Metabolic Activity of Subsurface Life in Deep-Sea Sediments

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Global maps of sulfate and methane in marine sediments reveal two provinces of subsurface metabolic activity: a sulfate-rich open-ocean province, and an ocean-margin province where sulfate is limited to shallow sediments. Methane is produced in both regions but is abundant only in sulfate-depleted sediments. Metabolic activity is greatest in narrow zones of sulfate-reducing methane oxidation along ocean margins. The metabolic rates of subseafloor life are orders of magnitude lower than those of life on Earth's surface. Most microorganisms in subseafloor sediments are either inactive or adapted for extraordinarily low metabolic activity.

During the past 15 years, studies of Ocean Drilling Program (ODP) cores have consistently identified abundant prokaryotes in deeply buried oceanic sediments (*1*). Microorganisms have been recovered from depths as great as 800 m below the seafloor (mbsf) (*2*). The potential for in situ activity of subseafloor microorganisms has been demonstrated by geochemical (*3*) and radiotracer (*1, 4*) experiments on sediments recovered from a range of burial depths. In recent contamination-tracer experiments, most of the microorganisms reported from ODP cores were inherent to the drilled sediments (*5*).

The number and mass of prokaryotes in subseafloor sediments have been estimated by extrapolation from direct counts of sedimentary microorganisms at a small number of ODP sites (*6, 7*). On the basis of that extrapolation, these prokaryotes constitute one-tenth (*6*) to one-third of Earth's biomass (*7*). In situ metabolic activity by at least some of these prokaryotes is spectacularly demonstrated by hydrates of methane (CH_4) produced in deep-sea sediments. These hydrates contain four to eight times the amount of carbon in Earth's surface biomass and terrestrial soils combined (*8*). Porewater chemical studies (*9*) and recent microbiological discoveries (*10, 11*) suggest that, on an ongoing basis, the CH_4 produced in deep-sea sediments may be primarily destroyed by sulfate-reducing activity of microorganisms in overlying sediments.

The activity of subseafloor microorganisms may directly affect the surface Earth. Intermittent release of CH_4 from marine sedimentary hydrates may have greatly affected the global climate and/or oceans several times in Earth history [e.g., (*12*)]. And relatively small changes in subsurface sulfate (SO_4^{2-}) reduction may have appreciably affected total oceanic alkalinity and, consequently, the partitioning of CO_2 between atmosphere and ocean over geologic time (*13*). Despite the large apparent mass and possible biogeochemical effects of subseafloor life, the magnitude of its metabolic activity in situ remains largely unknown. To assess this activity, we have compiled and analyzed sedimentary porewater chemical data from Deep Sea Drilling Project (DSDP) and ODP sites throughout the world ocean (DSDP Leg 1 through ODP Leg 182) (*14*).

We can infer that SO_4^{2-} reduction, methanogenesis (CH_4 production), and fermentation are the principal degradative metabolic processes in subsurface (>1.5 mbsf) marine sediments, for three reasons: (i) At the sediment-water interface, concentrations of dissolved SO_4^{2-} are more than 50 times as great as concentrations of all electron acceptors with higher standard free energies combined (*15, 16*). (ii) External electron acceptors that yield more energy than SO_4^{2-} typically disappear within the first few centimeters to tens of meters of sediment depth (*15*). (iii) Once all SO_4^{2-} has been reduced, methanogenesis and fermentation are the principal remaining avenues of metabolic activity.

The concentration of dissolved SO_4^{2-} in typical marine sediments results from the balance between diffusion of SO_4^{2-} from the overlying ocean and reduction of SO_4^{2-} by microbial activity in the sediments. Peak SO_4^{2-} concentrations typically occur at the sediment-water interface (Fig. 1). Sulfate concentrations are generally stable over stratigraphic intervals where little SO_4^{2-} reduction occurs (Fig. 1). At sites where subsurface microbial activity is consistently low, SO_4^{2-} concentrations are relatively high throughout the sediment column (Fig. 1, A and C). Where subsurface activity is relatively high, all dissolved SO_4^{2-} is consumed in the upper sediment column and microorganisms in deeper sediments produce CH_4, which diffuses up toward the sulfate-rich sediments (Fig. 1B). Consequently, peak CH_4 concentrations usually occur in sulfate-depleted sediments well below the seafloor (Fig. 1B). At sites where upward-diffusing CH_4 is entirely consumed by sulfate-reducing methane oxidation (*9*), CH_4 approaches laboratory-background concentrations within the sulfate reduction zone (Fig. 1, B and C).

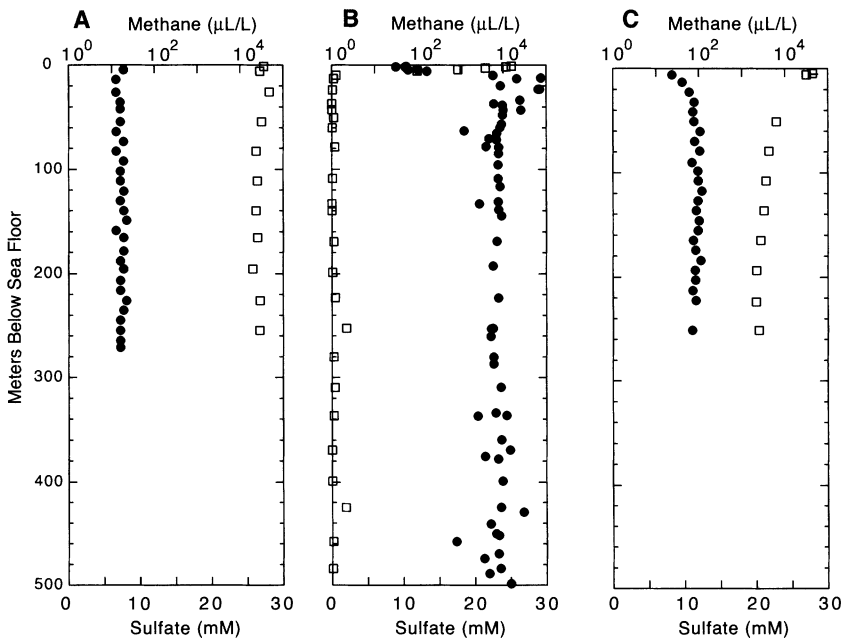

Fig. 1. Representative profiles of SO_4^{2-} (open squares) and CH_4 (solid circles) concentrations in deep-sea sediments: (**A**) open-ocean ODP Site 851, (**B**) ocean-margin ODP Site 798, (**C**) open-ocean ODP Site 846.

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To identify geographic patterns of SO_4^{2-} reduction and methanogenesis in deep-sea sediments, we created global maps of SO_4^{2-} and CH_4 concentration data from DSDP and ODP cores (Fig. 2). The maps exhibit two broad patterns in subsurface SO_4^{2-} and CH_4 concentrations. First, in open-ocean sediments, dissolved SO_4^{2-} concentrations are high and CH_4 concentrations are low throughout the entire sediment column (Fig. 2). Second, along ocean margins, dissolved SO_4^{2-} concentrations are essentially reduced to zero within a few tens of mbsf (Fig. 2A). Below this depth, CH_4 concentrations are high because microbial activity is generally limited to fermentation and methanogenesis (Fig. 2B).

The continuously high SO_4^{2-} concentrations and low CH_4 concentrations of open-ocean sites indicate that rates of SO_4^{2-} reduction and CH_4 production are very low in subsurface open-ocean sediments. In contrast, the general absence of SO_4^{2-} below a few tens of mbsf at ocean-margin sites indicates that the rate of subsurface SO_4^{2-} reduction is high relative to the rate of downward SO_4^{2-} diffusion in ocean-margin sediments. The absence of high CH_4 concentrations in the shallowly buried sulfate-rich zone of ocean-margin sites suggests that subsurface sulfate-reducing methane oxidation is the primary means of CH_4 destruction throughout the world ocean.

About one-sixth of all open-ocean sites (32 of 184 sites) contain abundant dissolved SO_4^{2-} and above-background CH_4 concentrations (~10 to 1000 ppm) (Fig. 2, A and B). These are typically sites with cool (<20°C) organic-poor open-ocean sediments that lack strong subsurface flow and lie hundreds to thousands of km from the organic-rich methanogenic zones of the oceanic margins (*17*). In general, CH_4 profiles mirror SO_4^{2-} profiles at these sites (Fig. 1C); CH_4 concentrations are stable and relatively high over intervals of stable SO_4^{2-} concentrations, but they decline to background values in the shallowly buried sulfate reduction zone. This finding indicates that methanogenesis commonly occurs in sulfate-rich open-ocean sediments. This occurrence conflicts with the generally accepted redox sequence, based on standard-state free energies of reaction (*18*), which predicts that sulfate will be depleted before methanogenesis occurs.

The occurrence of methanogenic activity in sulfate-rich open-ocean sediments may result from one or more causes. The methanogens and the sulfate-reducing microorganisms may rely on different electron donors (*19*). The relative in situ free energies of SO_4^{2-} reduction and CO_2 reduction may deviate from standard-state free energies. Ecological properties, such as relative predation susceptibility, may allow methanogens to persist in an environment energetically more favorable to sulfate reducers. Methanogens may be adapted to survive at lower rates of dissolved electron donor production.

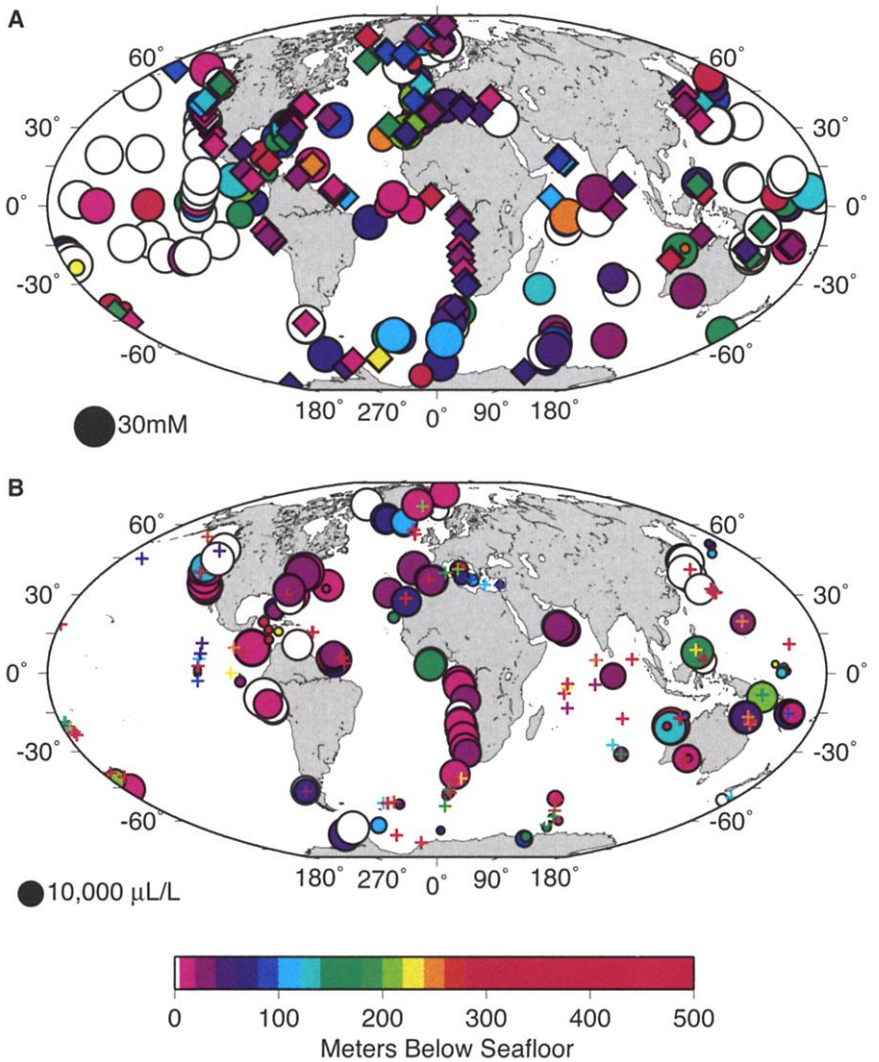

Fig. 2. (**A**) Global SO_4^{2-} map. Symbol color indicates the depth of the shallowest sample where subsurface SO_4^{2-} concentrations either stabilize at a nonzero value (circles) or reach zero (diamonds) (white, ≤5 mbsf). Circle size indicates the SO_4^{2-} concentration at which each subsurface SO_4^{2-} profile stabilizes. (**B**) Global CH_4 map. Circle color indicates the depth of the shallowest sample that exhibits a CH_4 concentration above the laboratory background level (white, ≤5 mbsf). Circle size indicates the peak subsurface concentration. Crosses mark sites where CH_4 never rises above laboratory background. Cross color marks the depth of the deepest sample analyzed (*36*).

In sedimentary ecosystems where SO_4^{2-} is the terminal electron acceptor (e.g., $3SO_4^{2-} + C_6H_{12}O_6 \rightarrow 3S^{2-} + 6CO_2 + 6H_2O$), the depth-integrated rate of SO_4^{2-} reduction is a direct measure of total dissimilatory activity. At open-ocean sites, where CH_4 concentrations are low, the dissimilatory activity of subsurface microorganisms can be approximated by the flux of dissolved SO_4^{2-} into the sediment (*20*). Along ocean margins, where subsurface CH_4 is destroyed by sulfate-reducing methane oxidation at the CH_4-SO_4^{2-} interface, total subsurface dissimilation can also be approximated by the flux of dissolved SO_4^{2-} into the sediment. In such regions, degradative metabolic activity in sediments deeper than the sulfate reduction zone is ultimately methanogenic (e.g., $C_6H_{12}O_6 \rightarrow 3CH_4 + 3CO_2$). Relative to CH_4, appreciable concentrations of hydrogen (*21*) and dissolved organic products of fermentation (*22*) do not occur at the CH_4-SO_4^{2-} interface or in the upper portion of the methane-rich zone. In these subsurface environments, SO_4^{2-} serves as the terminal electron acceptor for the ecosystem as a whole, because the CH_4 is consumed by SO_4^{2-} reduction as it diffuses up into the sulfate-rich zone ($SO_4^{2-} + CH_4 \rightarrow S^{2-} + CO_2 + 2H_2O$). The diffusive flux of CH_4 upward can be estimated by assuming that all of the SO_4^{2-} reduced in the CH_4-SO_4^{2-} transition zone is used for methane

Table 1. Rates of biological activity at representative sites (*23*). n/a indicates that SO_4^{2-} is present throughout the drilled hole and, consequently, that there is no base to the SO_4^{2-} reduction zone in the sampled sediment column.

Location	Base of SO_4^{2-} reduction zone (mbsf)	SO_4^{2-} flux downward to subsurface (mol cm^{-2} $year^{-1}$)	SO_4^{2-} flux due to CH_4 oxidation (% of total)	Total subsurface respiration (mol CO_2 cm^{-2} $year^{-1}$)	Photosynthesis of overlying ocean (mol CO_2 reduced cm^{-2} $year^{-1}$)
		Ocean-margin sites			
798B (Japan Sea)	10	$4.2 (\pm 1.3) \times 10^{-6}$	80	$8.4 (\pm 2.6) \times 10^{-6}$	2.3×10^{-3}
681C (Peru Margin)	30	$8.1 (\pm 2.5) \times 10^{-7}$	85	$1.6 (\pm 0.5) \times 10^{-6}$	4.9×10^{-3}
1175 (Nankai Trough)	11	$1.3 (\pm 0.6) \times 10^{-6}$	43	$2.6 (\pm 1.2) \times 10^{-6}$	1.8×10^{-3}
		Open-ocean sites			
851 (Equatorial Pacific)	n/a	$2.8 (\pm 2.5) \times 10^{-9}$	0	$5.6 (\pm 5.0) \times 10^{-9}$	9.3×10^{-4}
834 (Lau Basin)	n/a	$2.0 (\pm 2.2) \times 10^{-9}$	0	$4.0 (\pm 4.4) \times 10^{-9}$	6.7×10^{-4}
1149 (Izu-Bonin Trench)	n/a	$1.3 (\pm 0.6) \times 10^{-8}$	0	$2.6 (\pm 1.2) \times 10^{-8}$	4.8×10^{-4}

Table 2. Sulfate reduction per subsurface cell at representative sites (*27*). n/a indicates that there is no discernible subsurface methane oxidation zone at the site.

Location	Mean SO_4^{2-} reduction per cell in CH_4-depleted SO_4^{2-}-rich zone (mol $cell^{-1}$ $year^{-1}$)	Mean SO_4^{2-} reduction per cell in anaerobic methane oxidation zone (mol $cell^{-1}$ $year^{-1}$)
	Ocean-margin sites	
798B (Japan Sea)	$3.1 (\pm 1.3) \times 10^{-17}$	$2.6 (\pm 1.1) \times 10^{-16}$
681C (Peru Margin)	$1.4 (\pm 0.6) \times 10^{-19}$	$6.4 (\pm 2.7) \times 10^{-18}$
1175 (Nankai Trough)	$3.3 (\pm 1.4) \times 10^{-15}$	$7.5 (\pm 3.8) \times 10^{-15}$
	Open-ocean sites	
851 (Equatorial Pacific)	$1.2 (\pm 1.1) \times 10^{-19}$	n/a
834 (Lau Basin)	$1.5 (\pm 1.7) \times 10^{-20}$	n/a
1149 (Izu-Bonin Trench)	$9.5 (\pm 5.8) \times 10^{-20}$	n/a

oxidation. If the upward diffusion of CH_4 into the CH_4-SO_4^{2-} transition zone is in a steady-state balance with the rate of CH_4 production below, then (i) the total rate of microbial activity within the methanogenic zone can be directly estimated from the rate of SO_4^{2-} reduction in the transition zone, and (ii) the total respiration of the entire sediment column is approximated by the downward flux of SO_4^{2-} into the sediment column.

We have determined the downward flux of dissolved SO_4^{2-} at six representative ODP sites (Table 1) (*23*). Total rates of subsurface SO_4^{2-} reduction are at least two to three orders of magnitude higher at the methane-rich ocean-margin sites than at the sulfate-rich open-ocean sites (Table 1). At the open-ocean sites, total rates of subseafloor SO_4^{2-} reduction are so low as to be nearly indistinguishable from zero (Table 1). This finding of a large difference between SO_4^{2-} reduction rates at ocean-margin sites and those at open-ocean sites is consistent with an earlier study of DSDP sites (*24*), which found that SO_4^{2-} reduction can vary by a factor of more than 1000 from one marine environment to another.

On a more detailed level, these flux calculations suggest that subseafloor metabolic activity is greatly concentrated in relatively narrow zones of anaerobic methane oxidation along ocean margins. At the ocean-margin sites, most of the SO_4^{2-} flux downward past 1.5 mbsf is used to oxidize CH_4 created in the underlying sediments (Table 1). Recent studies have similarly shown that in sediments along the continental slope of Namibia (*25*) and in sediments of the Amazon Fan (*26*), nearly 100% of the downward SO_4^{2-} flux goes to anaerobic CH_4 oxidation. Comparison of these ocean-margin fluxes to the SO_4^{2-} fluxes at open-ocean sites (Table 1) suggests that anaerobic methane oxidation may be the dominant sink for SO_4^{2-} in marine sediments. Consequently, it may have a considerable long-term effect on oceanic alkalinity.

In terms of carbon content, the estimated mass of subsurface microorganisms in marine sediments (3×10^{17} g C) is two orders of magnitude greater than the mass of living organisms in the overlying ocean (4×10^{15} g C) (*7*). Despite its large inferred size, the annual metabolic activity of this subsurface world is extremely low relative to the annual metabolic activity in the overlying ocean. At the ocean-margin sites, the annual rate of biomass production in the sunlit water of the ocean surface is two or more orders of magnitude greater than the annual rate of subsurface respiration in the underlying sediments (Table 1). And at the open-ocean sites, the rate of oceanic biomass production is four or more orders of magnitude greater than the rate of respiration in the underlying sediments (Table 1).

The mean respiration per enumerated subsurface cell can be calculated from the flux estimates of Table 1 and previously published cell counts (*27*) (Table 2). Mean respiration per cell is highest in the anaerobic methane-oxidation zones of the ocean-margin sites and lowest in the methane-poor sulfate reduction zones of the open-ocean sites. Most rates of SO_4^{2-} reduction in Table 2 are orders of magnitude lower than per-cell rates of SO_4^{2-} reduction exhibited by pure sulfate-reducing bacteria cultures or radiotracer experiments with coastal marine sediments. Per-cell rates measured for pure cultures range from 7×10^{-14} to 1×10^{-11} mol SO_4^{2-} $cell^{-1}$ $year^{-1}$ (*28, 29*). Per-cell rates calculated from absolute cell numbers and radiotracer-based SO_4^{2-} reduction rates of marine coastal near-surface ($\leq$10 cm below seafloor) sediments (*30*) are in the range of 1×10^{-15} to 2×10^{-15} mol SO_4^{2-} $cell^{-1}$ $year^{-1}$ (*31*).

These comparisons suggest that very little adaptation to low metabolic activity is necessary for most enumerated subsurface microorganisms to be active in the anaerobic methane-oxidation zone at the sites of highest activity (1175 and 798B). They also indicate that most of the subseafloor microorganisms enumerated in most sediment at most sites must be either inactive or adapted for extraordinarily low metabolic activity.

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13. In modern seawater, SO_4^{2-} constitutes about 27 times as many equivalents as does alkalinity (*16*). Sulfate reduction followed by sulfide precipitation

results in the production of two equivalents of alkalinity per mole.
14. Sulfate is routinely accurately measured on ODP cruises. In contrast, because sediments outgas as cores are brought up through the water column, concentrations of CH_4 in deep-sea porewaters cannot routinely be accurately estimated from ODP CH_4 concentration data (headspace analysis). This quality of the CH_4 data does not preclude using these SO_4^{2-} and CH_4 data (i) to map downhole profiles of relative CH_4 abundance, or (ii), as described in the text, to estimate steady-state rates of sulfate-reducing methane oxidation and (by inference) CH_4 production. The DSDP and ODP shipboard data used for these profiles and maps were edited to remove samples affected by seawater contamination and sites where spot coring, poor core recovery, or intermittent porewater sampling caused large gaps that rendered profiles difficult to interpret. Sites with fewer than three samples in the zone of stable SO_4^{2-} concentrations were excluded from the SO_4^{2-} map. Because we limited our study to the diffusional realm typical of open-ocean sediments, this analysis omitted stratigraphic intervals from downhole SO_4^{2-} and CH_4 records in cases where porewater chemical profiles were unambiguously affected by hydrologic flow or pronounced lithologic breaks, subsurface anhydrite deposits, or sulfate-enriched brines. Sites identified as probably affected by $CaSO_4$ precipitation in the underlying basement were also deleted from the SO_4^{2-} map.
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Demographic Characteristics and Population Dynamical Patterns of Solitary Birds

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In birds and many other animals, there are large interspecific differences in the magnitude of annual variation in population size. Using time-series data on populations of solitary bird species, we found that fluctuations in population size of solitary birds were affected by the deterministic characteristics of the population dynamics as well as the stochastic factors. In species with highly variable populations, annual variation in recruitment was positively related to the return rate of adults between successive breeding seasons. In stable populations, more recruits were found in years with low return rates of breeding adults. This identifies a gradient, associated with the position of the species along a "slow-fast" continuum of life history variation, from highly variable populations with a recruitment-driven demography to stable, strongly density-regulated populations with a survival-restricted demography. These results suggest that patterns in avian population fluctuations can be predicted from a knowledge of life-history characteristics and/or temporal variation in certain demographic traits.

One of the challenges in ecology is to identify characteristics that can be used to predict interspecific differences in patterns of population fluctuations (*1*). Comparisons covering a wide range of taxa have shown a strong pattern of covariation of life history traits that divide species along a "slow-fast continuum" (*2–6*). Life history characteristics such as early onset of reproduction, rapid ontogenetic development, and large litter sizes are typical for species at one end of this continuum, whereas species with low reproductive rates, but longer life expectancies, are found at the other end. Several hypotheses have been proposed to explain this covariation among life history traits, e.g., density-dependent *r-K* selection (*3*), adaptive life history responses to differences in extrinsic mortality (*5*), or adaptations to variation in predictability or variability of the habitats (*7*). Few studies have, however, quantitatively examined how characteristics of the population dynamics are related to the species' position along this continuum of life history variation; an exception was Fowler (*8*, *9*), who showed that the pattern of density regulation was related to the rate of increase per generation. The presence of such patterns will enable characterization of patterns in population fluctuations from knowledge of basic demography or life history characteristics. Here we used data on the fluctuations of solitary bird populations to examine stochastic effects on population fluctuations. This enables us to quantitatively relate patterns in population dynamics to the position of the species along the slow-fast continuum of life history variation.

To examine how interspecific variations in population dynamical characteristics are affect-

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