Connectivity and Management of Caribbean Coral Reefs

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Science **278**, 1454 (1997);
DOI: 10.1126/science.278.5342.1454

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005.

ulation: Yanusari found that February characterizes the beginning of the El Niño cycle (*29*), and that in February (i) the amplitude and variability of the principal interannual atmospheric mode associated with the SO are highest (*30*) and (ii) the tropical convection that may lead to the onset of El Niño–Southern Oscillation (*31*) is strongest (*31*, *32*).

In conclusion, we have shown that an equatorial climatic mechanism produces strong variations of PP in the Indian Ocean. This mechanism is directly related to insolation and independent from global ice volume variations. It may be linked to past dynamics of the SO. If this mechanism acted over most of the equatorial ocean, the related PP variations could have produced a significant effect on global climates.

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$$\delta^{18}O = \frac{(\delta^{18}O/\delta^{16}O)_{sample} - (\delta^{18}O/\delta^{16}O)_{standard}}{(\delta^{18}O/\delta^{18}O)_{standard}} \times 1000$$

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25 March 1997; accepted 16 October 1997

Connectivity and Management of Caribbean Coral Reefs

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Surface current patterns were used to map dispersal routes of pelagic larvae from 18 coral reef sites in the Caribbean. The sites varied, both as sources and recipients of larvae, by an order of magnitude. It is likely that sites supplied copiously from "upstream" reef areas will be more resilient to recruitment overfishing, less susceptible to species loss, and less reliant on local management than places with little upstream reef. The mapping of connectivity patterns will enable the identification of beneficial management partnerships among nations and the design of networks of interdependent reserves.

Populations of marine organisms are typically much more open than terrestrial populations. The great majority of species have a dispersive pelagic larval stage, and many also disperse as eggs. Currents transport eggs and larvae, sometimes for long distances, generating interconnections among areas (*1*). Strong connectivity among areas implies that local populations may depend on processes occurring elsewhere. Consequently, local management initiatives may be ineffective in providing local benefits (although they may benefit other areas), and thus an increase in the scale of management may be necessary. Large-scale connectivity means that populations will often straddle political boundaries, sometimes several, and identifying which nations need to collaborate may seem to be a daunting task.

If a simplifying assumption is made—namely, that larvae are dispersed passively by currents—then surface current patterns should reveal routes of larval transport and patterns of connectivity (Fig. 1A). Potential connections among areas of the Caribbean (*2*) were mapped for dispersal periods of 1 and 2 months, which encompasses larval duration for the majority of reef species (*3*). For 18 locations with coral reefs, "transport envelopes" were mapped from which larvae spawned elsewhere could potentially arrive and to which larvae spawned locally could potentially be transported (Fig. 1, B and C). Measures of reef area within these envelopes reveal that from place to place in the Caribbean, there is an order of magnitude variation in both upstream and downstream reef area (Fig. 2).

Upstream reef area provides an indication of potential larval supply. At the low end of the scale, Barbados is almost entirely dependent on local larval production to replenish populations. By contrast, Andros Island, in the Bahamas, and reefs in the middle Florida Keys can draw larvae from very large catchments. Places with large upstream reef areas should be more resilient to recruitment overfishing (that is, fishing at intensities high enough that populations are limited by insufficient reproduction), because depletion of local populations may be offset by inputs of offspring spawned elsewhere. For example, Jamaica's reefs have been intensively fished since the end of the last century (*4*). Populations of many

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fish species on the north coast are almost entirely nonreproductive, as virtually all individuals are caught before sexual maturity (5). Such populations must be maintained by spawning elsewhere. The north coast of Jamaica has a relatively large upstream reef area, notably containing lightly fished reefs of the Turks and Caicos Islands (Fig. 2). In contrast to Jamaica, locations with little upstream reef will be more vulnerable to recruitment overfishing.

A corollary is that places with large upstream reef areas should be less dependent on local management to support fisheries or maintain biodiversity, whereas local management will be very important for places with little upstream reef. Overfishing has eliminated many large and vulnerable fish species from broad areas of the Caribbean—for example, groupers of the genus *Mycteroperca* (6). If a species like this were lost from Barbados, it might be a very long time before the population could be reestablished by larval input from elsewhere. A lack of larval supply is probably responsible for the slow rate of recovery of populations of large groupers after the establishment of a no-take marine reserve in Saba (7), an island with little upstream reef (Fig. 2).

Differences in downstream reef area of an order of magnitude can be expected to affect the performance of marine reserves, areas closed to fishing. Larval export provides the mechanism by which reserves can enhance fisheries (6, 8), but it could also mean that populations in reserves may not be self-sustaining. Replenishment is likely to depend, to a greater or lesser extent, on larval input from other sources. Consequently, isolated reserves will not necessarily maintain biodiversity over the long term, and there is a need to establish networks of interdependent reserves. This study suggests that reserves located in areas with large downstream reef area may be highly effective at supporting populations and fisheries elsewhere. McManus (9) and McManus and Meñez (3) have used such arguments in proposing the Spratly Islands in the South China Sea as a reserve that will benefit the fisheries of many neighboring countries.

The assumption of passive larval dispersal was necessary to make analysis of larval transport routes feasible. However, larvae of many species are likely to actively influence their dispersal to some extent, usually in the direction of greater local retention (*10–15*). Consequently, for most species the passive transport envelopes defined represent upper bounds to connectivity (maximum interaction distances) for larval durations of 1 and 2 months.

The use of current patterns to map linkages among reefs could aid the design of reserve networks. In areas with nonselective, multispecies fisheries (that is, most regions with coral reefs), reserves may be the only means of protecting large, long-lived, late-reproducing species such as many groupers (6). For reserves to interact effectively in maintaining biodiversity, they need to be located close enough together

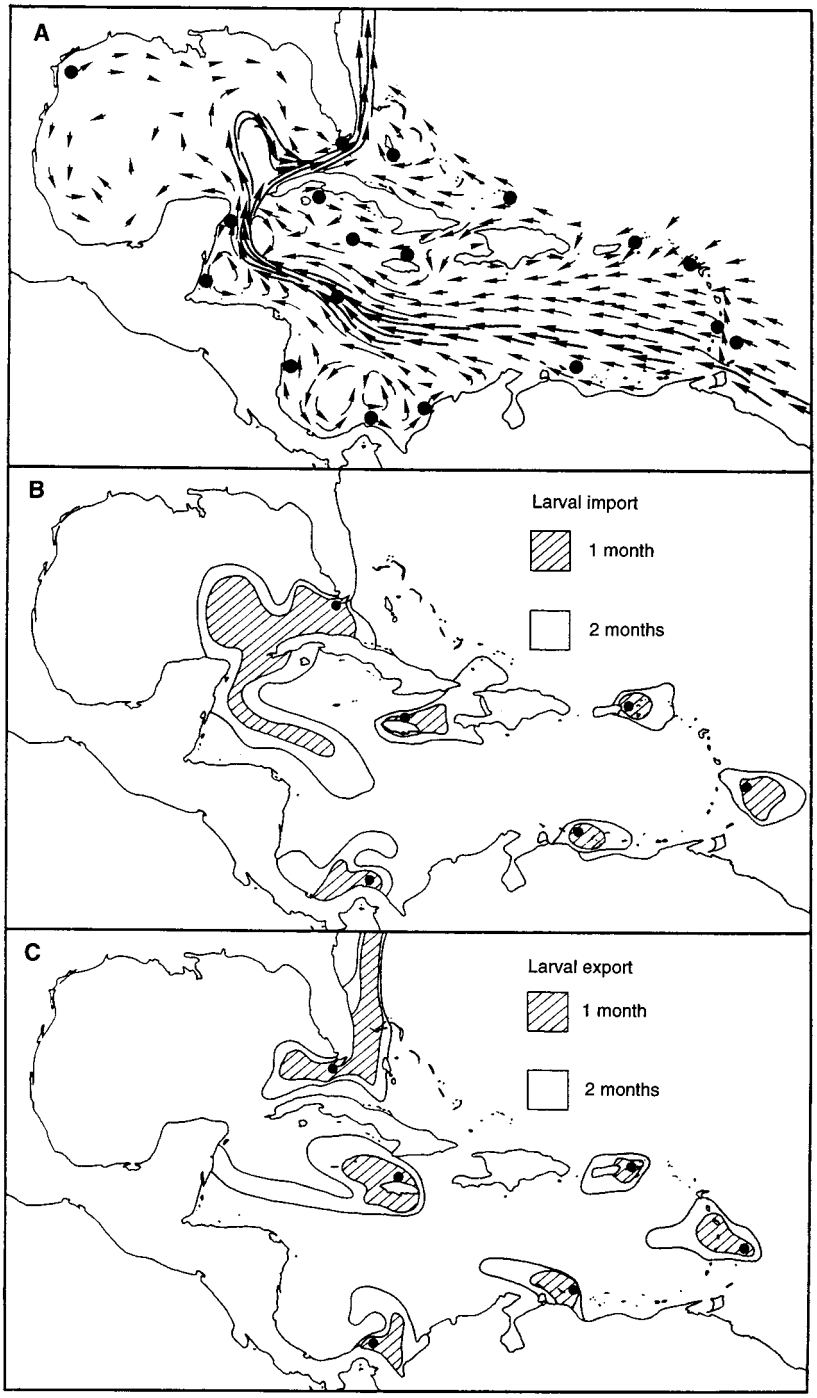

Fig. 1. (**A**) Major surface current patterns in the wider Caribbean region (*2*). The tail length and thickness of arrows are approximately proportional to current strength. There are weak nearshore countercurrent flows along most coastlines, but owing to scale constraints they are only shown for a few areas on this map. The 18 study locations are shown by dots. (**B**) One- and 2-month envelopes of potential larval transport showing upstream areas from which larvae could be imported to six of the 18 locations studied. Transport envelopes were calculated with the use of detailed data on current patterns and strength (*2*) surrounding each location and the distances a passively transported larva could travel to or from that point, calculated for 12 different directions around the compass, using the current speeds and the areas over which they would be experienced within each sector. (**C**) One- and 2-month envelopes of potential larval transport showing downstream areas to which larvae could be exported from the same six of the 18 locations studied.

that they can obtain larvae from upstream reserves and deliver them to downstream reserves. Although reserves can be expected to interact frequently within the 2-month larval transport envelope, the distances defined by the 1-month envelopes probably represent a safer maximum interaction distance (that is, minimum inter-reserve distance). Average interaction distances were 145 km for the 1-month envelope (both supply and delivery of larvae) and 212 and 219 km for the 2-month envelope (supply and delivery, respectively) (*16*).

Surface currents are vectors of gene flow for marine species with dispersive larvae, and future research into patterns of genetic similarity could test the validity of the transport envelopes described. Measured interaction distances among reefs imply high rates of gene flow leading to genetic similarity at a regional scale; this expectation has been confirmed by several studies (*17–21*). Shulman and Bermingham (*22*) recently found that genetic similarity among populations of eight fish species from six areas of the Caribbean did not obviously reflect current patterns. The most likely explanation is that the species examined were good dispersers. However, a few studies have shown regional genetic differentiation (*23, 24*), suggesting the existence of population-isolating mechanisms such as limited larval dispersal. Genetic data are likely to reveal transport routes most clearly for species that behave in ways that enhance local retention, thus increasing the number of generations required to circuit the region.

Mapped transport envelopes provide new insight into puzzling results from the Florida Keys about genetic patchiness in populations of a damselfish species, *Stegastes partitus*. Lacson and Morizot (*25*) identified significant genetic differences between populations separated by only a few kilometers. They reasoned that these populations had diverged as a result of a local genetic bottleneck caused by disturbance. A simpler alternative is that one sample originated through settlement from Central American sources while the other came from the Bahamas. Reefs in the Keys can be supplied with larvae from either area, but connectivity between the Bahamas and Central America is limited, suggesting the possibility of genetic differentiation of source populations. Two generations later, the genetic difference between populations of this short-lived species disappeared, suggesting subsequent recruitment to both from a single source region.

Patterns of interconnection among marine resources have long been recognized as an important management concern, but little action has been taken anywhere to link up management initiatives across international boundaries. The task of identifying linkages has seemed daunting, and the problem of reaching an agreement about management among a plethora of different nations almost intractable. Mapping connectivity patterns will enable the identification of key management partnerships that should be forged among Caribbean states. Numbers of core upstream partner nations—that is, those located within the 1-month envelope of larval transport—vary between 0 and 6, with an average of 2.1 nations (±0.4 SE) per reef location studied. Adding more distant partners—that is, those within the 2-month envelope—increases the average number of partner nations to 3.5 (±0.4 SE) with a range of 1 to 7. For example, core management partners for the U.S. Virgin Islands would include Puerto Rico and the British Virgin Islands; inclusion of partners within the 2-month transport envelope would add St. Martin, Anguilla, and the Netherlands Antilles (Fig. 1, B and C). A region like the Caribbean will contain many such local networks of management partners, each overlapping others. For a region so politically diverse, the numbers of partner nations within local management networks are actually rather small and lie well within the bounds of practicality.

A great deal more research will be needed to determine just how much influence species have over their dispersal as larvae. This study suggests that, even with passive dispersal, interaction distances among reefs are generally relatively short, and for marine reserves to be effective they need to be established in dense networks spanning international coalitions of management partners. For those cases where active dispersal enhances local retention, effective interaction distances will become smaller, and for reserves to effectively support populations in other reserves, they will need to be even more closely spaced. The most important implication of greater local retention is that local management actions are likely to generate larger local benefits. This is good news for those hoping to benefit local fisheries by creation of no-take reserves. It is good news also for places with very little upstream reef area. It means that in such areas, local management initiatives could achieve lasting security for reef resources.

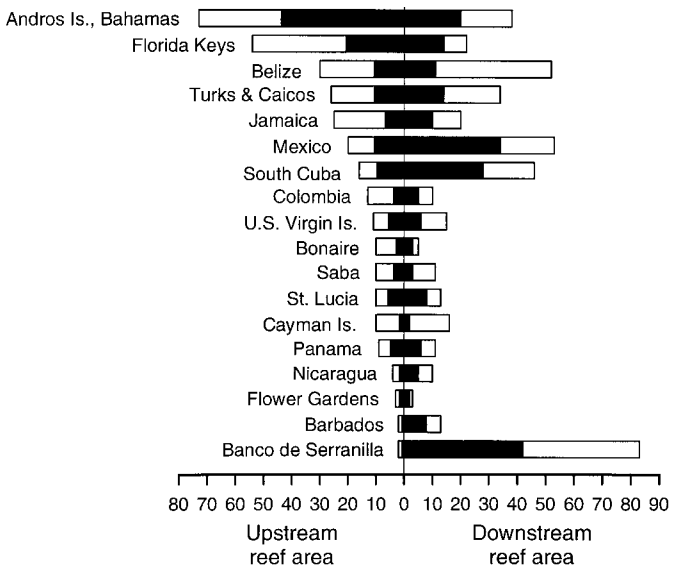

Fig. 2. Comparison of 1-month (solid bars) and 2-month (open bars) larval transport envelopes showing upstream and downstream reef area for each of the 18 locations studied, ranked in order of decreasing upstream reef area. Reef area is calculated as an index showing the number of 1/4° latitude (approximately 28 by 28 km) cells containing coral reefs that lie inside each envelope. Upstream reef area provides an indication of the likely magnitude of larval import to a location. Downstream reef area provides a measure of the likelihood of a larva spawned at a particular location finding a reef on which to settle and live. Both upstream and downstream reef area vary among locations by an order of magnitude. Although areas within dynamic current fields tend to have larger upstream and downstream reef area than those in weaker current fields, the similarity in size of areas of potential import and export is weak (Spearman's rank correlation of upstream versus downstream reef area = 0.49, $P = 0.04$).

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29 July 1997; accepted 8 October 1997

Crystal Structure of Methyl–Coenzyme M Reductase: The Key Enzyme of Biological Methane Formation

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Methyl–coenzyme M reductase (MCR), the enzyme responsible for the microbial formation of methane, is a 300-kilodalton protein organized as a hexamer in an $\alpha_2\beta_2\gamma_2$ arrangement. The crystal structure of the enzyme from *Methanobacterium thermoautotrophicum*, determined at 1.45 angstrom resolution for the inactive enzyme state $MCR_{ox1\text{-}silent}$, reveals that two molecules of the nickel porphinoid coenzyme F_{430} are embedded between the subunits α, α', β, and γ and α', α, β', and γ', forming two identical active sites. Each site is accessible for the substrate methyl–coenzyme M through a narrow channel locked after binding of the second substrate coenzyme B. Together with a second structurally characterized enzyme state (MCR_{silent}) containing the heterodisulfide of coenzymes M and B, a reaction mechanism is proposed that uses a radical intermediate and a nickel organic compound.

Methyl–coenzyme M reductase is the key enzyme of methane formation in methanogenic Archaea. It catalyzes the reduction of methyl–coenzyme M (methyl-CoM) [CH_3-S-CoM, 2-(methylthio)ethanesulfonate] with coenzyme B (CoB) (CoB-S-H, 7-thioheptanoyl-threoninephosphate) to methane and the heterodisulfide of CoM (CoM-S-H, 2-thioethane sulfonate) and CoB under strictly anaerobic conditions (*1*, *2*).

About 10^9 tons of CH_4 are produced per year by the reaction in Scheme 1. Part of it escapes to the atmosphere and acts as a potent greenhouse gas (*3*). Methyl-CoM reductase was first characterized by Ellefson and Wolfe (*4*) as a yellow protein of an apparent molecular mass of 300 kD composed of three different subunits arranged in an $\alpha_2\beta_2\gamma_2$ configuration. The hexameric protein contains two molecules of the tightly but not covalently bound coenzyme F_{430} (*4*), which is a Ni porphinoid (*5*).

Spectroscopic investigations of methyl-CoM reductase have revealed several Ni electron paramagnetic resonance (EPR) active and inactive states of the enzyme (*6*). After harvest of H_2-CO_2 grown cells, the enzyme is present in an inactive EPR silent state designated as MCR_{silent}. In this state, methyl-CoM reductase contains bound CoM (*7*) and CoB (*8*) and can only be partially reactivated by enzymatic reduction (*9*). When cells are gassed with H_2 before harvesting, the enzyme is present in an active MCR_{red1} state whose characteristic Ni(I) F_{430} EPR spectrum, designated red 1, can be correlated with the enzymatic activity in the enzyme (*10*). Even under strictly anaerobic conditions, the activity of the enzyme is completely lost within a few hours, and the enzyme enters an inactive EPR-silent Ni(II) state denoted as $MCR_{red1\text{-}silent}$. When cells are gassed with CO_2-N_2 before being harvested, the enzyme enters into the MCR_{ox1} state, which exhibits a Ni EPR spectrum, designated ox1, substantially different from that of the MCR_{red1} state. The MCR_{ox1} state has only very low activity but can be activated in vitro by reduction with Ti(III) citrate (*11*) into the MCR_{red1} state. Preparations in the MCR_{ox1} state slowly turn into an inactive EPR silent state, referred to as $MCR_{ox1\text{-}silent}$.

Methyl-CoM reductase (isoenzyme I) was aerobically crystallized in the enzymatically inactive enzyme states $MCR_{ox1\text{-}silent}$ and MCR_{silent}, as described by Shima *et al.*

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