

in a minor fraction of genes account for the adaptive differences that separate diverging species. If we had the sequence of several additional closely related sea urchin genomes, this model could be directly assessed. Another opportunity would arise if the genome sequences of two other widely used sea urchin species, *Lytechinus variegatus* and *Paracentrotus lividus*, were available: Comparison with the genome of *S. purpuratus* would yield a global map of conserved regulatory modules around every gene. Finally and most essentially, comparative regulatory genomics provides the key to unlock the basic processes of evolution. It has been possible to compare on a small scale the embryonic networks of two animals that have evolved independently for half a billion years, the sea urchin and the sea star (6). The comparison revealed both a shocking degree of architectural conservation in certain subcircuits and a shocking level of change of

others. This cuts close to the bone of the evolutionary processes by which body plans have diverged in evolution (7). Large-scale comparisons of regulatory gene networks between multiple species of different degrees of relatedness will provide a new dimension to our understanding of evolutionary mechanism and of network architecture and system design.

The sea urchin genome sequence did not open the door to a new pathway to knowledge; it opened the door to a nexus of such pathways. They lead in diverse directions, but their central and unifying reference is the genome sequence. Indeed, its central foundation in genomics will characterize a large area of bioscience, a reorganization that is already upon us, the coalescence of what might be called “informational bioscience.” This will consist of a scientific continuum over what used to be the distinct disciplines of regulation molecular bi-

ology, evolution, developmental biology, and genomics, together with their mathematical and computational support and more traditional descriptive knowledge. The sea urchin research community is now experiencing this intellectual revolution.

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PERSPECTIVE

Ecological Role of Purple Sea Urchins

John S. Pearse

Sea urchins are major components of marine communities. Their grazing limits algal biomass, and they are preyed upon by many predators. Purple sea urchins (*Strongylocentrotus purpuratus*) are among the best studied species. They live in environments that alternate between two stable states: luxuriant, species-rich kelp forests and sea urchin-dominated “barrens.” The transition from one state to the other can be initiated by several factors, including the abundance of algal food, predators, storm intensities, and incidence of disease. Purple sea urchins compete with other grazers, some of which are important fishery resources (such as abalones and red sea urchins), and they are harvested for scientific research. Revelations from their genome will lead to a better understanding of how they maintain their ecological importance, and may in turn enhance their economic potential.

Sea urchins are major grazers in shallow seas worldwide (1). Purple sea urchins (*S. purpuratus*) and other stronglycentrotid sea urchins of the Northern Hemisphere are particularly important and are the most intensively studied (2). A delicate balance between sea urchin grazing and kelp forest productivity leads to stable states that alternate between luxuriant kelp forests and relatively species-depauperate sea urchin “barrens” (3). Curiously, the densities of sea urchins are often similar within kelp forests and sea urchin barrens. Within kelp forests, sea urchins are nearly stationary, feeding on captured pieces of kelp litter (“drift kelp”) that are produced and shed in high quantities from the kelp plants. However, when the kelps are removed by storms or El Niño events, the remaining sea urchins actively forage on young kelp recruits and on drift kelp brought

in from elsewhere, preventing the reestablishment of the kelp forest. The sea urchins can be decimated by storms (4) or diseases (5), allowing the kelp forest to return to the area.

In addition to the alternation of kelp forests and sea urchin barrens, temporal and spatial variation in recruitment of sea urchins can greatly influence their abundance, and therefore their ecological role, within kelp forests. Infrequent peaks in recruitment can lead to spurts in sea urchin densities (6), sometimes triggering intense grazing that removes the kelp, transforming a kelp forest into a sea urchin barren (7) (Fig. 1). Recruitment intensity is determined mainly by the supply of sea urchin larvae, which in turn depends on the oceanographic conditions that bring the larvae to suitable areas to settle (8).

Predators almost certainly limited the abundance of sea urchins in the past, and the presence of sea urchin barrens around the world is due at least in part to decimation of predators by humans (9). In southern California, where

sea urchin-dominated barrens are common, major predators such as spiny lobsters, sheep-head fish, and sea otters have been greatly reduced during the past century (10). Sea otters, in particular, are effective in keeping sea urchin densities low throughout their range (11), which often tips the balance toward kelp forests and enhances kelp forest productivity and biodiversity (12). Other factors also can favor kelp forests or barrens, even in the absence of major sea urchin predators (13). For example, sea urchins compete with other grazers. Purple sea urchins compete in particular with abalones and red sea urchins (14). However, because both abalones and red sea urchins have experienced intensive fishing pressure for the past several decades, competitive interactions among these species have probably decreased, perhaps relieving purple sea urchins from adverse competition. On the other hand, juvenile purple sea urchins and abalones often are sheltered from predators under the spines of red sea urchins (15), and both may be negatively affected by heavy fishing of red sea urchins. The strengths of these interactions remain poorly known and are complicated by variation in fishing pressures. Red sea urchins have been the basis of a major fishery in the eastern Pacific for the past several decades. However, the U.S. sea urchin fishery has been in decline, mainly because of a decline in demand by the Japanese market (\$110 million worth of sea urchins were exported from the United States to Japan in 1993 compared with about \$36 million in 2003) (16). The smaller, less valuable, purple sea urchins have been a minor component of the fishery but continue to play an extensive role in scientific research (2).

Sea urchins are central in structuring marine benthic communities, both as grazers and prey, and are economically valuable in fisheries.

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Fig. 1. Purple sea urchins (*S. purpuratus*) grazing on the remains of a giant kelp hold fast after an unusually heavy recruitment in Carmel Bay, California (7). [Photo courtesy of J. M. Watanabe]

There are important differences among the different species: Some are more effective as grazers than others, and they vary in their diets,

growth rates, longevity, and importance in fisheries. Some show no sign of senility and live for well over a century (17). Elucidation of their

genomes will open new avenues of research into the underlying genetic and evolutionary bases of these variations.

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RESEARCH ARTICLE

The Genome of the Sea Urchin *Strongylocentrotus purpuratus*

Sea Urchin Genome Sequencing Consortium*†

We report the sequence and analysis of the 814-megabase genome of the sea urchin *Strongylocentrotus purpuratus*, a model for developmental and systems biology. The sequencing strategy combined whole-genome shotgun and bacterial artificial chromosome (BAC) sequences. This use of BAC clones, aided by a pooling strategy, overcame difficulties associated with high heterozygosity of the genome. The genome encodes about 23,300 genes, including many previously thought to be vertebrate innovations or known only outside the deuterostomes. This echinoderm genome provides an evolutionary outgroup for the chordates and yields insights into the evolution of deuterostomes.

The genome of the sea urchin was sequenced primarily because of the remarkable usefulness of the echinoderm embryo as a research model system for modern molecular, evolutionary, and cell biology. The sea urchin is the first animal with a sequenced genome that (i) is a free-living, motile marine invertebrate; (ii) has a bilaterally organized embryo but a radial adult body plan; (iii) has the endoskeleton and water vascular system found only in echinoderms; and (iv) has a nonadaptive immune

system that is unique in the enormous complexity of its receptor repertoire. Sea urchins are remarkably long-lived with life spans of *Strongylocentrotus* species extending to over a century [see supporting online material (SOM)] and highly fecund, producing millions of gametes each year; and *Strongylocentrotus purpuratus* is a pivotal component of subtidal marine ecology and an important fishery catch in several areas of the world, including the United States. Although a research model in developmental biology for a

century and a half, for most of that time, few were aware of one of the most important characteristics of sea urchins, a character that directly enhances its significance for genomic analysis: Echinoderms (and their sister phylum, the hemichordates) are the closest known relatives of the chordates (Fig. 1 and SOM). A description of the echinoderm body plan, as well as aspects of the life-style, longevity, polymorphic gene pool, and characteristics that make the sea urchin so valuable as a research organism, are presented in the SOM.

The last common ancestors of the deuterostomal groups at the branch points shown in Fig. 1 are of Precambrian antiquity [>540 million years ago (Ma)], according to protein molecular phylogeny. Stem group echinoderms appear in the Lower Cambrian fossil assemblages dating to 520 Ma. Cambrian echinoderms came in many distinct forms, but from their first appearance, the fossil record illustrates certain distinctive features that are still present: their water vascular system, including rows of tube feet protruding through holes in the ambulacral grooves and their calcite endoskeleton (mainly, a certain form of CaCO_3),

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