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24. All flume covers transmit ~90% of the photosynthetically active radiation (PAR; 400 to 700 nm). Flumes exposed to full-spectrum sunlight (PAR+UVA+UVB) were covered with either a film of UV-transparent polyvinylidine (PVI) (1991) or UV-transparent acrylic sheets, type OP-4 (CYRO, Toronto, Canada; 4.7 mm thick; 70 to 90% transmittance throughout the UVB and UVA) (1992 to 1993). Flumes protected from UVB were covered with Mylar-D (Du Pont, Wilmington, DE; (0.1 mm thick; 50% transmission at 318 nm) (1992 and 1993). Flumes shielded from both UVA and UVB were covered with UV-opaque acrylic sheets, type UF-1 (Rohm and Hass, West Hill Ontario, Canada; 6.4 mm thick; 50% transmission at 380 nm) (1991); or type UF-4 (Rohm and Hass; 6.4 mm thick; 50% transmission at 398 nm) (1992 and 1993). Neutral-density window screen placed over sections of flumes was used to reduce total incident solar insolation by 50%. All photo treatments were run in triplicate.
25. Discharge to troughs of 50 liters per minute produced supercritical flow conditions with water velocity, depth, and hydraulic residence time of ~50 cm s^{-1}, 1 cm, and ~4 s, respectively.
26. Areas cleared of diatoms by chironomid grazing activity (grazing scars) were readily visible. Chironomid tubes, formed by the adhesion of a diatom-detritus matrix around the larvae, were also visible (Fig. 5). Tubes were counted each day and used as an index of chironomid abundance in situ. Although the tubes visible to the unaided eye were only a fraction of the number of chironomids present, microscopic enumeration confirmed the relative chironomid abundances among treatments indicated by in situ tube counts.
27. Time course patterns in Chl a were also usually seen in algal cell numbers and biovolumes (*13*).
28. Three additional flumes exposed to 90% PAR were treated with the insecticide malathion (Dimethoxyphosphinothioyl thiobutanedioic acid diethyl ester), to exclude insect grazers chemically. Starting in the second week, 5-min pulses (final concentration of 2×10^{-3} % v/v) were metered into the flumes each day. This mild treatment retarded development of the chironomid community.
29. In 1991 and 1993, global UVB radiation and total-column ozone were measured with a Brewer Ozone Spectrophotometer (SCI-TEC Instruments, Saskatoon, Saskatchewan, Canada). During the daylight hours, automated scans were made at 30-min intervals forward and backward between 290 and 320 nm, and energy was recorded at 0.5-nm intervals. Daily ozone determinations were made with procedures outlined by J. B. Kerr, C. T. McElroy, R. A. Olafson, in *Proceedings of the International Quadrennial Ozone Symposium*, J. London, Ed., Boulder, CO, 4 to 9 August 1980 (International Ozone Commission, Boulder, CO, 1980), pp. 74–79. During 1992, global UVB, UVA, and PAR radiation were measured with an Optronics OL-752 spectroradiometer (Optronics Laboratories, Orlando, FL). Scans from 280 to 700 nm were made every 30 min during the daylight period, and readings were recorded at 2-nm intervals. In all three years, integrated PAR (400 to 700 nm) was continuously measured with a Li-Cor (Lincoln, NE) quantum cosine sensor (LI 190SA).
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42. On day 29, Chl a in PAR+UVA was lower than under PAR+UVA+UVB [Student-Newman-Keuls (SNK) $P < 0.05$]. However, PAR+UVA+UVB and PAR+malathion were similar (SNK, $P = 0.247$).
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Temperature and Water Viscosity: Physiological Versus Mechanical Effects on Suspension Feeding

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Water viscosity is inversely related to temperature. This simple physical relation couples two potential influences on organism performance. Seawater viscosity was manipulated, with and without temperature, to distinguish the physiological and mechanical effects of temperature on suspension feeding by ciliated echinoderm larvae. Change in viscosity alone accounted for half of the decline in the feeding rate at lower temperature. High viscosity shifted ingestion toward larger particles, which suggests that viscosity affects particle capture as well as rates of water processing. Temperature-induced change in viscosity, therefore, impacts suspension feeding independently of physiology and has implications for many small-scale biological processes.

Understanding the effects of temperature on biological activity and adaptation (*1*) requires the discrimination of temperature-dependent processes that underlie performance. Thermal biology has focused on physiological (biochemical) processes (*2*), but temperature can impact mechanical processes as well by influencing the viscosity (μ) of the ambient fluid (Fig. 1) (*3*).

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Such effects of temperature are potentially confounding for processes at a hydrodynamic scale where viscous forces dominate motion (*4*). For example, capture mechanisms involved in suspension feeding, which is commonly used by aquatic animals, depend on the viscous properties of water (*5–7*). Cilia, flagella, or setae are used to generate feeding currents and to capture particles, processes that may both be sensitive to temperature-induced viscosity change (*8*). However, the independent effects of temperature and fluid viscosity on feeding performance have not been measured experimentally.

The viscosity of seawater can be adjusted independently of temperature through the addition of high molecular weight polymers (*9*). I used this technique to separate temperature's mechanical and physiological effects on suspension feeding by planktonic larvae of the sand dollar *Dendraster excentricus*. Larvae generate water currents and collect food on a ciliated band that borders the larval arms. Most particles are captured through the reversal of ciliary beat on localized regions of the band where particles are detected (*10*). Viscous forces dominate the motion of cilia (*4*, *11*). By manipulating viscosity, it was possible to estimate the total effect of temperature on feeding in two steps: one that measures the effect of the viscosity change alone and one that measures the effects of temperature (Fig. 1).

To estimate feeding rates (*12*), I measured the accumulation of particles (*13*) in the guts of larvae during 10-min feeding trials. Six treatments were used to test for the effects of temperature, viscosity, viscosity acclimation, and polymer toxicity (Fig. 1) (*14*). (i) To measure the effect of viscosity alone, larvae were fed at a common temperature (22°C), with the viscosity adjusted from that characteristic of seawater at 22°C (μ = 1.02 cP, treatment A) to those characteristic of seawater at 12°C (μ = 1.30 cP, treatment B) and at 5°C (μ = 1.60 cP, treatment C) (*15*). (ii) To measure the combined effects of low temperature and high viscosity, larvae were fed at 12°C (treatment D). A comparison of treatments A and B delimits the effect of increased viscosity, whereas a comparison of B and D delimits other effects of temperature (Fig. 1). (iii) To test for short-term acclimation to high viscosity, treatment E differed from B in that the acclimation conditions included viscosity elevated to match the feeding conditions. (iv) To test for toxic effects of exposure to the polymer, in treatment F larvae were held in polymer solution for 3 hours before feeding in untreated seawater as in treatment A. To test for long-term feeding compensation in response to rearing conditions, the procedure was replicated for 16 cohorts reared at warm temperatures (20° to 22°C) and for 16 cohorts reared at cold temperatures (11° to 13°C) (*16*, *17*).

Larvae were fed a mixture of particle sizes (*13*) to test whether viscosity could influence the size of particles ingested. Recognizing the mechanism of ciliary reversal used in particle capture, I predicted that high viscosity might increase the detection of smaller particles that would be less likely to trigger reversal (*18*), which would shift the distribution of ingested particles toward smaller sizes. This hypothesis was prompted by the observation (*19*) that polar echinoderm larvae fed on bacteria, whereas related temperate species took only larger phytoplankton.

In untreated seawater, ingestion rate declined on average by 67% when temperature was reduced by 10°C (Table 1, A and D); this difference potentially includes both physiological and mechanical effects. The viscosity change alone (Table 1, A and B) was sufficient to account for 60.6% of this difference, which leaves 39.4% attributable to other effects of temperature (Table 1, B and D) (*20*). The ingestion rate declined further when viscosity was increased to that of seawater at 5°C (Table 1, A to C). Three-hour exposure to the polymer before feeding had no positive effect on ingestion, which would have been consistent with viscosity acclimation (B and E), nor a negative effect, which would have indicated toxicity (A and F).

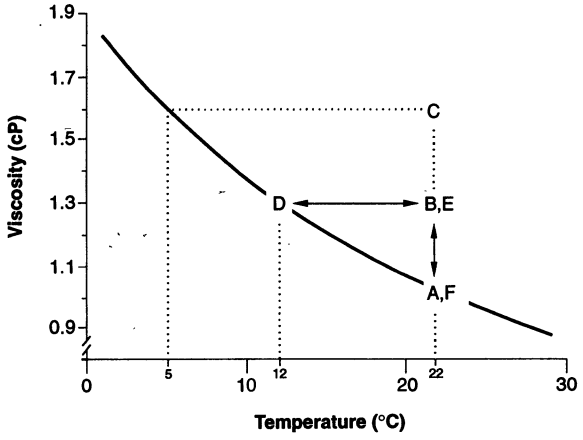

Fig. 1. Summary of seawater conditions in six treatments (A to F). The curved line shows the relation between temperature and viscosity for 30 per mil seawater (*3*). The position of each letter or pair represents a combination of temperature and viscosity conditions under which feeding was measured. Arrows show how an intermediate treatment (B) separates effects of viscosity (B versus A) from other effects of temperature (B versus D). In A to D, 3-hour acclimation to the feeding temperature was done in untreated seawater. In E and F, acclimation to the feeding temperature was done at the viscosity of 12°C seawater. Viscosities were increased through the addition of dextran (*13*).

Table 1. Mean number of particles (±1 SE) ingested per 10-min trial under different combinations of feeding viscosity and temperature. Data are pooled across rearing temperatures (N = 32). For reference, treatments (in parentheses) are positioned to correspond with those in Fig. 1. Before each trial, larvae were acclimated for 3 hours to the feeding temperature and to the normal viscosity for that temperature, except for the treatments listed in the second 22°C column, in which acclimation was carried out at an elevated viscosity of 1.30 cP. At feeding viscosities of 1.60, 1.30, and 1.02 cP the temperatures are normally 5°, 12°, and 22°C, respectively. The ANOVA showed a significant effect of treatment [$F_{(5,150)}$ = 39.0, P < 0.001]. Of the five a priori pair-wise comparisons (*17*), three were significant (A > B > C and D, P < 0.01) and two were not (E and B, A and F).

Feeding viscosity (cP)	Feeding temperature (°C)		
	12	22	22
1.60		15.3 ± 1.6 (C)	
1.30	14.0 ± 1.9 (D)	25.3 ± 2.2 (B)	22.9 ± 2.2 (E)
1.02		42.7 ± 4.6 (A)	43.1 ± 4.2 (F)

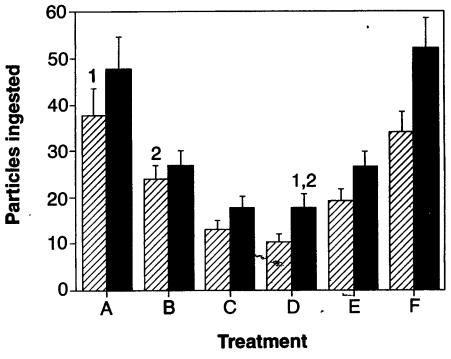

Fig. 2. Effect of rearing temperature on mean number of particles ingested per 10-min trial. Treatments are as indicated in Fig. 1. The ANOVA (*15*) showed that ingestion rates for cold-reared larvae (solid bars) were significantly higher than those for warm-reared larvae (hatched bars; t = 1.92, df = 30, P = 0.032; the rearing temperature by treatment interaction was not significant). The numbers on bars indicate groups used in two comparisons described in the text. Comparison 1: t_{30} = 2.96, P = 0.006. Comparison 2: t_{30} = 1.40, P = 0.17.

Within each treatment, larvae that were reared at cold temperatures fed at greater rates than those reared at warm temperatures (Fig. 2). Nevertheless, temperature compensation (*21*) for feeding was not complete: At their respective rearing temperatures, cold-reared larvae fed at lower rates than did warm-reared larvae (Fig. 2, comparison 1). Relative proportions of ingested particle sizes changed regularly as viscosity increased (Fig. 3). Contrary to the prediction, at higher viscosities the ratio of large (10-μm) particles increased significantly relative to smaller (2- and 5-μm) particles. Thus, hydromechanical factors alone do not explain the ingestion of smaller particles in polar waters; in fact, they appear to bias against it (*22*).

The physical properties of water are considered to play a major role in the evolution of aquatic feeding mechanisms (*5–7*). The results here support the hypothesis that mechanical effects of viscosity account for a large portion of the effects of temperature on feeding performance. Over the viscosity increase associated with a change from 22° to 12°C, the ingestion rate declined by 41%, whereas water movement by cilia of tethered larvae declined by only 19% (*11*). Thus, changes in viscosity affect not only rates of water processing but also the detection or capture of particles.

Effects on detection and capture are further supported by the shift in the size distribution of ingested particles. Size selectivity by planktivores commonly involves active discrimination or passive physical mechanisms that depend on characteristics of predators and prey (*23*). The results here suggest that physical characteristics of the fluid environment are sufficient to bias the size of particles taken. By affecting the steepness of velocity gradients, changes in viscosity could also influence particle selection by altering retention efficiencies on filters (*5–7, 24*) and concentrations of chemical stimulants around food particles (*23, 25*).

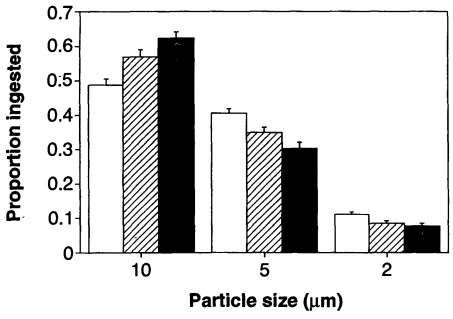

Fig. 3. Proportion of particles of different size ingested by larvae under increasing viscosity at constant temperature (22°C): open bars, 1.02 cP; hatched bars, 1.30 cP; solid bars, 1.60 cP. The proportion of 10-μm particles differed significantly among viscosity levels [$F_{(2,60)} = 31.6$, $P < 0.001$; the rearing temperature was not significant]. Proportions were arcsine square root–transformed before analysis.

By influencing exposure to planktonic mortality, growth rate through the larval period is a key variable in aquatic life histories (*26*). The mechanical and physiological effects of cold temperature on feeding likely lead to slower growth, though only when food availability limits growth rate (*27*). Feeding rates on microalgae are several times greater for temperate asteroid larvae than for polar relatives (*28*). Such effects on feeding could be one of several factors promoting a shift from feeding to nonfeeding larval development at higher latitudes (*29*).

Do larvae respond adaptively to the mechanical, as opposed to the physiological, challenges of temperature (*30*)? Feeding rate did not respond to a short (3-hour) exposure to high viscosity but did increase after development under chronic conditions of low temperature and high viscosity. The partial feeding compensation exhibited by larvae (Fig. 2, comparison 1) suggested that mechanical factors might limit the effectiveness of a physiological response (*21, 31*). To examine this hypothesis, I compared two groups of larvae feeding at their respective rearing temperatures but at a common (high) viscosity (Fig. 2, comparison 2). No significant difference in feeding rate between groups is consistent with the ability of larvae to show compensation that is more physiological than mechanical (*32*).

Given the similarities between suspension feeding and other processes involving contact between small particles, temperature-induced viscosity change likely impacts a range of biological processes at small scales, including the uptake of particulate and dissolved nutrients (*5–7, 33*), fertilization kinetics (*34*), viral transmission (*35*), and the sinking and aggregation of bacteria, phytoplankton, and other suspended material (*36*). Such considerations can suggest new empirical and theoretical approaches to biomechanical evolution, the dynamics and organization of planktonic communities, and material and energy flow through aquatic systems. The biological effects of viscosity may prove to be especially important in freshwater systems that are small in size and subject to large temperature fluctuation. To distinguish such effects is critical for an understanding of the ecological and evolutionary responses of organisms to temperature variation on local and geographic scales.

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3. Seawater dynamic viscosity (with a salinity of 30 per mil) more than doubles over a range of tropical (30°C) to polar (0°C) ocean temperatures (Fig. 1), whereas seawater density (ρ) increases less than 1% [N. E. Dorsey, Ed., *Properties of Ordinary Water-Substance* (Hafner, New York, 1968)]. Thus, kinematic viscosity (μ/ρ) changes with μ.
4. The hydrodynamic scale can be characterized by the dimensionless Reynolds number (Re = object length × velocity/fluid kinematic viscosity), which indicates the relative importance of inertial and viscous forces. When Re < 1, viscous forces dominate. For study organisms, $Re_{body} \approx 0.1$ and $Re_{cilia} \approx 0.01$.
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12. Experiments were conducted in summers 1991 and 1992 at the Friday Harbor Laboratories, San Juan Island, WA. Adult *D. excentricus* were collected from a beach near Olga, Orcas Island; larvae were cultured by standard methods [M. F. Strathmann, *Reproduction and Development of Marine Invertebrates of the Northern Coast* (Univ. of Washington Press, Seattle, 1987)].
13. Polystyrene beads (Duke Scientific, Palo Alto, CA) allowed control of the size, quality, and concentration of particles. Videotapes of freely swimming larvae showed that particles were readily ingested upon introduction, that the ingestion rate was repeatable, and that particle rejections were similar under all treatments. Before addition to vials, particles were suspended in distilled water and separated through sonication. In experiments, final concentrations of the mixture of 10-, 5-, and 2-μm beads were 2, 4, and 20 per microliter, respectively.
14. Larvae were acclimated for 3 hours as specified in Fig. 1. In each vial, approximately 15 larvae

were then fed for 10 min on the bead mixture suspended in 18 ml of 0.45-μm filtered seawater. The short period ensured that particles were not defecated. The acclimation and feeding containers were rinsed, 20-ml borosilicate vials. Temperatures were maintained by recirculating water baths, and vials were turned gently every 3 min to keep larvae suspended. Larvae were fixed and inspected at a magnification of ×400 to count particles in the stomach and intestine. The measurement recorded was the average number of particles ingested by all feeding larvae within a vial. I inspected on average 9.0 (SD = 1.8) larvae per vial (× 6 treatments × 16 cohorts × 2 rearing temperatures).

15. Concentrations of dextran needed to alter seawater viscosity from 1.02 to 1.30 cP and to 1.60 cP were 0.75 and 1.4%, respectively, as determined with a falling-ball viscometer (GV-2100, Gilmont Instruments, Barrington, IL).
16. For populations in Puget Sound, larval development is normal in this temperature range (*12*), and individuals may be exposed to this range during development near the ocean surface [R. B. Emlet, *Mar. Ecol. Prog. Ser.* **31**, 245 (1986)]. In addition, *D. excentricus* experiences a wide temperature range over its distribution from Baja California to Alaska. All larvae used in experiments were at the four-arm to early six-arm stage of development (*12*).
17. The six treatments were run in parallel for each cohort of larvae. The relevant predictions were (i) A > B > C, (ii) A > B > D, (iii) E > B, (iv) A > F, and (v) cold-reared > warm-reared. I performed a two-way nested analysis of variance (ANOVA) on particles ingested to test for effects of treatment and rearing temperature, with cohorts nested within temperature. The treatment predictions reduce to five a priori pair-wise comparisons (A > B and F; B > C and D; E > B), which I tested using planned contrasts and a Bonferroni adjustment to α for five comparisons (α = 0.01).
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37. I thank R. Strathmann, J. Pearse, the Rohwer manuscript group, and two anonymous reviewers for helpful comments on the manuscript and R. Emlet for encouraging my interest in this work. Supported by an NSF graduate fellowship, a University of Washington Graduate School Fund grant, and NSF grant OCE-9301665 to R. Strathmann.

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Deletion of a DNA Polymerase β Gene Segment in T Cells Using Cell Type–Specific Gene Targeting

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Deletion of the promoter and the first exon of the DNA polymerase β gene (*polβ*) in the mouse germ line results in a lethal phenotype. With the use of the bacteriophage-derived, site-specific recombinase Cre in a transgenic approach, the same mutation can be selectively introduced into a particular cellular compartment—in this case, T cells. The impact of the mutation on those cells can then be analyzed because the mutant animals are viable.

Gene targeting in embryonic stem (ES) cells provides a powerful tool for generating mice carrying predesigned mutations in the germ line (*1*). Current approaches to gene inactivation usually involve the introduction of a null mutation directly into ES cells from which homozygous mutant mice can be generated. Because the null mutation is carried in the germ line of the mutant animals, it will exert its effects from the onset of animal development. Although this approach to gene inactivation is valuable, for many applications it is important that the inactivation of a particular gene occurs in a conditional manner—for instance, in a predefined cell lineage or at a certain stage of development. Such conditional gene targeting would not only overcome problems posed by the fact that null mutations in the germ line are often lethal, but would also allow a more precise analysis of the impact of a mutation on individual cell lineages.

Somatic gene rearrangement and hypermutation at lymphocyte antigen receptor gene loci are unique events that require DNA repair (*2, 3*). The *polβ* gene has been shown to be one of various enzymes involved in the DNA repair machinery (*4*).

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