ities. The nutrient pulse from spawning is efficiently trapped, but this efficiency may become a threat on reefs exposed to continuous coastal eutrophication. Reefs within the Great Barrier Reef occur along gradients of water quality depending on their distances from point sources of pollution. Comparisons of ecosystem responses to spawning among these reefs may help to elucidate how these systems function under different levels of stress, as well as providing greater insights into coral reef functioning and resilience. References

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Diffusive random lasers, whose mechanism has

been elusive, are now explained by a general theory that encompasses conventional lasers.

10.1126/science.1155285

PHYSICS

A Unified Picture of Laser Physics

Jorge Bravo-Abad and Marin Soljačić

aser technology is present in our daily lives through literally thousands of applications, including surgical instruments, CD and DVD players, optical fiber communications, and even supermarket barcode readers. Despite the fast pace of laser research, the design of most laser devices relies on assumptions in the underlying theory that have barely changed since the early days of laser theory (1). However, this situation is problematic for two reasons. First, the rapid advance of nanofabrication techniques has led to the development of completely new lasing systems whose description falls outside the scope of conventional laser theory. Of these, random lasers (2) are perhaps the most challenging example. Second, more general models could enable the design of substantially different classes of lasers. With their contribution on page 643 of this issue, Türeci et al. (3) have substantially changed this picture. By developing a new theory in which the main properties of a laser can be physically understood as the result of strong nonlinear interactions between lasing modes, they have provided a substantially broader perspective of laser physics that unifies the physical description of many possible laser structures.

The most common description of a laser is that of an active lasing material, or gain medium (which could be an atomic vapor, a solid, or a dye), inside a resonant cavity formed by two mirrors. If the lasing material is properly pumped by an external excitation (which can be optical, electrical, etc.), most of the basic constituents of the lasing media (such as atoms, molecules, or ions) will be in excited states—it is said that the population inversion condition has been reached (1). Then, light of a certain frequency propagating through this medium will stimulate emission of radiation of the same frequency (and same direction) from the excited states. This process creates an amplifying medium: Light will be coherently amplified as it bounces back and forth inside the cavity, producing an output beam that is both highly directional and monochromatic (see the figure, left panel).

Standard laser theory explains the physics behind these devices, which resemble Fabry-Perot etalons and interferometers, provided that light is tightly trapped inside the cavity that is, when most of the energy of the amplified light remains inside the cavity for a long time (I). It also assumes that both the corresponding lasing frequencies and lasing modes are essentially determined by the modes and frequencies of the resonant cavity when the lasing material is not present.

The universality of this description has recently been challenged with the appearance of the so-called diffusive random lasers (4). A random laser consists essentially of a set of particles that scatter light and are embedded in a gain medium (see the figure, right panel). Most random lasers operate in the so-called diffusive regime, in which there are no lightconfinement mechanisms in the absence of the amplifying medium. Thus, diffusive random lasers apparently lack the strong lighttrapping mechanism that conventional laser theory regards as an essential ingredient for efficient light amplification.

At first glance, one might think that the physical mechanisms responsible for the lasing action in conventional and diffusive random lasers are very different. However, it has been shown experimentally that these two systems have the same basic features (4-7), which seems to suggest that a unified description should be possible. Until now, the theoretical analysis of random lasers has been restricted to fully numerical approaches (8), which, although interesting, do not offer a fundamental physical insight into mechanisms.

The theory developed by Türeci *et al.* to describe lasers provides the missing physical insight in an intrinsically elegant manner. By substituting the role of linear cavity reso-



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PERSPECTIVES

nances with a new set of modes—the constant-flux states—the authors find a simple analytical expression from which all of the properties of any laser structure can be obtained, given a knowledge of the dielectric constant profile of the system together with the main parameters characterizing the amplifying material (such as the amplification profile or the atomic frequency).

The versatility of their approach is demonstrated by applying it to the debate about the physical basis of lasing in diffusive random lasers. They show that for these kinds of structures, the lasing frequency predicted by standard laser theory is substantially modified by a new contribution that has no analog in conventional lasers. In addition, the theoretical framework developed by Türeci *et al.* allows us to track the competition between lasing modes within these systems as a result of a strong nonlinear interaction through the gain medium. More specifically, the authors show how pairs of modes of nearly identical frequencies compete with each other in a complex manner that ultimately determines both the emitted frequencies of the diffusive random lasers and their corresponding intensities; these predictions are in very good agreement with the recent experimental results (7). Finally, this new perspective on lasers reveals how the electric field profile in a diffusive random laser is more intense at the edge of the system than anywhere else in the sample—an interesting property that has also been observed in conventional lasers in which light is weakly confined.

In addition to its importance for understanding most of the physical properties discovered recently in diffusive random lasers, the theory of lasing provided by Türeci *et al.* may inspire the design of substantially different classes of structures that could be the basis of improved laser-based devices. From a more fundamental standpoint, this work could spark a new branch of nonlinear dynamics, in which phenomena such as optical bistability or multistability could be explored in novel types of lasing structures.

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10.1126/science.1157494

MOLECULAR BIOLOGY

The Paradox of Silent Heterochromatin

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ukaryotic chromosomes are generally partitioned into euchromatin and heterochromatin. The former is associated with actively expressed genes, whereas the latter has been considered to be inaccessible to RNA polymerase II, the enzyme that transcribes DNA to RNA. Heterochromatin is therefore transcriptionally silent. Paradoxically, to remain silent, heterochromatin that is located at a chromosome's centromerea region that is essential for chromosome separation during cell division-depends on both its transcription by RNA polymerase II and inhibition of its transcription by a mechanism called RNA interference (1-3). Two recent studies, by Kloc et al. (4) and by Chen et al. (5), demonstrate that transcription of this heterochromatin depends on the stage of the cell division cycle and thereby provides a possible solution to the paradox. According to the proposed model, the heterochromatic structure breaks up at the M phase (mitosis) of the cycle, enabling its transcription by RNA polymerase II, with subsequent reassembly

of heterochromatin and gene silencing.

The cell cycle of a eukaryotic cell is divided into four distinct phases: DNA replication at S phase; growth and preparation for division in G₂; nuclear division at M phase; and G₁, during which the cell may exit the cell cycle or continue dividing. Previously, heterochromatin has only been studied in asynchronous growing cell cultures, and cell cycle-dependent effects have not been appreciated. Kloc et al. and Chen et al. used synchronized cells to investigate the cell cycle dynamics of transcription and heterochromatin assembly at centromeres in the fission yeast Schizosaccharomyces pombe, the model organism in which the involvement of RNA interference in heterochromatin formation was first described (2). Both groups found that transcripts corresponding to centromeres (where there are large numbers of repeated DNA sequences) accumulate at S phase. This coincides with increased amounts of small interfering RNAs (siRNAs), which are derived from these transcripts. These siRNAs in turn silence the transcription of RNA from the centromeres by RNA interference. The assembly of heterochromatin at centromeres is also cell cycle dependent. Typical heterochromatic marks, such as the methylation of a lysine residue on Cell cycle control of heterochromatin disassembly may explain the paradox of heterochromatin gene expression.

histone 3 (H3K9me; histones are the major protein constituents of chromatin) and binding of the heterochromatin protein Swi6, decreased at S phase, causing the heterochromatin structure to become more loosely packed. Simultaneously, other marks that are associated with actively transcribed genes were detected. At the onset of M phase and remaining throughout the following S phase, there was a peak of phosphorylation of serine 10 on histone H3 (H3S10ph)-a mark antagonistic to Swi6 binding (6, 7)—together with methylation of lysine 4 on histone H3 (H3K4me). These changes further indicate that heterchromatin structure is changing and becoming more permissive to transcription.

These results support a stepwise model of cell cycle–regulated reassembly of heterochromatin at each cell division (see the figure). The densely packed structure of heterochromatin is dissolved at mitosis, followed by the binding of RNA polymerase II at S phase (5) and transcription. The transcripts are processed into siRNA that together with the RNA interference machinery directs the formation of heterochromatin to loci that are complementary to the siRNA. In addition, RNA polymerase II both directly and indirectly interacts (the latter, via nascent RNA)

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