生物策略表

類別	生物策略 (Strategy)
生物策略 STRATEGY	黏液過濾網捕捉小於網目的顆粒 (Mucus filters trap particles smaller than mesh size)
生物系統 LIVING SYSTEM	海樽 *Pegea confoederata* (Salp)
功能類別 FUNCTIONS	#獲取、吸收、或過濾生物 #獲取、吸收、或過濾固體 #排出液體 #排出固體 #Capture, absorb, or filter organisms #Capture, absorb, or filter solids #Expel liquids #Expel solids
作用機制標題	海樽的食物過濾網持續分泌黏液以最佳化穿過的水流，使其能捕獲小於網目的食物 (The food filters of *Pegea confoederata* salps capture food smaller than its mesh size by optimizing the water flow through their continuously secreted sticky mucus net.)
生物系統/作用機制示意圖	

作用機制摘要說明 (SUMMARY OF FUNCTIONING MECHANISMS)

雖然我們無法靠直覺想像過濾網竟能捕捉小於網目的顆粒，但指甲大小的海樽(Salp, *Pegea confoederata*) 卻靠此技能來存活。當海樽將周圍的海水吸入體內時，牠會使用肌肉來確保水流如同無風日的河流一般平靜有序。透過消除湍流（或紊流）的影響，小於網目的顆粒例如細菌、病毒和膠體物質 (colloidal mass) ，會以非常靠近網狀材料的距離通過。在離網一定距離處，它們會黏附在由海樽持續分泌的黏性網狀物上。甚至是比細菌、病毒和膠體物更小的顆粒則會直接擴散到過濾材料中。海樽在其過濾系統中創造的特定流體力學條件使其能夠捕獲直徑小至 0.01 微米的顆粒（病毒、膠體等），即使過濾網目尺寸約為 1.5 乘以 6 微米。這種適應性使得肉眼可見的海樽能藉由攝取已知最微小的生物生命形式而存活。

While it may not seem intuitive that filters can trap particles smaller than the size of their mesh, the fingernail-size marine salp (*Pegea confoederata*) depends on it for its survival. As the salp pulls the surrounding sea water into its body, it uses muscles to ensure the flow is as calm and orderly as a river on a windless day. By eliminating the effects of turbulence, particles smaller than the mesh, such as bacteria, viruses, and colloidal masses, pass extremely close to the net material. At a certain distance from the net, they adhere to the sticky netting material continuously secreted by the salp. Particles even smaller than bacteria, viruses, and colloidal masses diffuse right into the filter material. The specific fluid mechanical conditions which *P. confoederata* creates in its filtration systems enable it to trap particles with diameters as small as 0.01 micron (viruses, colloids, etc.) even though the filter mesh measures ~ 1.5 x 6 microns. This adaptation allows the macroscopic salps to survive on a diet of some of the tiniest biological life-forms known.

文獻引用 (REFERENCES)

「海樽在海洋水域中很常見，並且比任何其他以浮游動物 (zooplankton) 為食的濾食性生物 (filter feeder) 具有更高的個體過濾率⋯海樽過濾食物時是透過有節奏地將水泵入口吸管 (oral siphon) 中，通過咽腔 (pharyngeal chamber)，再從圍鰓腔吸管 (atrial siphon) 排出。進入咽腔的食物顆粒在通過持續分泌的黏液網時，會被捲成食物串並往後移向食道 (esophagus)…這種進食機制使其可以攝取任何進入圍鰓腔吸管並黏附在過濾網上的顆粒⋯在低雷諾數 (Reynolds number) ($Re \ll 1$) 時，黏性效應 (viscous effect) 具主導性，可以防止過濾網材周圍產生流動分離。海樽的過濾作用即在這種情況下進行，因為 Re $\sim 2\times10^{-3}$⋯低雷諾數過濾理論的經典原理指明，低 Re 的濾食性生物可以藉由簡單篩分 (simple sieving) 之外的機制來收集小於網目的顆粒。主要機制是直接攔截 (direct interception) 在流線上行進、且在距離過濾單元一個顆粒半徑範圍內的顆粒，以及由布朗效應 (Brownian effect) 或隨機運動 (random motility) 所引起的擴散沉積 (diffusional deposition)，這會使顆粒偏離流線 (streamline) 並使其與過濾網接觸…海樽可以捕獲亞微米 (submicrometer) 大小的顆粒，並以高過捕獲較大顆粒的速率進行。」(Sutherland et al. 2010: 15129)

「擴散沉積和直接攔截都對顆粒遇到過濾網 [規律間隔的矩形進食篩網，平均網目寬度和長度分別為 W = 1.5±0.5 μm 和 L = 6.0±1.5 μm] 起相當重要的作用，但對於粒徑 dP>0.05 μm 的顆粒來說，直接攔截為主要作用機制。對於粒徑 dP = 0.01-0.05 μm 的顆粒 (病毒、膠體)，擴散作用則是顆粒相遇的主要機制，儘管效率 < 2%⋯因為海洋中的小顆粒數量明顯較多，因此即使相遇效率相對較低，這些顆粒也可能不成比例地被攝入⋯粒徑在 0.01 到 0.1 微米範圍內（病毒、膠體）的顆粒相遇率是粒徑在 0.1 到 1 微米範圍內（亞微米顆粒 submicron particles、細菌、原綠球藻 Pro-chlorococcus）顆粒的兩百倍左右…簡單篩分模型是相對碰撞率的次級預測器 (inferior predictor)，且在預測最小顆粒的碰撞率方面特別差⋯測量到的速率與直接攔截模型預測的結果類似。」 (Sutherland et al. 2010: 15131)

「這些研究結果表明簡單篩分並非海樽得唯一攝食機制，相反地，低雷諾數過濾機制透過使海樽能捕獲亞微米顆粒而發揮主要甚而可能是主導的作用⋯我們的模型結果顯示擴散沉積允許最小的顆粒 (dP <0.05 μm) 相遇，儘管效率非常低。然而，即使黏附係數 (sticking coefficient) 小至 0.1，透過直接攔截也可以有效地遇到大部分亞微米顆粒 (0.05 μm < dP < W)，可以大幅或完全滿足海樽的能量需求⋯這些顆粒被包覆到由膜包圍的糞便顆粒 (fecal pellet) 中，由於多半未完全消化，因而富含碳、氮、和磷，及一些微

量元素（如鈣和鎂）。糞便顆粒迅速下沉，並被轉移到更深水中的長壽池 (longer-lived pool) 中，那裡的物質需要花費數年到數百年規模的時間才會被分解。」(Sutherland et al. 2010: 15132)

“Salps are common in oceanic waters and have higher per-individual filtration rates than any other zooplankton filter feeder…Salps filter feed by rhythmically pumping water into the oral siphon, through the pharyngeal chamber, and out the atrial siphon...Food particles entering the pharyngeal chamber are strained through a mucous net that is continuously secreted and rolled into a food strand that moves posteriorly toward the esophagus...This feeding mechanism results in ingestion of any particles that enter the atrial siphon and adhere to the filtering mesh...At low Re [Reynolds number] ($Re << 1$), viscous effects prevail and prevent flow separation around filter elements. Filtration in salps operates in this regime, as $Re \sim 2 \times 10^{-3}$...Classic principles of low-Re filtration theory show that low-Re filter feeders can collect particles smaller than the mesh spacing by relying on mechanisms other than simple sieving. The primary mechanisms are direct interception of particles traveling on streamlines that come within one particle radius of the filter element, and diffusional deposition caused by Brownian effects or random motility, which deflect particles from streamlines and cause contact with the filter... Salps can capture submicrometer particles, and do so at rates that exceed those of larger particles.” (Sutherland et al. 2010: 15129)

“Both diffusional deposition and direct interception play a role in determining particle encounter by the filtering mesh [a regularly spaced rectangular feeding mesh with a mean mesh width and length of $W=1.5\pm0.5$ μm and $L=6.0\pm1.5$ μm, respectively], but direct interception is dominant for particle sizes $dP > 0.05$ μm. For $dP = 0.01$-0.05 μm (viruses, colloids), diffusion is the primary mechanism of particle encounter, although efficiency is <2%...Because there are substantially higher numbers of small particles in the ocean, these particles can be disproportionately ingested even when encounter efficiencies are relatively low...particles in the 0.01- to 0.1- μm size range (viruses, colloids) are encountered at ~200× the rate of particles in the 0.1- to 1- μm range (submicron particles, bacteria, Pro- chlorococcus)... A model of simple sieving was an inferior predictor of relative encounter rates and was particularly poor at predicting encounter rates of the smallest particles...measured rates were similar to those predicted by the direct interception model.” (Sutherland et al. 2010: 15131)

“[T]hese findings suggest that simple sieving is not the sole feeding mechanism for salps, and instead that low Reynolds-number filtering mechanisms play a major and possibly dominant role by enabling salps to capture submicrometer particles...Our model results show that diffusional deposition allows encounter of the smallest particles ($dP < 0.05$ μm), although very inefficiently. However, a large fraction of submicrometer particles (0.05 μm $< dP < W$) can be efficiently encountered by direct interception and can largely or entirely satisfy salps’ energetic requirements even if the sticking coefficient is as small as 0.1...Particles are packaged into

membrane-bound fecal pellets that are often incompletely digested and therefore rich in carbon, nitrogen, and phosphorous, and contain trace elements (e.g., Ca and Mg). Fecal pellets sink quickly and are transferred to a longer-lived pool in deeper water, where material is sequestered on time scales of years to centuries.” (Sutherland et al. 2010: 15132)
參考文獻清單與連結 (REFERENCE LIST)
Sutherland, K. R., L. P. Madin, and R. Stocker. (2010). Filtration of submicrometer particles by pelagic tunicates. *PNAS* 107: 15129-15134. (https://www.pnas.org/content/107/34/15129)
延伸閱讀
生物系統延伸資訊連結 (LEARN MORE ABOUT THE LIVING SYSTEM/S)
撰寫/翻譯/編修者與日期
顏子傑翻譯 (2018/10/19)；譚國鋈編修 (2020/03/31)；紀凱容編修 (2021/07/01)
AskNature 原文連結
https://asknature.org/strategy/mucus-filters-trap-particles-smaller-than-mesh-size/