Predators Induce Cloning in Echinoderm Larvae

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Asexual propagation (cloning) is a widespread reproductive strategy of plants and adult and larval animals. Possible advantages of larval cloning include increased fecundity, dispersal, and salvaging of material otherwise lost at metamorphosis (*1*–*4*). These advantages require a larval environment conducive to growth and reproduction. In contrast, we show here that echinoderm larvae clone in response to cues from fish predators, that is, under conditions indicating potential risk to larvae. Our results suggest that asexual reproduction can be a strategy for rapid size reduction as a defense.

We exposed 4-day-old sand dollar (*Dendraster excentricus*) larvae (plutei) to external mucus from fish (predator cues) (*5*). Within 24 hours, clones formed as buds aborally (Fig. 1A) or by anterior-posterior fission of early-stage larvae. Cloning occurred in all treatments with fish mucus: 20% at 0.01 mg of mucus/ml of seawater, 40% at 0.1 mg/ml, 10% at 1.0 mg/ml. Cloning was not observed in controls without fish mucus. Buds detached as evenly ciliated gastrulae and developed into small larvae. All products of cloning by budding and fission were smaller than uncloned larvae.

The response to fish mucus suggests that larval cloning may counter a threat of predation. Slow-swimming plutei have no effective escape from predatory fish; cloning may provide a temporary refuge from predation by producing two smaller, less-detectable propagules, a gastrula-like bud and a smaller-than-usual pluteus. Size reduction by cloning is slow compared with a fish attack, but the stimulus is presence of fish, as indicated by mucus, not an immediate attack by a fish.

Small size can protect zooplankton against predators. Smaller size at a given stage reduces vulnerability of fish larvae to visual predators (*6*). Small sand dollar larvae (from half-embryos) are less vulnerable to a visual predator (postlarval fish) although more susceptible to some nonvisual predators (*7*). However, there is evidence that small size in some zooplankton decreases vulnerability to nonvisual predators (*8*). We hypothesize that reduced size in clones decreases detection and selection by visual predators and may reduce signals to some nonvisual planktonic predators.

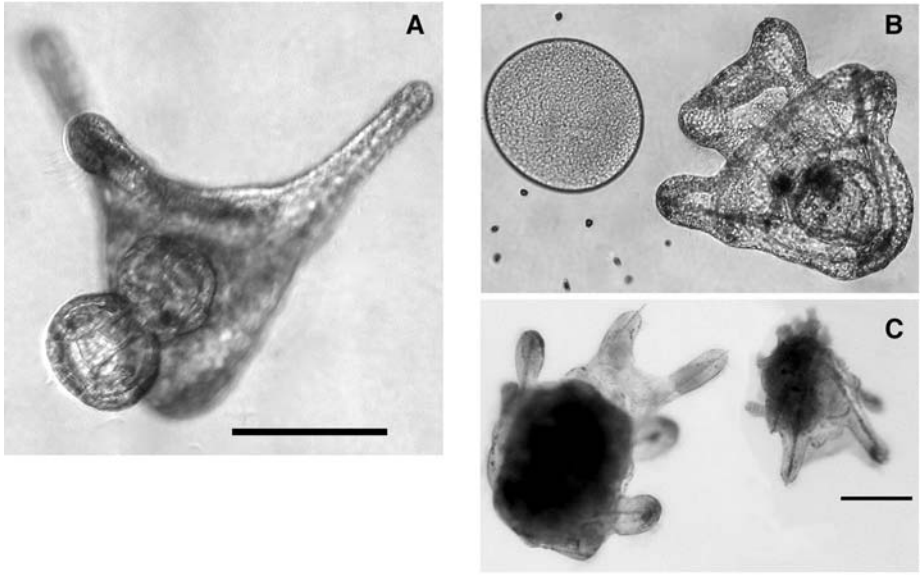

Fig. 1. Predator-induced cloning by early-stage sand dollar larvae (*Dendraster excentricus* plutei) and the effects of cloning on larval size. (**A**) A bud formed on the aboral surface of the primary larva that will subsequently be released as a gastrula-like individual. (**B**) A clone from asexual budding has developed to the six-arm stage but is only slightly larger than an egg (diameter of egg = 125 μm). (**C**) A late-stage clone with juvenile rudiment (right) and a sand dollar larva of the same developmental stage that was not exposed to fish-mucus stimuli (left). Scale bars indicate 100 μm in (A) and 200 μm in (C).

Reduced larval size resulting from predator-induced cloning also challenges the common assumption that bigger offspring are safer offspring. Cloning in plutei occurs in response to environmental information unavailable to parents on the sea floor. Adult sand dollars cannot assess risks to their planktonic offspring and adjust egg size accordingly. Instead, larvae may use information indicating risk in the plankton to adjust their size by cloning. Some cloned larvae were not much larger than conspecific eggs (Fig. 1B). Upon nearing metamorphosis, some clones were 2/3 the length (~1/3 the volume) of nonclones (Fig. 1C). Although size reduction may decrease vulnerability in the larval planktonic habitat, the persistence of small size implies that present risk for larvae is deferred to future risks for smaller juveniles on the sea floor.

Although larval cloning is known from all but one class of echinoderms (*1*), until now identified cues for cloning were limited to food and temperature favorable for growth and reproduction (*3*). Cloning in response to predators, like cloning in response to favorable conditions, can multiply each genet and increase fecundity, but advantages of predator-induced cloning do not depend on those features. If the small products of cloning are less vulnerable to predators, then cloning is adaptive whether all clonal products survive the process of division or only one.

Cloning by larvae in response to fish mucus suggests that even "restarting" development can provide a temporary escape from predation. We predict that cloning in response to predators will be found where safety lies in smaller size.

References and Notes

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Supporting Online Material

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Materials and Methods
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