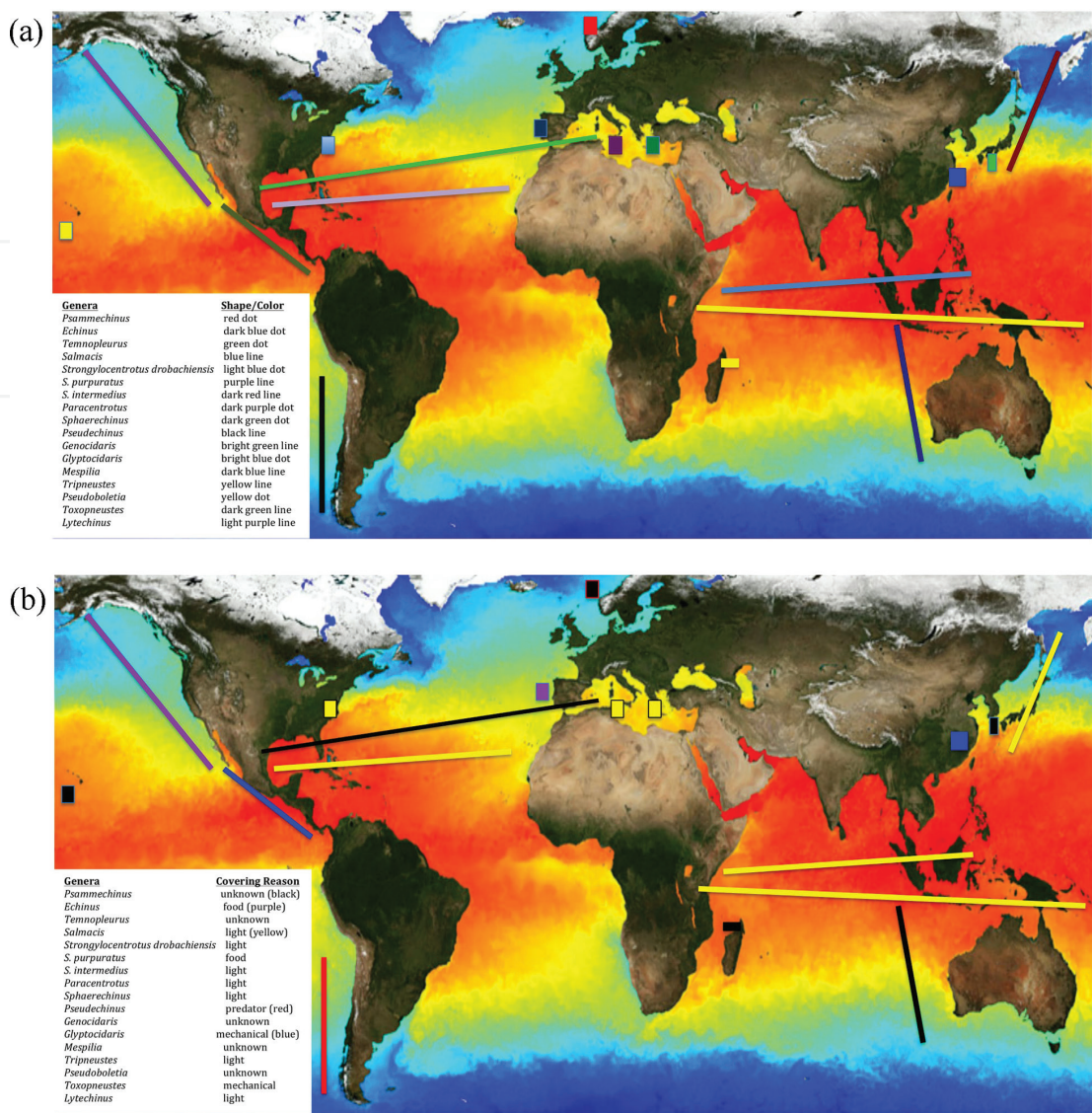


Figure 4. Map of urchins distribution and covering behavior. Distribution of the fifteen urchin genera considered, mapped onto an existing climate map (courtesy of NOAA). (a) Genera and shape/color, (b) genera and covering reason/color. The covering reasons were abbreviated to unknown, light, mechanical, food, and predator.

Climate(s)	Genera	Depth (meters)	Covering Use
Tropical	<i>Tripneustes</i>	0–75	L
	<i>Pseudoboletia</i>	0–100	U
	<i>Toxopneustes</i>	2–50	M
Tropical/Temperate	<i>Genocidaris</i>	12–420	U
	<i>Lytechinus</i>	0–250	L
	<i>Mespilia</i>	0–60	U

Climate(s)	Genera	Depth (meters)	Covering Use
Temperate	<i>Echinus</i>	0–1200	F
	<i>Temnopleurus</i>	5–65	U
	<i>Salmacis</i>	0–180	L
	<i>Strongylocentrotus drobachiensis</i>	0–1150	L/M
	<i>Paracentrotus</i>	0–35	L
	<i>Sphaerechinus</i>	0–100	L
	<i>Pseudechinus</i>	0–820	P
	<i>Glyptocidaris</i>	10–150	M
	<i>Strongylocentrotus purpuratus</i>	0–65	F
Temperate/Polar	<i>Psammechinus</i>	0–100	Up
	<i>Strongylocentrotus intermedius</i>	0–35	L

NOTE: U stands for unknown, L stands for sunlight/UV shielding, M stands for mechanical protection, and P stands for predator defense.

Table 2. Urchin covering by ocean climate: List of the 15 urchin genera and their use of covering behavior, organized by the climate(s) in which they are found.

4. Discussion

Phylogenetic relationships are a better tool than environmental considerations for predicting why sea urchin species use cryptic behavior. Urchins that are found closer to the equator are more likely to cover to shield themselves from light, but *Toxopneustes*, *Pseudechinus*, and *Mespilia* urchins are exceptions and several genera including *Paracentrotus*, *Temnopleurus*, and *Strongylocentrotus* cover to protect themselves from light despite being further from the equator (**Figure 4a, b**). These exceptions decrease the power of climate as a predictive tool for determining the function of covering. This study also found no relationship between reason for the behavior and depth at which urchins were found (**Table 1**). In contrast, more closely related urchin species cover for similar reasons (**Figure 3**). This may suggest a genetic basis for urchin crypsis and its species-specific uses.

The covering reaction remains nebulous. For several genera, no studies have been performed to determine the function of the behavior, leaving gaps in the phylogeny as well as the climate and depth tables that might have impeded otherwise prominent patterns (**Figure 3; Table 1; Table 2**). It is also worth noting that for other genera that were assigned a most likely reason for covering, alternative hypotheses often were not tested. *Glyptocidaris* urchins, for example, were found to most likely heap for mechanical defense, and their place in the phylogeny suggests that this may be the ancestral reason for sea urchin crypsis (**Figure 3**). However, the effects of light intensity or the presence of predators have not been studied

for *Glyptocidaris* and so cannot be conclusively ruled out as functions of their covering reaction. Of the urchin genera for which a most likely reason for covering was assigned, *Salmacis*, *Echinus*, *Sphaerechinus*, *Lytechinus*, *Toxopneustes*, and *Pseudechinus* all had at least one possible reason for the behavior that had not been explicitly tested. In other cases, multiple reasons for covering had convincing evidence, such as both food source and light protection for *Strongylocentrotus* urchins [7, 19].

It seems that heaping can perform several functions for a sea urchin, though within a genera there may be one primary reason for the behavior. *Tripneustes* and *Lytechinus* urchins primarily use the reaction to avoid bright light, but the importance of protection from wave surge has also been noted for both species [25, 33]. *Strongylocentrotus* urchins cover to shield themselves from light and use covering as a food source, but one study has also suggested the behavior might be used to prevent mechanical damage [17]. Because of this, it remains difficult to determine the reasons for a species cryptic behavior by any means apart from running experiments on the species in question. However, this study suggests that phylogenetic relationships provide a good framework for making predictions about the use of the covering reaction in other urchin species. For example, although the reason for the behavior is unknown for *Psammechinus* urchins, it is reasonable to predict that it also covers to defend itself from bright light because of its close relationship to *Paracentrotus* (**Figure 3**) and its noted phototactic ability [40].

This study has important implications for the study of sea urchin heaping as a whole because of its novel suggestion that there might be a relationship between the various uses of covering and other aspects of urchin biology, be they genetic or environmental considerations. Understanding covering in sea urchins is particularly important because the ability is crucial to survival; one study has even shown that some sea urchins die if not provided with sufficient material with which to cover themselves [25].

Sea urchin ecology is important because of their role in coral reef systems, where they consume and control populations of algae that threaten corals [43], as well as in aquaculture, where they are part of the diet of humans in many countries [44]. Additionally, understanding the covering reaction itself, and how it may be determined by genetic and environmental factors, is important when considering it in relation to the multitude of cryptic behaviors that exist within the animal kingdom. Further studies of covering in urchin genera with currently unstudied covering behavior would be especially insightful for this study. Additional studies might also include ruling out other uses of the behavior for which one primary use has been considered, or studying the phylogenetic relationships of all urchin genera that cover.

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