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Kleptoplasty in Sea Slugs: Nature's Photosynthetic Thieves

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SUMMARY

Kleptoplasty, is a phenomenon where sea slugs capture and retain functional chloroplasts from algae to perform photosynthesis. Sacoglossan sea slugs, such as Elysia viridis and Elysia timida, ingest algae, selectively retaining chloroplasts in their digestive cells. These chloroplasts can photosynthesize for weeks or months, providing energy to the sea slug. Kleptoplasty offers ecological advantages like camouflage and survival during food scarcity, but it faces challenges: missing algal genes, chloroplast degradation over time, and the need for periodic feeding. Despite these, kleptoplasts provide a significant nutritional source. The phenomenon showcases nature’s adaptability and holds potential for applications in solar energy systems. However, further research is needed to fully understand the processes and limitations of kleptoplasty.

INTRODUCTION

Kleptoplasty derives its name from the Greek word *kleptes*, meaning "thief," and *plastid*, which refers to organelles involved in photosynthesis. Kleptoplasty is a biological phenomenon in which one organism captures and retains functional chloroplasts (the organelles responsible for photosynthesis) from another organism, typically algae, and incorporates them into its own cells. These stolen chloroplasts, or "kleptoplasts," remain temporarily functional and allow the host organism to perform photosynthesis, thereby producing energy from sunlight. Within the Metazoa, only sacoglossan sea slugs (Heterobranchia = Opisthobranchia) are known to display this type of association. The sea slugs which will ingest algae, extract their chloroplasts, and integrate them into their own tissues. The retained chloroplasts can continue photosynthesizing for weeks or months, enabling the host to derive nutrients directly from sunlight. Due to these remarkable features, sacoglossan sea slugs have been frequently termed ‘leaves that crawl’ or ‘solar-powered sea slugs’.These organisms have a wide geographical distribution, being present in the majority of shallow tropical and temperate marine environments. The most well-studied species of sacoglossans displaying the ability to retain functional chloroplasts in their animal cells include: *Elysia viridis* the coast of Scandinavia, *Elysia timida* occurring in the Mediterranean coast, *Elysia clarki* and *Elysia chlorotica* that occur in the southeast coast of North America. (Figure 1)

Figure 1: *Elysia viridis* and *Elysia chlorotica*

Mechanisms of Kleptoplasty in sea slug

The sea slug uses its radula (a specialized tooth-like structure) to puncture algal cells and suck out their contents, which include chloroplasts, cytoplasm, and other organelles. Unlike most herbivores that digest these components entirely, the sea slug selectively retains chloroplasts. After ingestion, chloroplasts are transported through the slug’s digestive tract and selectively incorporated into the cells lining its digestive diverticula (branched structures extending throughout the slug’s body). These diverticula are highly vascularized, providing chloroplasts with nutrients and gases needed for photosynthesis. Within the cells, the chloroplasts are enclosed in vacuolar membranes, which protect them from degradation. This step requires active cellular transport systems, including vesicle trafficking and cytoskeletal elements like actin and tubulin, to position the chloroplasts strategically. A critical aspect of kleptoplasty is the long-term maintenance of functional chloroplasts. Normally, chloroplasts depend on the host algal nucleus to produce essential proteins for photosynthesis, yet in sea slugs, these proteins are somehow provided despite the absence of the algal nucleus.

Over evolutionary time, sea slugs have incorporated genes from algae into their own genome. These genes are expressed in the sea slug's cells to produce proteins essential for:

- Chloroplast repair and maintenance (e.g., D1 protein repair in Photosystem II).
- Photosynthetic activity stabilization (e.g., production of enzymes like RuBisCO).

This HGT process is unprecedented among animals, making sea slugs a unique model for studying gene transfer between species.

Once sequestered, chloroplasts within the digestive diverticula are exposed to light through the slug's semi-transparent body. These chloroplasts use sunlight to drive photosynthesis, converting carbon dioxide and water into glucose and oxygen. Sea slugs exhibit unique adaptations to house and sustain chloroplasts:

- Digestive Cell Specialization: Cells in the digestive diverticula are modified to accommodate and maintain chloroplasts, including the presence of specific vacuolar and cytoplasmic structures.
- Cytoskeletal Rearrangements: Actin filaments and microtubules help position chloroplasts near cell surfaces for optimal light exposure.
- Molecular Chaperones: These proteins assist in the folding and stabilization of chloroplast-derived enzymes and proteins.

Despite its advantages, kleptoplasty faces several challenges: Not all algal genes needed for chloroplast maintenance are transferred to the sea slug's genome. Scientists are still studying how sea slugs compensate for missing algal proteins; Over time, chloroplasts degrade due to the absence of the algal nucleus. Sea slugs rely on periodic feeding to replenish chloroplasts.

The Role of Kleptoplasts in Sea Slug Physiology

Protection from predation

In kleptoplast-bearing sea slugs, the macroalgal chloroplasts are phagocytized by cells of the digestive tubules, which ramify throughout most of the sea slug's body. Hence, one of the most noticeable characteristics of these sea slugs is their green coloration, which allows them to blend with the environment dominated by macroalgae and pass unnoticed to predators such as fish and crabs. Avoiding predation might have been an important evolutionary drive in the acquisition of chloroplasts by some sacoglossans. However, crypsis is also an ability of sea slugs that acquire nonfunctional chloroplasts, such as *Placida dendritica*.

Enhanced survival during food scarcity

Evidence of kleptoplast photosynthesis minimizing weight loss and increasing survival in periods of food scarcity in sea slugs such as *E. viridis*, *E. timida, E. chlorotica,* and *P. ocellatus*. metabolites produced by kleptoplast photosynthesis are continuously made available to the sea slugs by rapid translocation into kleptoplast-free tissues, it is also possible that under prolonged starvation sea slugs obtain nutritive benefits by targeting kleptoplasts for degradation and using their starch reserves. The studies showed increased growth efficiency in *E. viridis* fed on *C. fragile* under regular light compared to quasi-dark, which correlated to increased photosynthesis (Baumgartner and Toth, 2014) however by contrast *E. viridis* feeding on *Cladophora rupestis* did not display an increase in growth efficiency under light conditions due to the highly limited functionality of the algal chloroplasts. Nevertheless, the authors concluded that kleptoplast photosynthates formed a significant nutritional source for animals in periods of food shortage.

Higher reproductive output

It was recently hypothesized that kleptoplast photosynthesis could support the reproductive output of sacoglossan sea slugs. It is reasonable to consider that better-nourished individuals, including sea slugs able to obtain metabolites from kleptoplast photosynthesis, have more resources to allocate to reproduction and consequently display higher fecundity. The sea slug *E. atroviridis* was shown to spawn a higher number of eggs when fed under regular light than under quasi-dark conditions. This shows that under limited kleptoplast photosynthesis due to reduced light levels, the sea slugs clearly changed their reproductive energy investment by decreasing the number of spawned eggs.

Enhanced mucus production

Mucus secretion is paramount for mollusks, playing different roles in processes such as locomotion, feeding, reproduction, or protection, including reducing exposure to predation or physical stress. When exposed to desiccation stress, sea slugs with active kleptoplasts produce significantly more mucus. This mucus acts as a protective barrier against environmental stressors, demonstrating the role of photosynthetically derived metabolites in enhancing mucus production during challenging conditions. Research using carbon labeling has shown that 5–30% of the carbon fixed by kleptoplasts is incorporated into the secreted mucus. This highlights the direct biochemical contribution of kleptoplast-derived carbon to mucus synthesis.

Challenges and limitations of kleptopasty

Sea slugs rely on particular algal species to obtain functional chloroplasts. A decline in these algae can directly impact their survival. Not all sea slugs possess the genes necessary for maintaining chloroplasts. Horizontal gene transfer is species-specific and incomplete, leading to varying efficiencies of kleptoplasty. Without the algal nucleus, chloroplasts eventually degrade. Despite adaptations, sea slugs must feed periodically to replenish them. Supporting foreign organelles within cells requires significant cellular resources, including antioxidants and repair proteins, which can strain the host's metabolism. Photosynthesis produces reactive oxygen species (ROS), which can harm both the chloroplasts and host cells. Sea slugs must actively mitigate this damage.

CONCLUSION

Kleptoplasty in sea slugs is an extraordinary example of adaptive evolution that illustrates the complexity of interspecies interactions and resource utilization. It highlights the ability of these organisms to harness photosynthetic capabilities from their algal prey, providing them with significant ecological advantages. Future research is needed which has potential implications in biotechnology, such as designing more efficient systems for solar energy capture. Ultimately, the study of kleptoplasty in sea slugs showcases nature's remarkable creativity and boundless ability to adapt and innovate.

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