MEMBRANE LIPID PROBE TECHNIQUES INDICATE MINIMAL TEMPORAL CARBON COUPLING BETWEEN BENTHIC ALGAL AND BACTERIAL POPULATIONS OF ARTHUR HARBOR, ANTARCTICA

Glen A. Smith,[1#] David B. Ringelberg[1], James B. Guckert[1] and David C. White[1]

[1] Institute for Applied Microbiology/Oak Ridge National Laboratory, 10515 Res. Dr., Suite 300, Knoxville, TN., 37932-2567.

Keywords: algal-bacterial carbon coupling, lipids, microbial benthic communities.

[#] To whom correspondence should be addressed.

ABSTRACT

Sediment microbial carbon transfer for an Arthur Harbor, Antarctic Peninsula site was investigated utilizing lipid membrane techniques as direct measures of temporal carbon coupling. The incorporation of radiolabeled carbon from [^{14}C]-sodium bicarbonate and [2-^{14}C]-sodium acetate into algal specific or bacterial specific membrane lipids were utilized to provide direct information on the conceivable carbon coupling of algae and bacteria within a benthic near-shore environment. Over a 72 hour incubation period with radiolabeled sodium bicarbonate and ambient light conditions there was no apparent transfer of fixed algal carbon into bacterial lipids. Monounsaturated bacterial fatty acids remained throughout the incubation at approximately 5-8%, indicating no transfer from algal-fixed carbon. This result is contrasted with the ability of acetate to radiolabel the bacterial lipids. Large sediment fluxes of POC (2gm/M^2/d) is suggested as a "short circuiting" mechanism for close benthic algal-bacterial carbon coupling.

INTRODUCTION

Little information is available on the ecology of benthic microbial communities within the Antarctic near-shore environment. This has left a sizeable void in global carbon flux determinations. Utilizing biochemical methods we have recently

begun to investigate some primary aspects of benthic microbial ecology for this region (White et al., 1985; Smith et al., 1986, 1989a, 1989b in press). This work is complimented by information provided by others utilizing somewhat more classical techniques (Azam et. al., 1979; Palmisano et al., 1985; Dayton et. al., 1986). In addition, several important ecological and physiological investigations of antarctic sea-ice microbial communities have been made over the last 20 years (Ackely et al., 1979; Bunt and Wood, 1963; Sullivan and Palmisano, 1984; McConville and Wetherbee, 1983; Palmisano and Sullivan, 1982, 1983; Kottmeier et al., 1987).

It is apparent that both sea ice and sediment biomasses are substantial and the sediment microbial communities are comparable to more temperate and tropical regions (Smith et al., 1986, 1989b in press). Following studies of microbial biomass, community composition and bacterial activity (estimated by biochemical methods), our research turned to the influence of benthic algal-fixed carbon on the benthic bacterial populations. In this investigation we have chosen to elucidate the carbon transfer question by means of a direct technique utilizing membrane lipids as population-specific probes for radiolabeled incorporation. More specifically, information is provided on the apparent uncoupling (temporal, < 72 hrs.) of the abundant algal-bacterial

component within benthic Arthur Harbor sediments during this spring phytoplankton bloom. The question of algal-bacterial coupling has grown in prominence recently as investigations into their close physical association in various systems has been noted. Murray et al., (1986) has shown that algal exudates can stimulate bacterial DNA synthesis in attached algal-bacterial consortia. Cole (1982) determined that within a closed system, devoid of nutrient regeneration and respiration from heterotrophic activity, autotrophic growth would be impossible. Realizing that bacteria are essentially opportunist Bell et al. (1974) postulated that they would be attracted to a zone he referred to in pelagic systems as a 'phycosphere', in which phytoplankton can produce extracellular compounds at rates 5-30% of net photosynthesis.

To date only two indirect studies of sea-ice microbial communities have demonstrated any evidence substantiating possible algal-bacterial coupling within Polar environments. Kottmeier et al. (1987) observed a lag in bacterial secondary production of approximately three days with respect to primary production during a spring ice algal bloom in McMurdo Sound. While for an arctic ice algal community, Smith et al. (1989a) noted dual phase dynamics in bacterial cell numbers, which increased while ice algal biomass (Chl a, measurements) was both

increasing and decreasing during a vernal bloom. This was observed for both epiphytic and unattached bacteria. However, epiphytic bacteria were found to be somewhat more abundant during the bloom when compared to unattached bacteria. In this investigation we describe a direct assessment of temporal carbon coupling of benthic algal-bacterial populations of Arthur Harbor, Antarctica. Secondly, what effect does the annual spring phytoplankton bloom and it's subsequent contribution of carbon to the benthos have on sediment microbial communities.

MATERIALS AND METHODS

Solvents were all of residue or ultra high purity quality (Burdick and Jackson Co., Muskegon, MI). Sodium [^{14}C]-bicarbonate (40-60 mCi/mmol) and sodium [2- ^{14}C]-acetate (45-60 mCi/mmol) were purchased from New England Nuclear (Boston, MA).

Study site

A site in Arthur Harbor adjacent to Elephant Rocks (Fig. 1), was examined based upon information from previous sediment microbial studies. This site at a depth of 26 m has been determined to contain a surface (top 2-3cm) sediment size distribution of mostly fine material, with 20% and 45% (by weight) retained on a 0.125mm and 0.062mm sieve respectively, and a C:N of 6 (Smith et al., in press). Interstitial porewater was

determined to be approximately 15% within the surface sediments. Overlying seawater physio-chemical conditions averaged: salinity 30 ppt., pH 7.8, dissolved oxygen 10.5 mg/l, and Temperature 1.5 °C over the 28 day field period (Dec. 26, 1988 to Jan. 22, 1989). Light at the sediment surface was 1.4-2.2% of ambient seawater surface light during the study period, with a mean of 13.7 + 5.3 uM-Photon/M^2/s. There was during our study no sea ice at this site, either annual or permanent (only an occasional accumulation of brash ice). Nutrients for sediment porewater and overlying seawater were analyzed utilizing commercial prepared field assays (HACH Co., Loveland, CO).

Sample Collection

Sediment cores were collected by SCUBA divers at the Elephant Rocks site (Fig. 1). Upon returning the 5cm i.d. cores to the Palmer station laboratory under ambient conditions and within 30 min., they were sub-sampled with 1.8 cm i.d. cores containing silicone injection ports for radioisotope introduction. The sub-sampled sediment was carefully adjusted so that injection ports were approximately 2-3 mm below the sediment surface within the core. This provided a sub-cored sediment sample of approximately 5-5.5 gm dry weight (GDW).

The sub-cored samples were inoculated with either 50 uCi/core ([^{14}C]-sodium bicarbonate), or 5 uCi/core ([2-^{14}C]-sodium acetate). Injections were accomplished by making 2 x 25 ul injections through the silicone septa in a V-shape to facilitate distribution of the label. Killed controls were injected with radioisotopes in the same manner and 3 mls of 10% formalin in 0.45 um filtered seawater was immediately added to the overlying water and gently pulled down into the core sediments by adjusting the syringe plunger. These techniques have been shown to minimize any disturbance artifacts introduced by other commonly used methods of radiolabel introduction (Carman et al., in press). Likewise, this technique also provided a mechanism for maintaining the overlying water in it's totally unaltered condition. The sub-sample cores (including killed controls) were then placed into a test tube rack and positioned in an outside aquaria which served as a circulating ambient temperature sea-water bath. This maintained the inoculated sediments and overlying water at + 0.5°C of ambient sea-water temperature throughout the incubations. The aquaria was then covered with window screening to provide a light level reaching the core sediments comparable to those determined in their benthic environment. All light measurements were made using a Li Cor, model Li-193-SA quantum spherical radiometer (Lincoln. NB.), with

a Fluke - 8050A digital multimeter display (Fluke Manufacturing Co., Evert, WA.). At designated time points incubated sediments were extracted by a single phase methanol:chloroform:buffer (2:1:0.2) modification (Guckert, et al., 1985) of the Bligh and Dyer, (1959) technique. Total lipid fractions were collected, dried under nitrogen in a teflon lined screw cap test tube. The samples were then capped and stored under nitrogen at -70°C for transportation and further analysis at the University of Tennessee-Knoxville (UTK).

Sedimentation Traps

Traps were deployed in a stationary and vertical position by SCUBA divers near the study site. The top of the trap was maintained 1.5m from the sediment surface and trap design incorporated aspects determined by Hargrave and Burns (1979) (ie., a height:diameter ratio of 5, and a baffled opening) to facilitate collection of only non-resuspended sedimenting material. A 10% formalin-sucrose solution in removable collection tubes was used as a preservative. Samples were recovered on two twelve day intervals, as divers carefully removed the collection tubes, capped it, and placed another preservative containing tube on the trap. Recovered collection tubes were centrifuged at 6000-8000 g, for 20 min., and the overlying water was decanted. At

that point the pelletized material was frozen at -70°C and lyophilized for transportation and further analysis at (UTK). Lyophilized sediment trap material was weighed for total dry weight on a Metler AE-100 analytical balance (Metler Inst. Corp., Highstown, NJ) and homogenized before a portion was collected for particulate organic carbon (POC) determination. POC was determined by ash free dry weight (AFDW) analysis in pre-fired ceramic crucibles combusted at 500°C for 5 hr.

Lipid Analysis

Total lipids from radiolabeled time course work at Palmer were fractionated by silicic acid (Unisil 100-200 mesh, Clarkson Chemical Co., Williamsport, PA.) column chromatography (Kates, 1986; Guckert et al., 1985). Consecutive washes of increasing mobile phase polarity: chloroform, acetone and methanol, yielded fractions of neutral, glyco-and phospholipid respectively. Fractions were concentrated by evaporation under nitrogen, resuspended in a known volume of chloroform and a aliquot counted in 2 mls of Ecoloume (ICN Biomedical, Inc., Irvine, CA). Phospholipids were then transesterified to their methyl esters (Guckert et al., 1985) and further separated by silver nitrate TLC (Christie, 1973; Guckert et al., 1987), into saturated, monounsaturated and polyunsaturated fatty acids. Dried

phospholipids were taken up in a known volume and an aliquot counted in 2mls ecoloume.

Lyophilized sedimentation material from traps was extracted by procedures discussed above to provide total lipid (by weight). Percent composition of lipid within the POC fraction was then calculated.

Radioisotope Counting

Dried lipid aliquots in 6 ml high-density polypropylene scintillation vials (Sarstedt Co., Newton, NC), were resuspended in 2ml Ecoloume and counted for 10 min. Counting was performed on a LKB 1212 Rackbeta liquid scintillation counter operated in the standards ratio method. Corrections for quench and counting efficiencies were made using external standard curves generated from standards (Packard Inst. Co., Dovers Grove, IL). External standards were run and counting efficiencies calculated for every set of samples counted. Background radiation was subtracted and all samples were normalized to GDW of sediment. Dark incorporation of [^{14}C]-sodium bicarbonate was never greater than 1% of total lipid recovered.

RESULTS

Nutrient Determinations

A comparison of nutrient concentrations within the sediment porewater and overlying seawater indicated no depletion of the four nutrients assayed (Table 1). In fact, both phosphate and silicate were more concentrated in the porewater than the overlying seawater.

Sedimentation fluxes

The results of this investigation are shown in Table 2, with a comparison to other polar, temperate and tropical sediment flux studies. The Arthur Harbor flux of 2 gm POC/M^2/d, of which 70 mg/M^2/d was lipid, is among the highest values observed.

Radiolabel incorporation into total lipid

The 72 hour time course patterns for [^{14}C]-bicarbonate and acetate into total extractable lipid is shown in figures 2a and 2b, respectively. Radiolabel in lipid accounted for 6-16% of the total [^{14}C]-bicarbonate and 4-6% of the total [2-^{14}C]-acetate added. A regression line calculated for the bicarbonate data (fig. 2a) indicates a relatively linear incorporation over the 72 hours (r^2 = 0.82) following an initial lag of approximately 20 hours (fig. 2a). Incorporation from acetate did not show a similar lag (fig. 2b), however the data did not fit the calculated regression line as well (r^2 = 0.60). The pattern of the acetate time course suggest a rapid incorporation into total lipid over the first 45 hours with the total lipids becoming

saturated after this point (fig. 2b).

Radiolabel incorporation into lipid classes

Fractionation into lipid classes revealed different intracellular allocation patterns for phototrophs ([^{14}C]-bicarbonate) and heterotrophs ([2-^{14}C]-acetate). For the bicarbonate incubation, neutral lipid ranged from approximately 30% to 55% of recovered lipid over 72 hours. (Fig. 3a), and loosely resembled the pattern of assimilation into total lipid (Fig. 2a). Glycolipid conversely, deceased nearly synchronously with neutral lipid increase, from approximately 43% to 33% of recovered lipid over the same time period. Phospholipid on the other hand remained at approximately 10-12% throughout the time course (Fig. 3a).

Patterns of allocation into lipid classes for [2-^{14}C]-acetate were quite different from that of the bicarbonate. All fractions approached 35% after 30 hours and remained at this level for 72 hours. (Fig. 3b). Prior to 30 hours. glycolipid assimilation predominated (18 hours, 72%), followed by neutral lipid and phospholipid. There was also a greater proportion of phospholipid synthesis from acetate (8-38%) than with bicarbonate.

Radiolabel incorporation into membrane fatty acid fractions

Membrane phospholipid fatty acid fractions consisting of; saturates, monounsaturates and polyunsaturates were monitored as

a direct technique to specifically monitor algal vs. bacterial populations. Allocation into polyunsaturates remained predominant throughout the time course for both radiolabeled bicarbonate and acetate (fig. 4 a & b). However, polyunsaturates for the bicarbonate study were higher (65-82%), than acetate (42-62%) during the incubation period. Conversely, monounsaturates in the radiolabeled acetate study were higher (18-25%), compared to bicarbonate (5-8%). Proportions of saturates remained relatively stable for both incubations at approximately 20%.

DISCUSSION

Various radiolabeling techniques have been used in past investigations of carbon assimilation and intracellular allocation within Polar microbial communities. These environments dominated by phototrophic organisms have received considerable investigation by radiotracer and subsequent biochemical techniques. Investigations to date have focused primarily on determining the partitioning of fixed carbon into end products of photosynthesis (ie. protein, carbohydrate, small molecular weight compounds, and lipid). In addition the majority of past work has concentrated on water column phytoplankton (Li and Platt, 1982; Sargent et. al., 1985) and sea ice microbial communities (Palmisano and Sullivan 1985; Palmisano et al., 1988; McConville,

1983, 1985; Smith et al., 1987, 1989a,b) while benthic communities have not been investigated. These past techniques for investigations of algal-bacterial coupling have concentrated upon somewhat more indirect methods. Such studies have observed changes in bacterial growth dynamics when closely associated with photosynthesizing sea-ice algal communities. Demonstrated from these investigations is a lag in bacterial growth with respect to sea-ice algal growth during seasonal blooms for both Arctic (Smith et al., 1989a) and Antarctic (Kottmeier et al., 1987) regions.

The linear pattern of assimilation into total lipid from our study gave little indication of radiolabel recycling over the 72 hour incubation for [^{14}C]-bicarbonate (Fig. 2a). Additionally, our investigations support those of Smith et al. (1987), in which assimilation into lipid end products of photosynthesis remained predominantly linear over 70 hours. Radiolabeled acetate on the other hand indicated a somewhat non-linear pattern of assimilation into total lipid. Previous incubation time courses for high latitude environments have typically ranged form 6 to 24 hours, with the one report of 70 hours by Smith et al. (1987). The rational for this is the relatively slow metabolic rate of incorporation by microorganisms in low temperature environments. Likewise, incorporation rates for this site during a previous

study (Smith et al. in press) have indicated similar slow [^{14}C]-sodium acetate incorporation into lipids. Our extended incubation periods were for this reason required for complete realization of radiolabel precursor incorporation into intracellular lipids.

The most informative investigation of intracellular lipid allocation presented in this study is provided by the separation of radiolabeled membrane phospholipids by silver nitrate TLC (fig. 4 a & b). By following assimilation and subsequent allocation of radiolabeled precursor carbon into phospholipid fatty acid (PLFA's), taxonomic discrimination of metabolic groups is possible (White 1983; Nichols 1983; Gillan 1981; Lechevalier 1977). Examination of these PLFA's by lipid metabolic techniques indicated minimal algal-bacterial coupling over our temporal investigation. For if radiolabeled carbon from algal polyunsaturated fatty acids (Ackman et al., 1968; Chuecus and Riley, 1969; Harwood and Russell, 1984) were being utilized extracellularly by any coupled bacteria, than assimilation into predominantly bacterial saturated and monounsaturated fatty acids (Lechevalier 1977; Gillan and Johns, 1986; Harwood and Russell, 1984) would be expected. This process was not apparent from our investigations using radiolabeled [^{14}C]-bicarbonate as a precursor into phototrophs during a 72 hour ambient light incubation.

The parallel radiolabeled acetate study under dark conditions demonstrated the ability of bacteria to fix substantial amounts of carbon into monounsaturated fatty acids (fig. 4b). The fact that proportions of radiolabeled monounsaturated fatty acids in the bicarbonate study remained at such low levels (fig. 4a) indicates minimal transfer of algal-fixed carbon to bacterial lipids. However, slightly increased proportions of saturated fatty acids at 42 hours during the bicarbonate study (fig. 4a), may indicate some coupling is occurring. A somewhat confusingly high proportion of polyunsaturated fatty acids are present in the acetate study. At this point it is uncertain whether these are actually unusual components of antarctic sediment bacteria, or derived from other non-photosynthetic microeucaryotic grazers. The increase in these polyunsaturated fatty acids during the actetate time course may indicate the later as bacteria are grazed by microeucaryotes.

Indications from a preliminary Arthur Harbor sedimentation flux study revealed a large pool of organics in the form of water column phytoplankton (Table 2). This bloom was shown to produce as much as 2 gm $POC/M^2/d$ during the period of our study. This could be a key component in the indication from our investigations that minimal algal-bacterial coupling is occurring. Such a flux of organics from primarily senescent or

moribund phytoplankton would effect a dilution consequence and a "short circuiting" of bacterial coupling with viable algae. For if bacteria are, as reported by Cole 1982, efficient opportunist, than their preference for senescent phytoplankton would prevent our detection during such blooms. Conversely, close coupling of bacteria to algae during low light, aphotic, and/or non-bloom periods remain a plausible heterotrophic mechanism for sediment bacteria.

In addition, lipid class determinations provided a means of following physiology within the benthic microbial community without confounding disturbance artifacts. Recent investigations have utilized these and other lipid techniques in ice algal communities to determine carbon allocation patterns and physiological responses on a seasonal scale (Palmisano et al., 1988; Nichols et al., 1989), and on a spacial scale (Li and Platt, 1982). By utilizing two precursors with specificity for different components of the benthic community (ie. phototrophs and heterotrophs), a primary interpretation of lipid metabolic processes within these communities was possible. Therefore, from the interpretation of the linearity for total lipid assimilations (Fig. 1a vs.1b) it becomes apparent that acetate is more readily assimilated into lipids when compared to bicarbonate. This is felt to reflect a more rapid metabolic incorporation of acetate

by heterotrophic bacteria.

Variations in assimilation of radiolabeled substrates; bicarbonate (light), vs. acetate (dark), displayed distinctive patterns of allocation into lipid classes. Patterns determined by Palmisano et al. (1988) for an ice algal community in which the lipid classes of neutral and glycolipid varied more dramatically on a seasonal scale with respect to phospholipid were also noted for these benthic microbial communities. Even though no direct correlation of our results can be made with such seasonal studies, the similarities may represent the dynamics of intracellular lipid metabolism on a shorter temporal scale. As a whole these patterns are believed to indicate a physiological response of phototrophs. That is, responses in which they allocate carbon within lipids to either neutral lipid (storage), or photopigment associated glycolipids, depending on ambient environmental conditions and/or life cycle dynamics. During such shifts in carbon allocation between neutral lipids and glycolipids, structural membrane phospholipids remained essentially constant (for both bicarbonate and acetate), indicating a viable, metabolically sound community.

Assimilation of acetate on the other hand provided an interesting signal early (18 hours), with glycolipids being greater than either neutral or phospholipid. Allocation of

radiolabeled carbon into glycolipids could, as suggested by Rivkin and Putt (1987), reflect phototrophic assimilation of organic acids under low light conditions. This would fit into ecological considerations of Polar phototrophs, which may posses mechanisms for utilization of these acids when exposed to seasonally low light levels. If this is the circumstance, then allocation into photopigment associated glycolipids could be a mechanism for either utilizing extreme low light, and/or, a physiological preparation for utilizing increased light when available. This recent information by Rivkin and Putt (1987) along with our determined glycolipid allocation pattern for [2-^{14}C]-acetate (Fig. 3b) focuses attention on relatively rapid incorporation of organic acids into lipids under certain conditions. These in situ physiological processes clearly deserve further elucidation.

Past this initial point at 18 hours. allocation of carbon from [2-^{14}C]-acetate indicated little variation within lipid classes (Fig. 3b). To our knowledge this lipid class analysis has never been conducted under any conditions, or environment. Only one similar investigation conducted by Sargent et al. (1985) for Phaeocystis pouchetii has indicated that [^{14}C]-bicarbonate allocation into polarlipids (ie., glycolipid + phospholipid) was greater than free fatty acids (typically a minor component of the

neutral lipid fraction) during a 7 hour incubation. Consequently information needed make comparisons with this pattern is unavailable. However this pattern, apart from the early glycolipid signal, does seem intuitively appropriate and indicates no interfering aberrations from disturbance artifacts.

Ecological considerations

From these observations one must certainly obtain an awareness for the importance that the sedimentation fluxes (ie., phytoplankton blooms) have on sediment trophic responses in Arthur Harbor. To date it would be somewhat premature to make any broad prediction of sedimentation flux effects on antarctic near-shore environments. However, this spring bloom is very well documented throughout the peninsula region, and similar benthic microbial trophic responses as discussed above are very plausible. Concurrent with this effect is the need for continued stability of present environmental conditions which facilitate this seasonal phytoplankton bloom. Any aberration with a deleterious consequence on the timing or magnitude of this bloom and it's subsequent sedimentation flux could surely create adverse repercussions within sediment microbial communities, and therefore the whole of the antarctic near-shore microbial ecology.

ACKNOWLEDGEMENTS

The authors wish to thank the excellent ITT/ANS staff at Palmer Station, and the crew of the Polar Duke. Mr. Baldo Marinovic is thanked for his diving support in sediment core collections and laboratory sample preparations. Dr. R.E.H. Smith is thanked for his helpful comments during manuscript preparation. This research was funded by a NSF/DPP grant #86-13248 awarded to Dr. David C. White.

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FIGURE LEGEND

Fig. 1. Arthur Harbor study site. ER = Elephant Rocks at 26 m.

Fig. 2. Assimilation of precursor [^{14}C]-sodium bicarbonate, (A, light), $y = 47133x + -1.19 \times 10^6$, $r^2 = 0.82$, at $P < 0.01$, (n=4), and [2-^{14}C]-sodium acetate (B, dark), $y = 639.01x + 2.66 \times 10^4$, $r^2 = 0.60$, at $P < 0.01$, (n=4), into total lipid.

Fig. 3. Allocation of radiolabeled carbon into lipid classes of neutral, glycolipid and phospholipid. Bicarbonate (A, light; n=4) and acetate (B, dark; n=4).

Fig. 4. Allocation of radiolabeled carbon into phospholipid fatty acid groups of saturates, monounsaturates and polyunsaturates. Bicarbonate (A, light; n=4), and acetate (B, dark; n=4).

Table 1.

Nutrient determinations for sediment porewater and overlying water of the Elephant Rock (26m), Arthur Harbor study site

	Porewater uM	Overlying seawater uM
Nitrate-N	10.0	11.8
Nitrite-N	3.3	nd[a]
Phosphate-P	1.3	0.4
Silicate-Si	188.0	43.0

a. nd = not detected

Table 2.

Sediment fluxes of POC and lipid for Polar and various temperate and tropical sites

	Location	Depth (m)	POC $mg/M^2/d$	Lipid $mg/M^2/d$
POLAR				
Frobisher Bay, Southern[a] Baffin Is., Arctic	63° N : 68° W	33	72	
King Geo. Is., Antarctic, Peninsula[b]	62° S : 57° W	323	132	
Risser-Larsen Ice Shelf[c] Weddell sea, Antarctica	72° S : 18° W	80	17	
Arthur Harbor, Antarctic, peninsula[d]	64° S : 64° W	26	2000	70
TEMPERATE AND TROPICAL				
Peru upwelling[e]	15° S : 75° W	15	700	90
California current[e]	35° N :122° W	100	70	20
Central No. Pacific[e]	15° N :150° W	400	3	0.2
Equatorial No. Atlantic[e]	12° N : 50° E	400	6	2
Sargasso Sea[e]	30° N : 52° E	5200	1	

a. From Atkinson and Wacasey, (1987) Polar Biol., 8:3-7.

b. From Bodugen, B. v., (1986) Polar Biol., 6:153-160.

c. From Bodugen, et al., (1988) Comp. Biochem. Physiol. 90B (3):475-487.

d. This study.

e. From Wakeham, et al., (1984) Deep-Sea Res. 31(5):509-528.

Fig. 1

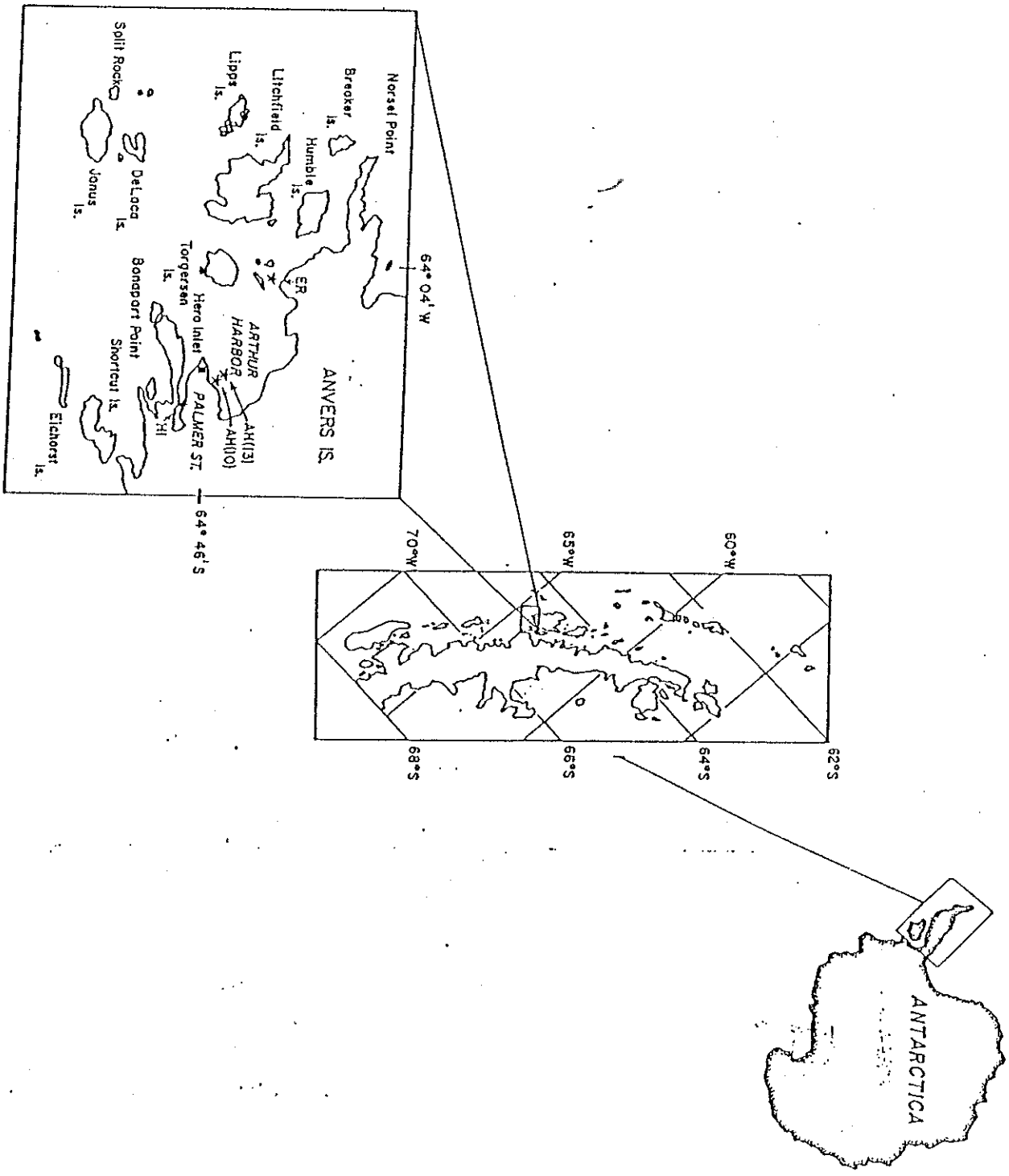

Norsel Point
Breaker Is.
Humble Is.
Litchfield Is.
Lipps Is.
Split Rock
DeLaca Is.
Janus Is.
Torgersen Is.
Hero Inlet
Bonaparte Point
Shortcut Is.
Elchorst Is.
ER
ARTHUR HARBOR
PALMER ST.
AH(13)
AH(10)
ANVERS IS.
64° 04' W
64° 46' S
70°W
65°W
60°W
68°S
66°S
64°S
62°S
ANTARCTICA

Fig. 2.

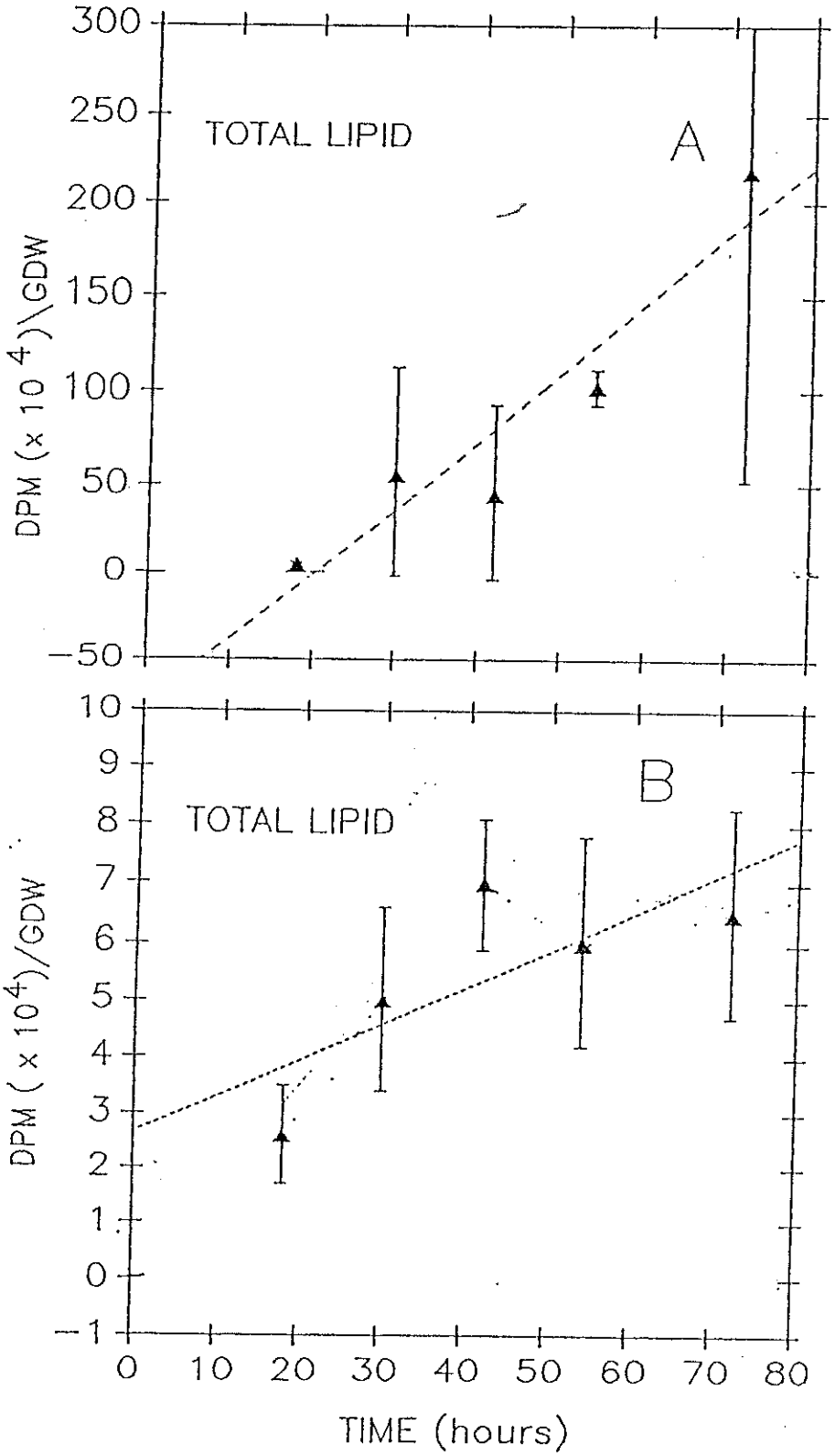

TOTAL LIPID
A
DPM (x 10 4)\GDW
300
250
200
150
100
50
0
−50
TOTAL LIPID
B
DPM (x 10 4)/GDW
10
9
8
7
6
5
4
3
2
1
0
−1
0
10
20
30
40
50
60
70
80
TIME (hours)

FIG. 3

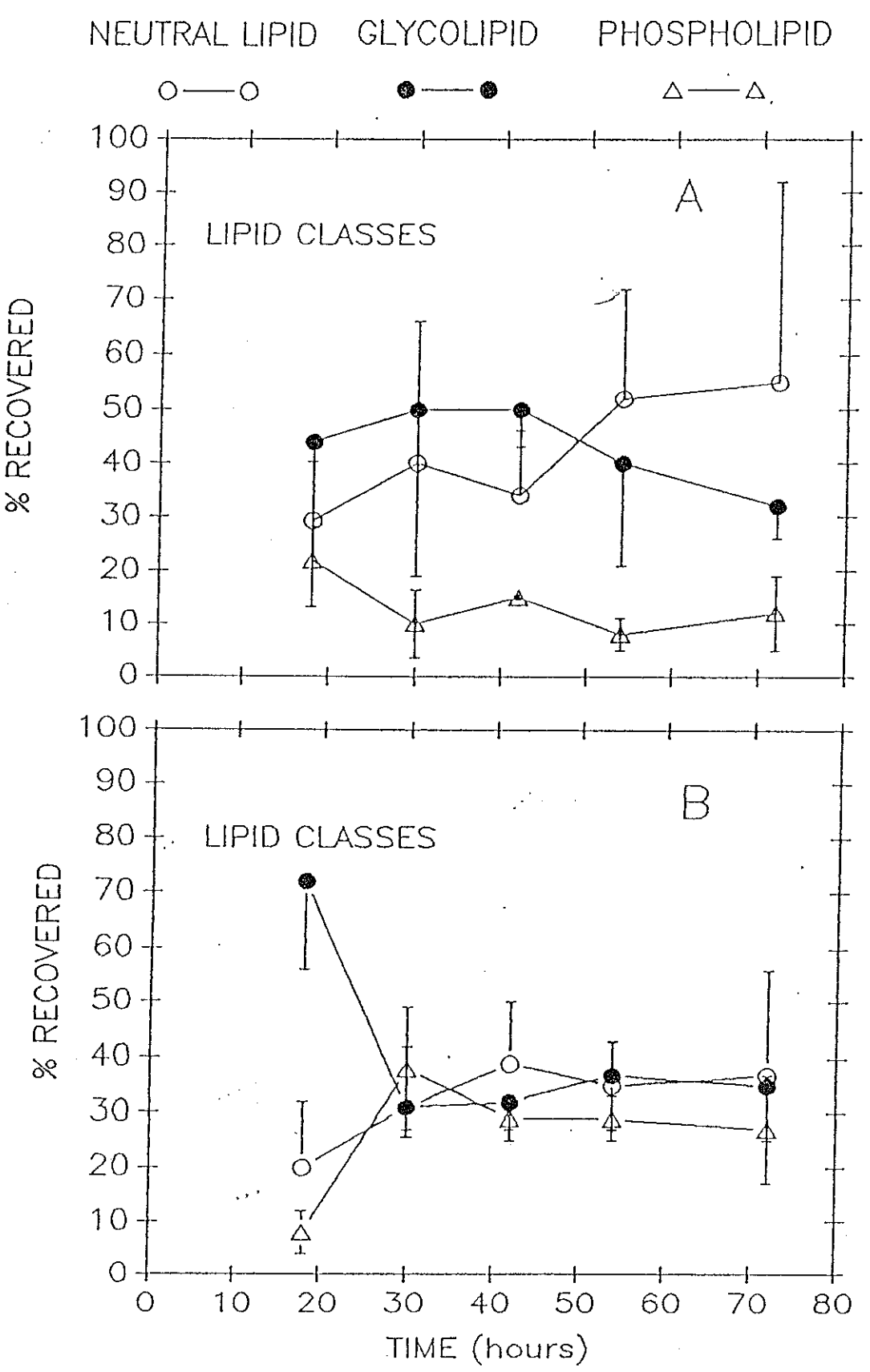
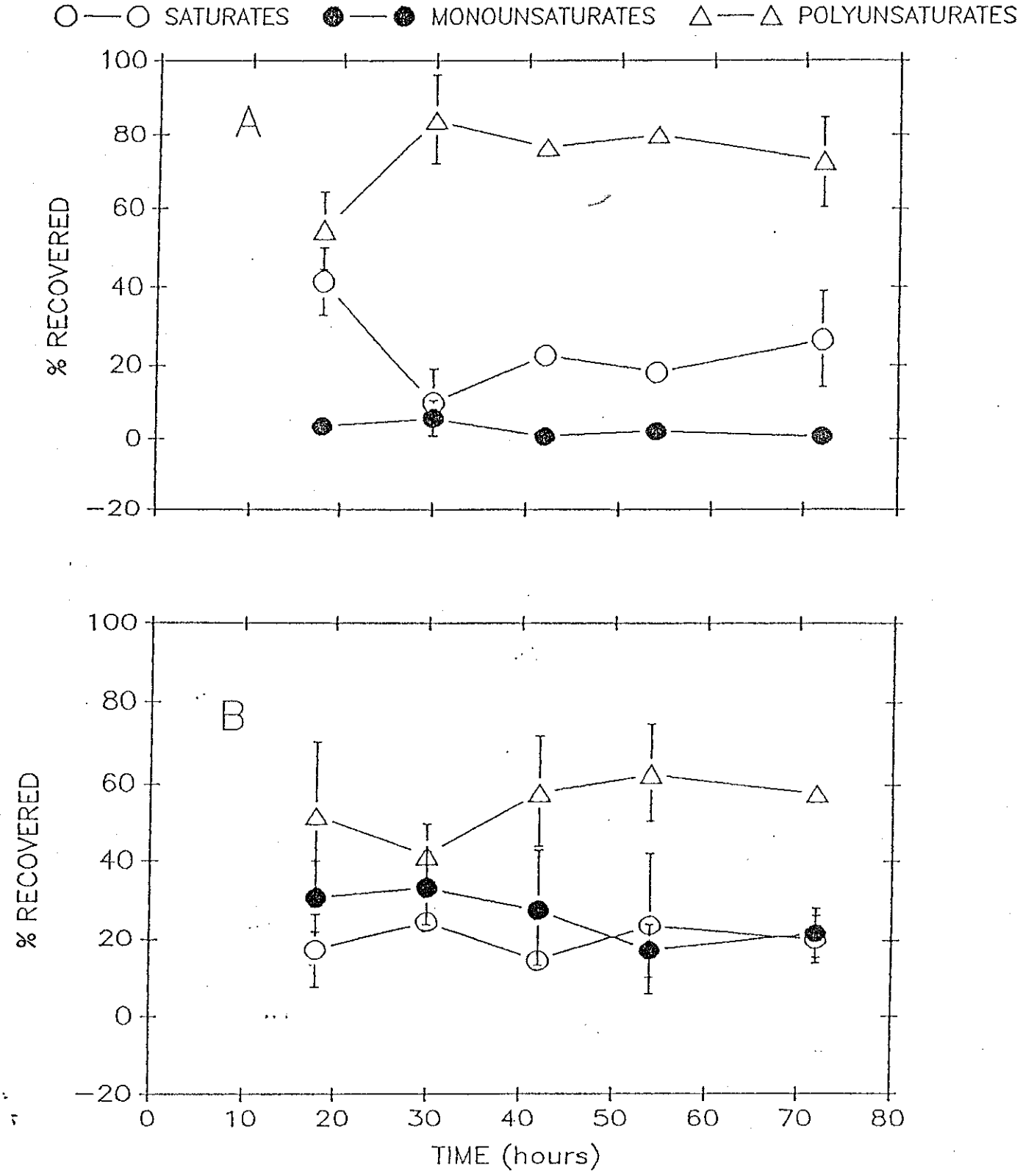

NEUTRAL LIPID
GLYCOLIPID
PHOSPHOLIPID
A
LIPID CLASSES
% RECOVERED
B
LIPID CLASSES
% RECOVERED
TIME (hours)

FIG. 4.


SATURATES
MONOUNSATURATES
POLYUNSATURATES
A
B
% RECOVERED
% RECOVERED
100
80
60
40
20
0
-20
0
10
20
30
40
50
60
70
80
TIME (hours)