

PREY INGESTION REVEALED BY OESOPHAGUS AND STOMACH TEMPERATURE RECORDINGS IN CORMORANTS

A. ANCEL*, M. HORNING† AND G. L. KOOYMAN

Center for Marine Biotechnology and Biomedicine, Scripps Institution of Oceanography, La Jolla, CA 92093-0204, USA

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Summary

We examined the accuracy of both stomach and oesophagus temperature sensors – deployed on captive Brandt's cormorants – for determination of the mass of food ingested and the number of prey items swallowed. The oesophageal temperature sensor was a better detector of all feeding events, including that of small prey which were missed by the stomach sensor. Adapted to free-ranging animals (and coupled to data loggers for recording seawater temperature), oesophagus temperature

recorders, in conjunction with both recordings of energy expenditure (e.g. doubly labelled water, heart rate) and determination of position (e.g. Argos transmitter, time/depth recorder), should provide further important insights into the foraging success of marine endotherms.

Key words: stomach temperature, oesophagus temperature, food intake, telemetry, seabird, cormorant, *Phalacrocorax penicillatus*.

Introduction

For more than a decade, information has been gathered on the foraging behaviour of many seabirds and marine mammals (for a review, see Kooyma, 1989; Le Boeuf and Laws, 1994; Williams, 1995) following improvements in data recording and transmitting devices (Trivelpiece *et al.* 1986; Jouventin and Weimerskirch, 1990; Wanless *et al.* 1991; Ancel *et al.* 1992). However, none of these studies has investigated the efficiency of foraging (i.e. the energy expenditure in relation to the amount of food consumed, but see Chappell *et al.* 1993; Wilson *et al.* 1993, 1994), and none has reliably detected when individual prey items are actually captured. Both the timing and the amount of prey captured by marine endotherms need to be determined if foraging behaviour is to be well enough understood to extrapolate this information to the effects of these predators on the food web.

Some studies have characterized diet, from analyses of either pellets (Duffy and Laurenson, 1983) or from stomach contents (e.g. Croxall *et al.* 1995). Other methods have estimated the food consumed by seabirds and marine mammals from ejected meals (Van Dobben, 1952), stomach samples (Wilson, 1984), isotopic methods (Gales and Green, 1990) and stomach temperature recordings (Wilson *et al.* 1992, 1995; Gales and Renouf, 1993; Grémillet and Plös, 1994).

Nevertheless, each method has limitations, and the quantification of food consumption has remained problematic (Pütz and Bost, 1994; Hedd *et al.* 1996). Specifically, these methods do not deliver sufficiently accurate information

regarding either the number of prey items eaten or the amount of food consumed. Until now, the most promising technique was the measurement of variations in stomach temperature, as first proposed by Wilson *et al.* (1992). Questions that arise from this technique are: where is the best place to record a temperature drop due to prey ingestion? Is the stomach a good place to quantify the food intake? These questions have been addressed in a comprehensive review by Wilson *et al.* (1995).

Hitherto, the stomach has been chosen as the site for recording temperature fluctuations because of the technical ease of placing the sensor in the stomach. However, it is now known that the stomach is not an entirely satisfactory site for detecting the ingestion of small prey items or for estimating the amount of food consumed because the temperature sensor may be covered by warm food, thus rendering it insensitive to newly ingested material (Wilson *et al.* 1995). These authors also noted that the closer the sensor was to the entrance of the stomach, the more accurate was the recording of food ingestion. Thus, placement of the sensor in the oesophagus should render a prey ingestion detection system more effective. We therefore chose to study temperature drops caused by ingestion of cold prey, simultaneously in the stomach and oesophagus.

Materials and methods

To record the temperature inside the lumen of the stomach

*Permanent address: Centre d'Ecologie et Physiologie Energétiques, Centre National de la Recherche Scientifique, 23 rue Becquerel, 67087 Strasbourg Cedex 02, France (e-mail: andre.ancel@c-strasbourg.fr).

†Present address: Dept of Marine Biology, Texas A&M University, 5007 Avenue U, Galveston, TX 77551, USA.

and inside the lumen of the oesophagus simultaneously, we used two types of miniaturized electronic temperature recorders. Both types of devices were designed and built by one of us (M.H.).

The first type of recorder (stomach temperature recorder) consisted of two separate devices (to prevent the loss of data due to regurgitation): a temperature-sensing radio transmitter pill and a separate radio receiver with integrated data recorder. The temperature sensor/transmitter pill incorporated two YSI thermistors, electronic circuitry and a lithium battery encapsulated in physiologically inert resin. The oval-cylindrical sensor pill was 45 mm long and had a maximum diameter of 20 mm. Pill mass was 20 g at a density of 1.67 g ml^{-1} . The pill integrated temperature over the two thermistors, located at the tips of the unit. The temperature signal was sent as a short-range pulse-interval-modulated extremely low-frequency transmission. The receiver/recorder unit measured $55 \text{ mm} \times 32 \text{ mm} \times 15 \text{ mm}$ and had a mass of 35 g. It incorporated the radio receiver/decoder and a data recorder with 10 bit resolution and 128 kbytes of static RAM, encapsulated in electronic resin. Data transfer to an external PC was by optical communication, using a special interface box.

The second type of temperature recorder was identical to the first except for the absence of the radio receiver/decoder. Instead, a single YSI thermistor was connected directly to the data recorder unit via a 50 cm long, 1.5 mm diameter coaxial butyl-sheathed cable. The thermistor was coated in physiologically inert resin, forming a pear-shaped bead of approximately $2.5 \text{ mm} \times 5.0 \text{ mm}$. The recording device measured $50 \text{ mm} \times 30 \text{ mm} \times 14 \text{ mm}$ and had a mass of 32 g.

Both recorders were set to sample continuously at a fixed interval of 4 s for a total recording period of 6 days.

The temperature sensors of both recorders were calibrated before deployment. Calibration curves were established in a Precision R10a refrigerated constant-temperature water bath (CGA) before and after the experiment over the usable temperature range $0\text{--}50^\circ\text{C}$. Reference temperatures were taken with a NIST-certified mercury thermometer (Thompson Scientific, -1 to 51°C at 0.1°C intervals). The temperature recording systems had a nonlinear resolution of better than 0.1°C at 50°C and 0.2°C at 0°C , corresponding to a nine-bit data bandwidth over the usable temperature range. Absolute accuracy was better than $\pm 0.2^\circ\text{C}$. Hysteresis was less than 0.05°C . The response speed of both systems was determined by transferring the sensors from a water bath at 36.5°C to another at 16.0°C . Initial response of the pill was $0.01^\circ\text{C s}^{-1}$; that of the thermistor cable was 0.1°C s^{-1} . Thus, the cable sensor had a faster initial response than the pill by a factor of 10.

To assess the validity of the temperature recorders as a detector of food intake, a trial with three captive Brandt's cormorants (*Phalacrocorax penicillatus* Brandt) was undertaken in July 1994. The cormorants were captured in San Diego Bay. They were housed in a 200 m^2 outdoor pool at the Scripps Institution of Oceanography (University of California

at San Diego). The pool, equipped with sites for the birds to roost, was filled to a depth of approximately 1 m with sea water, continuously pumped from a pipe inlet 300 m offshore. The experiment started after the birds had become accustomed to their new situation (captivity, feeding and human presence), about 5–8 days after capture. The birds were fed by the same person throughout the experiment. All birds maintained a constant body mass for the duration of their captivity and were released in apparently good health.

Data recorders were attached to the dorsal feathers of the birds, between the wings, using a 1 s glue with accelerator (Loctite 422) or TESA 5020-19 textile tape (Beiersdorf). The stomach temperature pill alone was inserted into a fish and fed to the bird. For simultaneous deployments of both recorder types, the cable sensor for the oesophagus was linked by an 18–20 cm long silk thread to the stomach radio pill. The sensor pill was then placed in a fish and fed to a bird. Upon eating the fish, the bird automatically swallowed the cable sensor, which trailed the fish. The cable sensor thus lodged in the oesophagus and was held in place by the heavier pill located in the stomach. The sensor cable was secured to the corner of the beak with a small break-away dab of Loctite glue, at a distance of 20 cm from the sensor. The remainder of the cable was secured along the neck with short break-away pieces of TESA tape. This ensured that, after regurgitation of the transmitter pill and cable sensor, these two devices hung off the back of the bird without deleterious effects.

The birds were fed during daylight on thawed herring (*Clupea harengus*) and smelt (*Salmo eperlanus*) of known mass (range 16–143 g) and temperature (core and external temperatures were the same, range $1.5\text{--}25.5^\circ\text{C}$), and the exact time of feeding was recorded. As soon as the stomach sensor was regurgitated, all equipment was removed and data were transferred to a PC.

The data obtained were the number of items ingested, their mass and temperature, the time at which they were swallowed, and the temperature of both the oesophagus and the stomach before, during and after the feeding events.

Results

The birds retained the temperature sensors for periods averaging 32 h for the stomach pill only (range 12–118 h, 18 deployments) and 25 h for the simultaneous deployment of both sensors (range 16–45 h, five deployments). During the feeding sessions, the birds equipped with cable sensors seemed as eager to eat as the birds equipped solely with a stomach pill. On average, the birds ate $400 \text{ g fish day}^{-1}$, which amounted to approximately 20% of their body mass ($1.9 \pm 0.1 \text{ kg}$, mean \pm S.D., $N=3$). During the feeding sessions, the birds did not seem encumbered in moving around the tank, in reaching for the fish or in swallowing them; they were no more shy or more reluctant to eat. Between the feeding sessions, their body temperature oscillated around $40.0 \pm 0.5^\circ\text{C}$ (S.D.) during the day and $39.2 \pm 0.2^\circ\text{C}$ (S.D.) at night. The stomach and oesophagus baseline temperatures were identical.

Fig. 1. Simultaneous profiles of changes in stomach (solid line) and oesophagus (dotted line) temperature recorded in a captive cormorant while it ingested meals of fish. The starts of the five feeding sessions (three single prey ingestions, SP1, SP2 and SP3, and two multiple prey ingestions, MP1 and MP2) are shown by the arrows. The numbers above the arrows indicate prey mass (g) and prey temperature ($^{\circ}\text{C}$). Note that, before event SP1, the bird's stomach already contained a 25 g meal swallowed 1 h earlier with the temperature sensors. The sampling interval for both temperature sensors is 4 s.

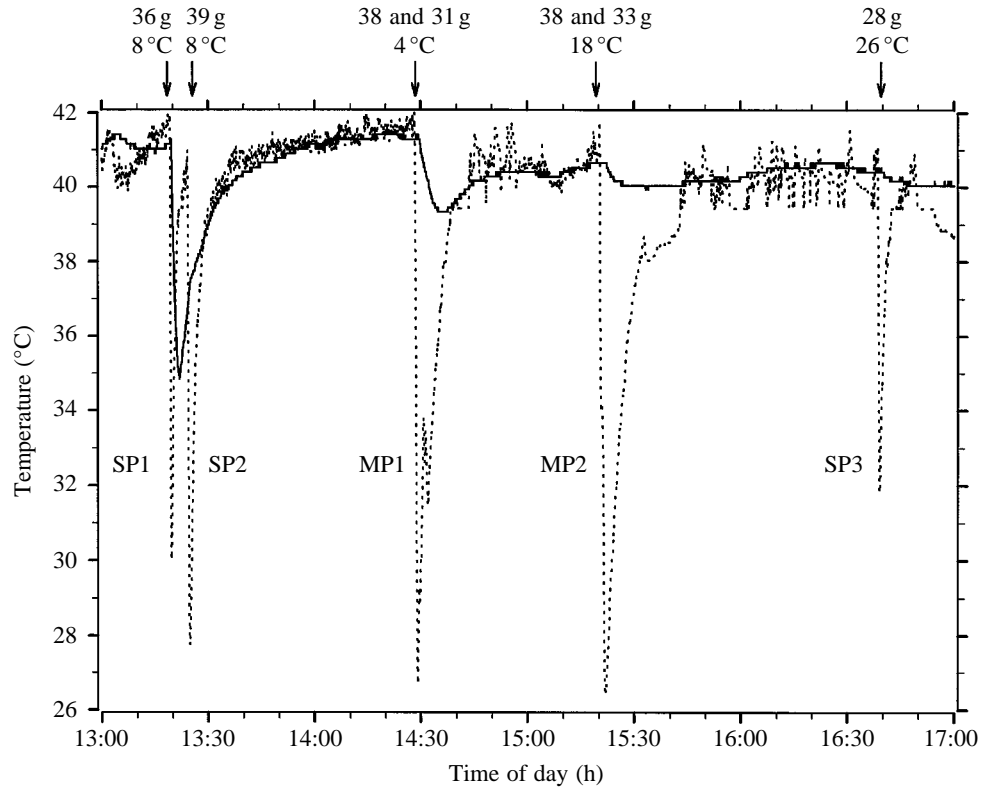
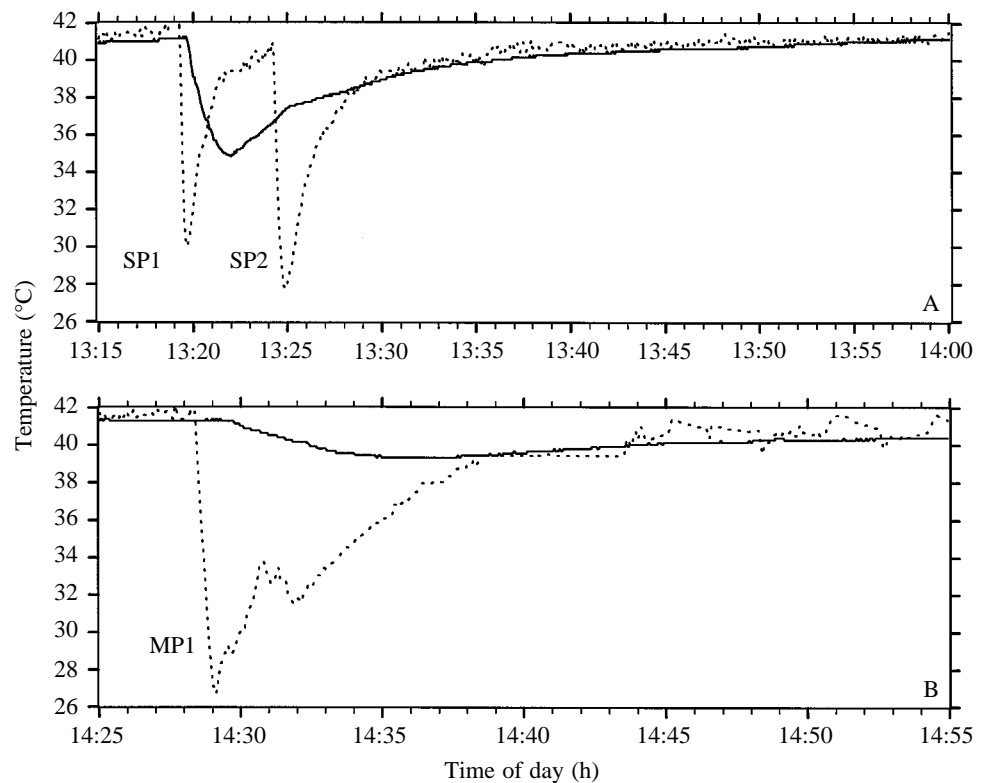


Fig. 2. Enlarged portion of Fig. 1, detailing feeding sessions SP1, SP2 and MP1. (A) One smelt (36 g at 8°C) swallowed at 13:19 h and a second (39 g at 8°C) at 13:24 h. (B) Two smelts swallowed simultaneously at 14:28 h (38 g at 4°C and 31 g at 4°C). Solid lines, stomach temperature; dotted lines, temperature in the oesophagus.



When a bird swallowed a fish, head first, both sensors recorded a drop in temperature followed by an exponential rise (Fig. 1). Although the two sensors recorded identical

temperature levels between the feeding sessions, the shape of the temperature-change curves recorded by each sensor differed (Figs 1, 2). In the oesophagus, ingestion of prey

caused a precipitous drop in temperature for every fish eaten. This was not the case for the sensor located in the stomach. In cases of multiple sequential feeding events, the stomach sensor recorded only one drop (Fig. 2). During the course of the day, as the stomach was gradually filled with food, the stomach sensor became increasingly less sensitive to the food intake, in contrast to the oesophagus sensor (Fig. 1). In the same way, during the course of the first two feeding events of the day, the time delay between ingestion and the onset of the temperature drop for the stomach sensor increased from 52 s (Fig. 2A, feeding event SP1) to 104 s (Fig. 2B). The time lag for the oesophagus sensor was a constant 8 s.

We obtained usable temperature readings during 28 meals of fish from the stomach recorder and eight from the recorder in the oesophagus. An additional 39 feeding sessions for the stomach and seven for the oesophagus were deemed non-usable because (a) we could not clearly determine whether the bird in question had in fact eaten all prey items, (b) prey items were not eaten immediately and could have warmed up before ingestion, or (c) no significant temperature deviation was observed for stomach temperature values on a full stomach. The integral of the area above the curve, from the minimum temperature recorded until the pre-prandial value had been regained (i.e. the exponential rise described in details by Grémillet and Plös, 1994), was highly correlated to the meal mass (Fig. 3). The use of regression equations relating the mass and the temperature of the prey (in most cases for marine endotherms, the temperature of the prey is the same as that of the surrounding water) to the rewarming period area leads to high correlations (Fig. 3). Despite a smaller sample size, the correlation coefficient was much higher for oesophageal than for stomach temperatures ($r^2=0.96$ for oesophagus and $r^2=0.45$

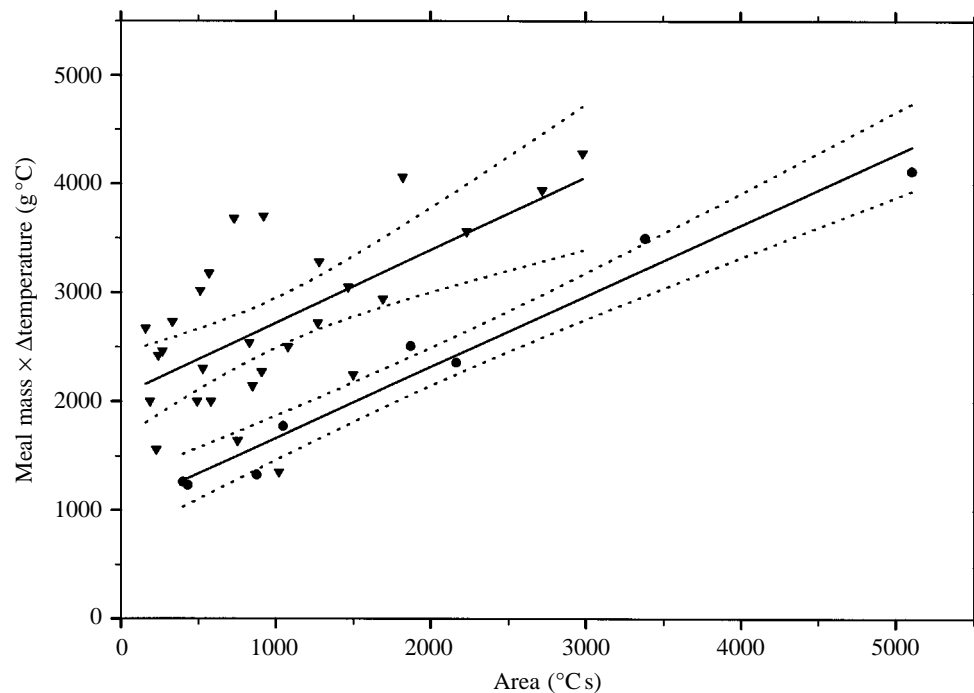
for stomach). Most oesophageal data points were within or close to the 95 % confidence limits, whereas stomach values showed a much larger deviation (Fig. 3).

Discussion

We have tested a new system for the continuous measurement of temperature in freely moving birds maintained in captivity. The 2–5 day recordings indicated the accuracy and reliability of this recording system. The oesophagus sensor provides a reliable means for the detection of feeding events and for the accurate estimation of food intake in seabirds. Furthermore, the procedure did not seem to affect the birds' performance: their feeding behaviour was not altered, their initial and final masses were similar (on average 1.9 kg), and the daily food consumption was slightly higher than previously reported for captive cormorants (16–18 % of body mass reported by Junor, 1972, and 18–20 % by Zijlstra and Van Eerden, 1995). However, retention times were shorter for the dual sensor set-up, indicating that the oesophageal cable was an irritant. Nevertheless, no other efforts were made to quantify the effect of the sensors on the birds' behaviour. As reported here, the variations of baseline temperature values between day and night may serve to indicate endogenous circadian rhythms in endotherms.

The effects of the the location of the temperature sensor within the stomach or within the oesophagus have never been investigated, except for a first attempt to analyze sinking *versus* floating devices (Wilson *et al.* 1995). Our data indicate that the oesophagus may be a more suitable location in which to quantify food intake, in terms of both number of prey items and ingested mass. The stomach sensors we employed were

Fig. 3. Relationship between prey mass ingested and area related to fish ingestion (integral above temperature curve and below baseline temperature asymptote; starting when minimum temperature was reached and ending when initial body temperature was regained). The regression lines are shown with 95 % confidence limits (dotted lines): $m \times \Delta T = 2048.7 + 0.67A$ ($N=28$, $r^2=0.45$, $F=18.5$, $t=4.3$, $P<0.005$) for the stomach sensor (triangles) and $m \times \Delta T = 1012.6 + 0.65A$ ($N=8$, $r^2=0.96$, $F=167.5$, $t=12.9$, $P<0.005$) for the oesophagus sensor (circles), where m is the mass of the fish (g), ΔT is the difference between the bird temperature and the fish temperature (or surrounding water temperature, °C) and A (°Cs) is the area above the curve (to a temperature equal to the pre-ingestion value) in the temperature *versus* time graphs (see Figs 1 and 2).



not capable of resolving ingestion events separated by less than 27 min, when the stomach was empty. The oesophagus sensor, however, was able to distinguish two small prey items ingested within seconds of each other (Fig. 2B). This difference in sensitivity is probably due to the smaller mass, and thus lower thermal inertia, of the cable sensor, which was 10 times faster during a transfer from a warm to a cold water bath. In addition, of the two thermistors in the stomach pill, only one is likely to come into contact with the cold food upon ingestion. The second sensor will not respond until the entire pill has begun to cool down. The response time of the stomach sensor seemed to be influenced by the degree of stomach fullness (Fig. 1, from SP1 to SP3). This progressive decrease in response is probably due to the sensor being covered by warm food. Wilson *et al.* (1995) suggested that this problem can be avoided by designing stomach sensing devices that float in the contents of the stomach and/or that are very large (>12 % of the maximum stomach volume), with a thermally conductive surface. This approach is problematic: large devices are more likely to interfere with a bird's behaviour. In diving animals, floating devices might still not remain in place close to the oesophageal opening, where they would be more exposed to ingested food, owing to frequent changes in orientation of the diving bird. Placing the temperature probe in the oesophagus circumvents these problems. The initial response delay between cable and pill sensors of only 52 s, in conjunction with the very rapid rewarming of the cable sensor (5 min for event SP1), indicates a rapid passage of swallowed fish beyond the oesophagus and into the stomach. This implies that the actual position of the cable sensor within the oesophagus is much less critical than that of the pill sensor in the stomach. This would be particularly important for species with delayed gastric emptying for the purpose of carrying food inside the stomach for their chicks (Wilson *et al.* 1989). Longer retention of prey in the oesophagus should be reflected in a more gradual return to pre-ingestion temperature values in the oesophagus sensor. This did not occur: rewarming times remained more or less constant for a given meal size, even after several feeding sessions filled the stomach (e.g. events SP1 and SP3 in Fig. 1). Thus, neither increasing meal size nor increasing stomach fullness seemed to affect passage time through the oesophagus in our study.

The use of oesophageal temperature sensors may have additional advantages that were not investigated in our experiments: little is known at present about how the magnitude of the diving response affects the warm-up of stomach contents. Initial evidence suggests that warm-up of stomach contents may be delayed under intense diving conditions (Bevan and Butler, 1992; Pütz, 1994; Culik *et al.* 1996). If reduced intestinal perfusion during diving delays the warming of stomach contents, then calibrations of a stomach temperature-recording system would become very difficult, unless realistic diving conditions could be simulated. Such limitations should be less severe for oesophageal recordings.

The oesophageal recording system described here should enhance the quantification of food intake in free-ranging

homeotherms that ingest prey items colder than their own body. The resolution of the system seems to be sufficient to quantify ingested mass, number of items ingested and even the mass of individual prey items. The ultimate usefulness of this system will require tests on free-ranging birds and mammals.

P. Heineke's help was 'instrumental' for the circuitboard production for the electronic recorders at the Max-Planck-Institute, Seewiesen, Germany. Also at Max-Planck, W. Mohren wrote the software required for data downloading and viewing. Assistance in San Diego was kindly provided by T. Mau, L. Starke, R. Van Dam and L. Winter. This work was supported by grants USPHSHL17731 and NSFDP92-19872 to UCSD.

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