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Algivore or Phototroph? *Plakobranchus ocellatus* (Gastropoda) Continuously Acquires Kleptoplasts and Nutrition

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The sea slug *Plakobranchus ocellatus* (Sacoglossa, Gastropoda) retains photosynthetically active chloroplasts from ingested algae (functional kleptoplasts) in the epithelial cells of its digestive gland for up to 10 months. While its feeding behavior has not been observed in natural habitats, two hypotheses have been proposed: 1) adult P. ocellatus uses kleptoplasts to obtain photosynthates and nutritionally behaves as a photoautotroph without replenishing the kleptoplasts; or 2) it behaves as a mixotroph (photoautotroph and herbivorous consumer) and replenishes kleptoplasts continually or periodically. To address the question of which hypothesis is more likely, we examined the source algae for kleptoplasts and temporal changes in kleptoplast composition and nutritional contribution. By characterizing the temporal diversity of *P. ocellatus* kleptoplasts using *rbcL* sequences, we found that *P. ocellatus* harvests kleptoplasts from at least 8 different siphonous green algal species, that kleptoplasts from more than one species are present in each individual sea slug, and that the kleptoplast composition differs temporally. These results suggest that wild *P. ocellatus* often feed on multiple species of siphonous algae from which they continually obtain fresh chloroplasts. By estimating the trophic position of wild and starved P. ocellatus using the stable nitrogen isotopic composition of amino acids, we showed that despite the abundance of kleptoplasts, their photosynthates do not contribute greatly to the nutrition of wild P. ocellatus, but that kleptoplast photosynthates form a significant source of nutrition for starved sea slugs. The herbivorous nature of wild P. ocellatus is consistent with insights from molecular analyses indicating that kleptoplasts are frequently replenished from ingested algae, leading to the conclusion that natural populations of P. ocellatus do not rely on photosynthesis but mainly on the digestion of ingested algae.

Keywords: kleptoplasty, sacoglossan, ulvophyceae, symbiosis