Energy-Transfer Dynamics in Three Light-Harvesting Mutants of *Rhodobacter sphaeroides*: A Picosecond Spectroscopy Study†

C. Neil Hunter,*,‡ Hans Bergström,§ Rienk van Grondelle,∥ and Villy Sundström§

Department of Physical Chemistry, University of Umeå, S-90187, Umeå, Sweden, Krebs Institute for Biomolecular Research, Department of Molecular Biology and Biotechnology, University of Sheffield, Western Bank, Sheffield S10 2TN, U.K., and Department of Biophysics, Physics Laboratory, Free University De Boelelaan 1081, HV 1081 Amsterdam, The Netherlands

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ABSTRACT: Picosecond absorption spectroscopy has been used to investigate energy-transfer dynamics within the LH1 and LH2 light-harvesting complexes of three mutants of *Rhodobacter sphaeroides*. We demonstrate that both complexes are inhomogeneous; each contains a specialized pigment pool which absorbs maximally at a longer wavelength. Within LH2 (mutant NF57), Bchl850 transfers energy to Bchl870 in 39 ± 9 ps; within LH1 (mutants M21 and M2192), energy is transferred from Bchl875 to Bchl896 in 22 ± 4 and 35 ± 5 ps, respectively. Examination of the decay of induced absorption anisotropy indicates that each of these specialized pools exists in a state which is highly organized with respect to the remainder of the pigments. Such an arrangement may facilitate and direct energy migration toward the reaction center.

The photosynthetic apparatus of the purple bacterium *Rhodobacter sphaeroides* is composed of two light-harvesting complexes, LH1 and LH2, which surround and interconnect photochemical reaction centers (Monger & Parson, 1977; Vos et al., 1986; Hunter et al., 1989a). Illumination of the light-harvesting antenna with weak picosecond excitation flashes produces absorption transients which can be probed with delayed laser pulses; the analysis of absorption recovery data yields valuable information on excited-state dynamics in antenna systems (Sundström et al., 1986). This approach has recently been extended through the use of low temperature (77 K) to establish unidirectional excitation transfer between pigments by diminishing equilibration processes within the antenna (van Grondelle et al., 1987). In unidirectional transfer, excitations move from pigments absorbing at higher energy to those absorbing at lower energy. For *Rb. sphaeroides* at 77 K, the measured picosecond absorption kinetics were interpreted to give the following sequence of energy-transfer events and time constants (van Grondelle et al., 1987; Bergström et al., 1989):

$$\underset{\text{LH2}}{\text{Bchl800}} \xrightarrow{2\text{ ps}} \underset{\text{LH2}}{\text{Bchl850}} \xrightarrow{40\text{ ps}} \underset{\text{LH1}}{\text{Bchl875}} \xrightarrow{20\text{ ps}} \underset{\text{LH1}}{\text{Bchl896}} \xrightarrow{35\text{ ps}} \text{RC}$$

Fluorescence polarization data at room temperature and 4 K (Bolt et al., 1981; Kramer et al., 1984) had already clearly identified the existence of an energetically low-lying minor antenna component, bacteriochlorophyll 896 (Bchl896),[1] also suggested by other authors (Borisov et al., 1982; Sebban et al., 1985). Picosecond studies of membranes from the wild-type strain produced further evidence for the long-wavelength component Bchl896 which was suggested to act as a "sink" for excitations so they are focused prior to transfer to the reaction center where useful photochemistry takes place (van Grondelle et al., 1987, 1988). The complex energy-transfer kinetics observed in *Rb. sphaeroides* membranes at 77 K around 870 nm suggested the presence of still another component, the existence of which had also been inferred from singlet–singlet excitation annihilation studies and deconvolution of the absorbance spectrum of a mutant, NF57, which synthesizes only the LH2 complex (Vos et al., 1988; van Dorssen et al., 1988). However, the complexity of the wild-type membrane system makes it difficult to obtain detailed information regarding the dynamics and pathways of energy transfer in this wavelength region. One way to simplify the situation is to solubilize and purify each complex; for the LH1 complex, this approach enabled Bergström et al. (1988) to measure the Bchl875 → Bchl896 transfer time as being 15 ± 5 ps. In this paper, we have employed an alternative approach and have used mutants which possess the following complexes: NF57 (LH2), M21 (LH1 and RC), and M2192 (LH1). The energy-transfer and trapping dynamics demonstrate the presence of an additional long-wavelength component in the antenna of NF57, and confirm the presence of Bchl896 as an intrinsic component of LH1.

Materials and Methods

The isolation and biochemical characterization of mutants NF57 and M21 have already been described (Ashby et al., 1987; Hunter & van Grondelle, 1988; Hunter et al., 1988). Spectral characterization by low-temperature polarized absorption and fluorescence spectroscopy and excitation annihilation has been described (van Dorssen et al., 1988; Vos et al., 1988). M2192 was constructed from M21 using transposon Tn5 mutagenesis to disrupt *puf* L encoding the reaction center L subunit (Hunter et al., 1989b). Membranes were prepared from mutant strains by using methods described by Vos et al. (1988). Samples were buffered with 50 mM Tris, pH 8.0, and prepared in glycerol to give a maximum absorbance of approximately 0.3 mm^{-1}; a glycerol:water ratio of approximately 3:1 ensured that an optically clear glass was maintained at 77 K.

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* Correspondence should be addressed to this author.
‡ University of Sheffield.
§ University of Umeå.
∥ Free University De Boelelaan 1081.

[1] Abbreviations: RC, reaction center; Bchl, bacteriochlorophyll; P^+, "special pair" of reaction center bacteriochlorophylls in the oxidized (closed) state.

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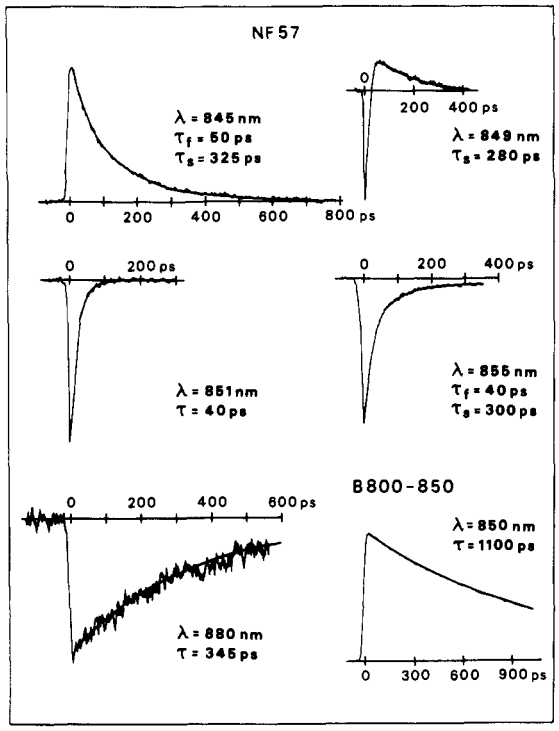

FIGURE 1: Isotropic kinetics of the LH2 complex of mutant NF57 at 77 K. The kinetics of the LH2 (B800–850) complex solubilized and purified from membranes of the wild type are included for comparison.

Absorption recovery measurements were performed at 77 K in the 800–900-nm region using pump and probe pulses of 10-ps duration as described previously (Sundström et al., 1986; van Grondelle et al., 1987; Bergström et al., 1988). The intensity of the excitation pulses was carefully chosen to be low enough to avoid artificial kinetics due to exciton annihilation effects. All results reported here for those membranes with reaction centers present refer to the situation of "closed" reaction centers; that is, no charge separation is possible due to the preoxidation of the special pair P by the continuous high-frequency train of laser pulses. Specifically, the closing of reaction centers as $P^+ HQ_A^- Q_B^-$ was achieved by purging the membrane solution with nitrogen gas prior to cooling. During the cooling from room temperature to 77 K, the sample was illuminated with white light from a slide projector to accumulate the reaction centers in the P^+ state. This state was maintained for the duration of the measurements by virtue of the high repetition rate (800 kHz) of the excitation pulses.

Results

Mutant NF57. Isotropic absorption recovery kinetics were measured at a range of wavelengths. It is apparent from Table I and Figure 1 that there are two distinct phases of decay; the ratio of relative amplitudes of these phases was observed to be wavelength dependent. From the average of a number of measurements, these two components emerge as $\tau_f = 39 \pm 9$ ps and $\tau_s = 300 \pm 50$ ps. In addition to kinetic information, the decay curves in Figure 1 also yield spectral information. The trace obtained at 849 nm displays the two kinetic components τ_f and τ_s with opposite sign, τ_f as a bleaching (negative ΔA) and τ_s as an increased absorption (positive ΔA). At shorter wavelengths, e.g., 845 nm, both components appear in absorption whereas at longer wavelengths, for example, 855–880 nm, both components are observed as a bleaching. This spectral variation of the amplitudes of τ_f and τ_s proves that they are related to two species with different absorption

Table I: Summary of Isotropic Lifetimes of Light-Harvesting Mutants of *Rb. sphaeroides* at 77 K

mutant	wavelength (nm)	τ_f (ps)	τ_s (ps)	comments
NF57	840	33	286	
	845	50	320	
		34	250	
	849		273	
	851	40		λ_{iso} Bchl870 = 851 nm[a]
	855	40		
	880		270	
			286	
			347	
			340	
		39 ± 9	300 ± 50	
M21	870	25	177	
	875		170	close to λ_{iso} Bchl875
	880	17	150	low intensity; close to
	890	25	175	λ_{iso} Bchl896
		22 ± 4	168 ± 11	
M2192	870		298	
	881		306	
	886	30	220	λ_{iso} Bchl896 = 886 nm
	889	36	355	
	896	32	355	
	900	40	380	
	910		370	
		35 ± 5	335 ± 40	

[a] This is the isosbestic wavelength.

Table II: Summary of Limiting Values of Anisotropy for Light-Harvesting Mutants of *Rb. sphaeroides* at 77 K

mutant	wavelength (nm)	$r(0)$	$r(\infty)$
NF57	870	0.25 ± 0.03	0.15 ± 0.093
	880	0.30 ± 0.03	0.20 ± 0.03
M21	870	0.05 ± 0.02	0.03 ± 0.01
	890	0.15 ± 0.02	0.05 ± 0.02
M2192	900	0.15 ± 0.02	0.05 ± 0.01

spectra. Inspection of Table I shows that the fast component has an isosbestic wavelength at 847–849 nm. However, the kinetic curve at 851 nm in Figure 1 only contains the fast (40 ps) component, which demonstrates that the slow component has an isosbestic point at 851 nm; it represents the decay of the terminal emitter in the complex of this mutant. Inspection of the trace obtained at 880 nm (Figure 1), where this terminal emitter is selectively excited, reveals a monophasic decay which reflects the quenching of excitations within this antenna component. In Figure 1, we compare the absorption recovery of fast and slow components in NF57 with the monophasic recovery of the isolated LH2 complex; the striking absence of a fast phase for the isolated complex is in agreement with the lack of absorbance on the red side of the 850-nm maximum of this complex at 4 K with respect to NF57 (van Dorssen et al., 1988). Thus, we interpret the fast 40-ps component as energy transfer from the main Bchl850 pigment to a minor red-shifted pigment, Bchl870. Previous work on mutant NF57 has shown that the absorption maximum of the additional pigment is 870 nm at 4 K and the emission maximum 889 nm (van Dorssen et al., 1988). Moreover, it has been shown that at high excitation densities annihilation preferentially occurs in these long-wavelength pigments which appear to form an aggregate of at least a few Bchl870 molecules (Vos et al., 1988).

The measurements of induced absorption anisotropy are displayed in Table II. High values are obtained in the red wing of the absorption band which suggests that only limited

depolarization occurs within the Bchl870 pigments, where $r(0) = 0.30$ and $r(\infty) = 0.20$. This is consistent with the idea that domains of Bchl850 and Bchl870 pigments are relatively restricted at 77 K; at 4 K, they are approximately 30 and 8 Bchls, respectively (Vos et al., 1988). It is reasonable to assume that the Bchl870 pool in particular consists of an array of highly organized chromophores.

The data presented here confirm the presence of a new pigment, Bchl870, in the antenna of NF57 and show for the first time that it participates in the energy-transfer dynamics of LH2. It is distinguished from the Bchl875 chromophore of LH1 by virtue of its absorption and emission maxima (van Dorssen et al., 1988) and its isosbestic point (851 nm, compared with 870 nm for Bchl875). Moreover, it possesses a high anisotropy value, $r(0)$, at 870 nm of 0.25, compared with $r(0) < 0.1$ for Bchl875 within wild-type membranes (Sundström et al., 1986), the isolated LH1 complex (Bergström et al., 1988), and mutant M21 (see below). These properties are notably analogous to those observed for Bchl896 in the LH1 antenna.

The energy-transfer kinetics obtained previously from wild-type membranes at 77 K could only be interpreted with an additional pigment, intermediate between Bchl850 and Bchl875 (van Grondelle et al., 1987). On the other hand, Freiberg et al. (1988, 1989) performed time-resolved fluorescence measurements at 77 K on wild-type membranes of *Rb. sphaeroides* which displayed a very fast rise time (~10 ps) of the Bchl875/896 fluorescence; this was interpreted as arising from a direct pathway of energy transfer from Bchl850 to Bchl875. Time-resolved fluorescence spectra of *Rb. sphaeroides* cells at 77 K measured by Shimada et al. (1989) revealed the presence of three different fluorescence components which were attributed to B850, to B875, and to an additional long-wavelength antenna component designated B890. The observed fluorescence kinetics were interpreted as a consequence of sequential energy flow in the order B800, B850, B875, B890, and RC, similar to earlier conclusions from picosecond absorption work (Sundström et al., 1986; van Grondelle et al., 1987). However, in contrast to the 40-ps lifetime at 77 K found by van Grondelle and co-workers for the Bchl850 → Bchl870/875 transfer, these authors report a lifetime for the Bchl850 → Bchl875 process of less than 6 ps; moreover, no heterogeneity of B850 was distinguished. There is an important difference between the absorption measurements of van Grondelle et al. (1987) and the fluorescence measurements of Shimada et al. (1989). In the former case, selective infrared excitation of the individual pigments was used, whereas Shimada and co-workers employed the much less selective 590-nm excitation into the Bchl Q_X band which is bound to produce substantial direct optical excitation of Bchl875. Since this will result in an apparently faster rise time of the Bchl875 fluorescence, it may be an explanation for the differing results obtained in the fluorescence and absorption measurements. The most straightforward interpretation of the role of the pigment identified in mutant NF57 as Bchl870 is that it receives excitations from Bchl850 and transfers them to Bchl875 pigments in LH1. It is not possible to say whether or not Bchl870 forms an obligatory link between LH2 and LH1 or whether energy is also relayed directly from Bchl850 to Bchl875.

Mutant M21. Mutant M21 lacks LH2 and contains only the core antenna LH1 together with the reaction center. From an energy-transfer point of view, this mutant could be expected to behave similarly to membranes of *Rhodospirillum rubrum*, which has only one major antenna complex, LH1, containing

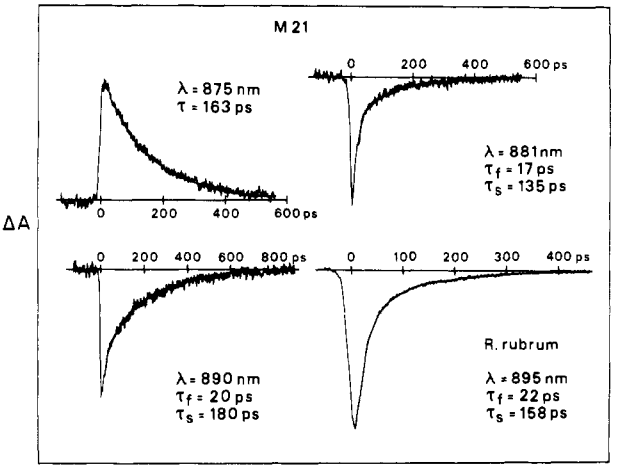

FIGURE 2: Isotropic kinetics of the LH1 complex of mutant M21 at 77 K. The kinetics of membranes isolated from *Rhodospirillum rubrum*, which also contains only LH1 and RC complexes, are included for comparison.

a minor Bchl896 component (Sundström et al., 1986). The energy-transfer kinetics show that this comparison is quite realistic; the kinetics observed for membranes prepared from mutant M21 are very similar to those previously reported for membranes of *Rs. rubrum* at 77 K (van Grondelle et al., 1987). Thus, upon excitation of the main antenna of M21, the excitation energy is transferred to the red-shifted Bchl896 pigment with a time constant of about 20 ps (see Figure 2). On a slower time scale, τ_s = 170 ps, the energy is then quenched by the closed reaction center (P^+). This latter time constant is also similar to that observed from *Rs. rubrum* under similar conditions (van Grondelle et al., 1987). The relative amplitude of the two decay components exhibits a wavelength dependence, which indicates that they arise from pigments with different absorption spectra. This is illustrated in Figure 2, where very little of the 20-ps component is observed at 875 nm, which is close to the isosbestic point for Bchl875. On the other hand, 881 nm is close to the isosbestic wavelength of Bchl896, and the decay is dominated by the 20-ps lifetime which reflects energy transfer from Bchl875 to Bchl896. At longer wavelengths, the slow phase (τ_s = 170 ps) increases in amplitude, to the point where it is the sole component at wavelengths greater than 910 nm (results not shown). This behavior is very similar to earlier observations of the *Rs. rubrum* and *Rb. sphaeroides* wild-type strains made at 77 K (van Grondelle et al., 1987) and reflects the fact that Bchl896 is selectively excited at the longest wavelengths and that the excited state of Bchl896 is quenched by the closed reaction center. Isotropic kinetics measured at several different wavelengths are summarized in Table I.

Time-resolved anisotropy was also measured for mutant M21. The results (see Table II) show that the initial anisotropy is relatively high, $r(0) = 0.15$, in the red wing of the absorption band ($\lambda > 890$ nm) but very low, $r(0) = 0.05$, at shorter wavelengths. This is the same observation as those previously made at 77 K, both with membranes prepared from the wild-type strain of *Rb. sphaeroides* (van Grondelle et al., 1987) and also with the isolated LH1 (B875) complex (Bergström et al., 1988), and it is another piece of evidence that Bchl896 is a distinct antenna component having a functional role in the pigment system of several purple bacteria.

Mutant M2192. In this mutant, only the core antenna LH1 is present; it is derived from mutant M21 (see Materials and Methods). We have followed the same approach as for the other two mutants and have attempted to relate observations

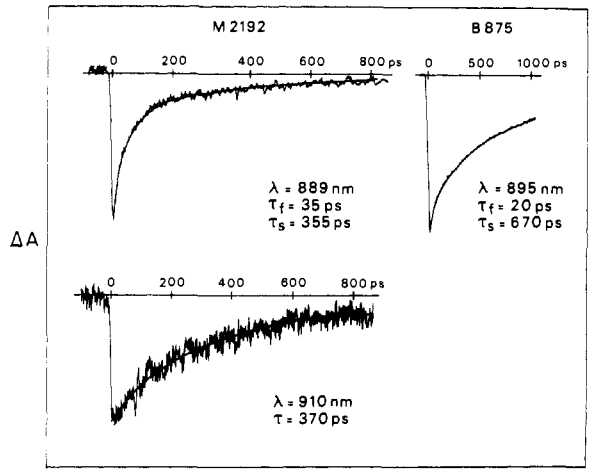

FIGURE 3: Isotropic kinetics of the LH1 complex of mutant M2192 at 77 K. The kinetics of the LH1 (B875) complex solubilized and purified from membranes of the wild type are included for comparison.

made on membranes of the mutant to a previously studied and well-known situation, in this case the isolated LH1 complex of *Rb. sphaeroides* (Bergström et al., 1988). The kinetics displayed in Figure 3 and summarized in Table I exhibit a similar decay pattern for the two preparations, and it is clear that the dominating feature of the kinetics is the fast energy transfer from Bchl875 to Bchl896 with a time constant of 15–35 ps. The upper limit refers to results for the mutant. It is interesting to note that the domain sizes obtained from singlet–singlet excitation annihilation measurements of M2192 and the isolated LH1 complex (approximately 125 Bchl and 6–8 Bchl, respectively; Vos et al., 1988; van Grondelle et al., 1983) appear to influence the rate of decay measured here (τ_f = 35 ± 5 and 15 ± 5 ps, respectively). We assume that the 35-ps decay in the mutant with relatively large domains reflects fast excitation transfer within the minimum LH1 unit as well as a slower migration between units. It is also interesting to compare this decay in mutants M2192 and M21; the somewhat longer time constant for the Bchl875 to Bchl896 transfer in M2192 compared to M21 may reflect some changes in the organization of the antenna pigments upon deletion of the reaction centers, or it may suggest that in M21 there is some direct energy transfer from Bchl875 to the special pair of the reaction center. The results provide more evidence that Bchl896 is an integral part of the LH1 core antenna and plays an important role in energy trapping.

The quenching of excitations in Bchl896 described by the time constant τ_s = 300–680 ps is somewhat faster in M2192 when compared with the isolated LH1 pigment–protein complex. This could be a result of a quenching process introduced by interactions between Bchl896 pigments within M2192 promoted by the absence of the reaction center complex. In the model of Hunter et al. (1989b), no such interactions are presumed to exist in the small LH1 units of the isolated complex. In this connection, comparison of the limiting values of anisotropy $r(0)$ and $r(\infty)$ reveals that this parameter is time dependent in M2192 (Table II) whereas in the isolated complex the anisotropy is time independent at 905 nm (Bergström et al., 1988). A measurement of the time-resolved absorption anisotropy within M2192 (Figure 4) reveals a gradual depolarization as a result of energy transfer among identical Bchl896 chromophores. This is consistent with the low polarization of fluorescence emitted from Bchl896 within the mutant at 4 K (Hunter et al., 1986b) in comparison with the isolated complex (Kramer et al., 1984) and can be explained by a model in which Bchl896 chromophores are separated in

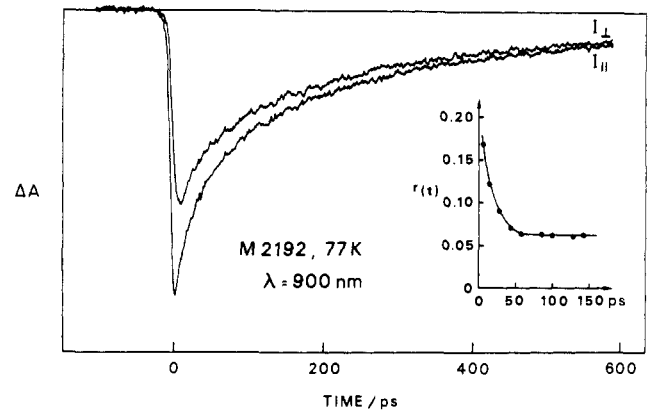

FIGURE 4: Time-resolved decay of anisotropy, $r(t)$, of mutant M2192 at 77 K. The measurements were recorded at 900 nm.

the minimal units of the isolated LH1 complex, but brought in proximity for energy transfer by the absence of reaction centers in the core antenna of M2192 (Hunter et al., 1989b).

Discussion

These kinetic studies on membrane-bound antenna complexes have confirmed that minor spectral components exist in LH2 and LH1. We have demonstrated that these components, Bchl870 and Bchl896, can participate in the energy-transfer dynamics of each antenna and that they do not arise from detergent isolation procedures. Indeed, the detection of Bchl870 in the LH2 antenna of mutant NF57 appears to depend upon the absence of the detergents LDAO and Triton X-100; other detergents may not cause this effect, however. This point should be investigated further. Another possibility, that these small pools of pigment arise from special environments created by points of contact between LH2 and LH1, for example, can be discounted since these pools are observed in homogeneous antenna systems (Kramer et al., 1984; van Dorssen et al., 1988; Bergström et al., 1988; Hunter et al., 1989b). The aggregation state of the antenna may influence the absorbance of small pools of pigment, but there is no evidence for this possibility from the studies conducted here on mutant and solubilized antenna systems. Singlet–singlet annihilation measurements of the aggregation state of LH2 in mutant NF57 or in the detergent-solubilized complex yield a domain size of the order of hundreds of Bchl molecules in each case (Vos et al., 1988; van Grondelle et al., 1983), but there is no Bchl870 in the latter complex. Conversely, the domains in the LH1 antenna of mutant M2192 or the solubilized complex are significantly different, at 150 and 6–8 Bchl*a*'s, respectively (Vos et al., 1988; van Grondelle et al., 1983), but both contain Bchl896.

It should be pointed out that mutations that remove major membrane complexes may also give rise to pleiotropic effects on membrane morphology and to the associations between light-harvesting complexes. For example, the results of sedimentation, ultrastructural, and chromatographic analyses of mutant M21 membranes demonstrate that lipid-enriched, tubular structures and vesicles of greatly increased size are formed, rather than the normal intracytoplasmic membrane vesicles seen in wild-type strains [Hunter et al., 1988; see also Kiley et al. (1988)]. This has been interpreted as evidence for the involvement of LH2 in the invagination process (Hunter et al., 1988; Sturgis et al., 1989). Despite such morphological differences, the mutant strains examined here have provided us with model systems in which the kinetics of energy transfer within each antenna species are in good agreement with results obtained with membranes isolated from the wild type. Since

the complexes within each mutant are disconnected, there is, however, a pronounced effect on the lifetime of the terminally emitting antenna pigment in each case. This is most clearly seen when comparing the effects of open and closed reaction center traps on the lifetime of the Bchl896 excited state. For membranes from the *Rb. sphaeroides* wild type at 77 K, this lifetime is approximately 40 ps with open traps (Bergström et al., 1989) and increases to approximately 180 ps when the traps are closed. In the present study, 168 ps was obtained for mutant M21 (closed traps), but for M2192 and the solubilized LH1 complex, other factors must influence the increase in the Bchl896 excited-state lifetime to 335 and 670 ps, respectively. These differences can be attributed in part to the presence or absence of reaction centers, with attendant effects on the aggregation of Bchl896 pigments, and, for the solubilized LH1 complex, the effect of detergent in creating small aggregates. These lifetimes and aggregation states can also be correlated with measurements of anisotropy decay (Table II; discussed in the previous section) and fluorescence polarization (Hunter et al., 1989b). This accumulation of biophysical and biochemical data has still not enabled us to explain the origin of these small pools of pigments in LH1 and LH2. We will continue to use a combination of spectroscopy, biochemistry, and molecular biology to examine this problem further.

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