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Comparison of several techniques for mobility and activity estimates of smallmouth bass in lentic environments

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Mean daily mobility estimates for smallmouth bass *Micropterus dolomieu* from mark-recapture (47·5 ± 12·5 m) were less than from conventional telemetry (77·1 ± 10·6 m). The relationship developed in a respirometer between the activity transmitter and swimming speed (r^2=0·99, P<0·001, n=6) when applied to field activity data estimated mean daily movement at 27 408 ± 4085 m, i.e. >100 times mark/recapture or telemetry estimates. Using these estimates in the activity parameter of a bioenergetics model resulted in different model outputs. These results highlight the potential underestimates in activity associated with using traditional mark-recapture and locational telemetry and reaffirm that fish expend a significant portion of their activity budgets undertaking localized movements.

Key words: smallmouth bass; movement; telemetry; anchor tags; EMG*i*; activity; bioenergetics.

INTRODUCTION

Mobility and activity estimates of free-swimming fish, although difficult to obtain (Beamish, 1978), are important aspects of fish ecology. Managers rely upon accurate estimates of mobility for conducting stock assessments and implementing management strategies. Activity estimates are important in bioenergetics models, which are used as simulation tools to predict food consumption rates and growth (Ney, 1993). Activity has been identified as an integral component of bioenergetics modelling (Boisclair & Leggett, 1989*d*; Boisclair & Sirois, 1993) because energy costs related to activity may represent one of the most important determinants of variation of growth rate between populations (Boisclair & Leggett, 1989*a*,*b*,*c*,*d*). Direct assessments of fish activity are rare, with most activity estimates derived from mobility studies, frequently from different species. This is due in large part to the lack of either swimming-speed field measurements or knowledge of the proportion of time spent swimming by fish (Hinch & Collins, 1991). Better methods of assessing activity are required to provide more accurate information on behaviour and energetics of free-swimming fish.

Several methods have been used to estimate activity of free-swimming fish. Direct underwater observation using snorkeling and SCUBA have been used

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sporadically (Emery, 1973), but it is limited in its ability to document the activity of individual organisms over extended periods. Direct underwater observation using videography provides some additional insights into the free swimming activity of fish (Boisclair, 1992; Trudel & Boisclair, 1996) however, it is not particularly useful for highly mobile species. Data can be collected only when a fish is within the field of view, when water is sufficiently clear, and when densities of fish are high (Boisclair, 1992; Krohn & Boisclair, 1994). In addition, during the night, videography requires infrared lights and infrared sensitive cameras to record activity (Collins *et al*., 1991; Hinch & Collins, 1991). Hansen *et al*. (1993) and Ney (1993) proposed that bioenergetics modelling will benefit from the advent of physiological telemetry and hydroacoustics. Since this prognosis, both of these techniques have become more commonly available, with physiological telemetry being used successfully to estimate metabolic rates (Lucas *et al*., 1993).

Conventional means of collecting information on fish mobility have focused on mark-recapture studies with tag returns from anglers, electrofishing and netting, conventional locational telemetry involving manual tracking, and fixed telemetry systems. Gowan *et al*. (1994) highlighted and reviewed the biases and limitations associated with different techniques for assessing fish mobility and concluded that in many cases, the results obtained were a function of the methodology employed. They also highlighted the potential significant implications of underestimating fish mobility.

Generally, lake dwelling smallmouth bass *Micropterus dolomieu* (Lacépède) exhibit restricted movements (Ridgway & Shuter, 1996). Methods to determine both movements and activity of smallmouth bass have included most techniques available. Consequently, smallmouth bass serve as an excellent model for comparing activity and mobility estimates directly. Mark-recapture programmes based upon angler tag returns (Stone *et al*., 1954; Webster, 1954; Forney, 1961; Latta, 1963; Pflug & Pauley, 1983), electrofishing (Pflug & Pauley, 1983) and netting (Fraser, 1955; Latta, 1963) provided the first evidence that lake dwelling smallmouth bass exhibit restricted movements. Similar findings have been reported by researchers using conventional telemetry involving manual tracking (Hubert & Lackey, 1980; Kraai *et al*., 1991; Savitz *et al*., 1993; Ridgway & Shuter, 1996; Cole & Moring, 1997) and those employing continuously monitored fixed telemetry systems (Cooke *et al*., 2000). Activity of nest guarding male smallmouth bass collected using videography (Hinch & Collins, 1991) provided some of the first insights into the activity patterns of free-swimming fish. Although fish did not move over a wide area, they were extremely active. More recently, Demers *et al*. (1996), using electromyogram (EMG*i*) telemetry to assess the activity patterns of free swimming smallmouth bass, often found elevated EMG*i* activity among apparently stationary fish. They concluded that fish activity at spatial and temporal scales too small for detection by conventional tracking may account for a significant portion of the daily activity budget. Applying mobility estimates to activity components of bioenergetics models may provide erroneous results if the mobility estimates do not incorporate fine scale movements.

This study aimed to compare differences in lentic smallmouth bass activity and mobility using mark-recapture, a continuously monitored fixed telemetry system, and telemetered signals of locomotor activity, identifying and describing the

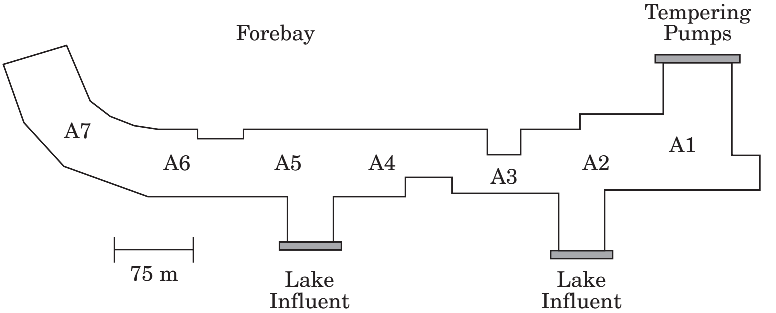

FIG. 1. Map of the thermal generating station forebay where the study was conducted. Water was drawn into the forebay through the influents and exited the forebay either *via* tempering pumps or a series of screened condenser pumps. A1–A7, antennae 1–7.

biases and limitations associated with each method. The utility of each of these methods for achieving specific research objectives was considered.

MATERIALS AND METHODS

STUDY SITE CHARACTERISTICS

The field component of this study was based on data collected during the summer of 1998 in the intake forebay (Fig. 1) at a thermal generating station on the north shore of Lake Erie. This coal-fired station uses a once-through condenser cooling water system, taking water from Lake Erie via two submerged intakes that extend *c*. 550 m offshore. Prior to being used for condenser cooling or discharge canal tempering, the water is held in the intake forebay. The forebay creates a safe and secure area from which to draw water, and allows year round operation by adding heated water to prevent frazil ice formation in winter.

Numerous fish species reside in the forebay, with smallmouth bass being the most prevalent. During the study period, the stomachs of numerous smallmouth bass were examined using gastric lavage. The gut contents were varied and there appeared to be sufficient food in the forebay (S. J. Cooke, unpubl. data). Anecdotal observations using underwater videography and diet analysis confirmed that the smallmouth bass fed in the forebay.

Water and fish enter the forebay constantly through the lake intakes, but exits are limited. Daily records are kept for fish that are filtered from the cooling water intake. Smallmouth bass were a small constituent of these fish and during the study no tagged individuals were impinged on the travelling screens. Occasionally fish could swim through the tempering pumps and then enter the discharge canal but such movement was rare (S. J. Cooke, unpubl. data). Security of the site ensured that study fish would not be removed by recreational or commercial anglers. Only project personnel were permitted to angle in the forebay.

MARK-RECAPTURE

At least three times weekly, from 18 May until 4 August 1998, three researchers angled within the forebay for 6 h. Standard spinning and baitcasting equipment used to capture the fish produces negligible mortality in smallmouth bass (Dunmall *et al*., in press). Fish were placed in a cooler then measured (L_T mm) and weighed (g) before tagging in the dorsal musculature, between the soft and the spiny dorsal fin with an individually identifiable anchor tag. The date and site of capture were recorded prior to release. Recaptured fish were treated in the same manner, but were not tagged. The date and location of recapture was noted and the fish was released. Angling effort was spread throughout the study site to minimize bias in the results based upon unequal effort and to minimize the detection biases associated with mark-recapture studies (Gowan *et al.*, 1994). The interval in days between mark and recapture was calculated and the distance between sites of mark and recapture measured to the nearest 5 m from a map. Mean daily movement was calculated by dividing the distance between mark and recapture by the time interval.

FIXED CONVENTIONAL TELEMETRY

An array of seven antennae was used to monitor continuously movements of fish in the study area (Fig. 1). Antennae were placed evenly every 75 m within the intake forebay. The antennae most extreme to either end were aerial. Antenna one was an H-antenna and antenna seven was a four element yagi. Aerial antennae with the concomitant increases in reception were required to compensate for signal attenuation in the long coaxial cable (Cooke & Bunt, in press). Antennae two to six were anchored to a depth of 4 m and were comprised of coaxial cable with 3 cm of the shielding removed. All cables used were RG58c/u and ran to a central antenna switching box (ASP-8, Lotek Engineering Inc.). An SRX_400 receiver (Lotek Engineering Inc.) with W-17 software scanned the seven antennae continuously each for 3 s. To minimize scan time, coded radio-transmitters were operated on one of four frequencies (channels) and all fish had one of 16 distinct codes. The transmitters emitted a pulse every 2·5 s. Therefore, every antenna reception zone was scanned for every fish at 84-s intervals. The receiver was downloaded to a field computer on a weekly basis.

Transmitters were inserted into fish collected by angling on 15 June 1998, landed in <20 s, and placed in coolers. Fish were anaesthetized using a 60 ppm induction bath of clove oil and ethanol (Anderson *et al.*, 1997). Equilibrium was lost after several minutes and then fish were measured (L_T, mm) and weighed (g) before being placed ventral side up in foam padding on a surgery table. A maintenance dose of anaesthetic (30 ppm) in oxygenated water irrigated the gills continuously.

A 15-mm incision was made slightly dorsal to the ventral midline, just posterior to the pelvic girdle of the fish. Then the transmitter was inserted gently into the coelomic cavity. The incision was closed using three independent sutures of 3/0 non-absorbable braided silk (Ethicon Inc.). The entire surgical procedure took <3 min. Then fish were returned to lake water, where they were allowed to recover for several minutes prior to release at the site of capture. All fish were captured and released at the same location (antenna six). A concurrent study confirmed that neither the burden of the radio transmitters nor the surgical procedure itself altered the swimming performance of smallmouth bass (Cooke & Bunt, in press).

LOCOMOTOR ACTIVITY TELEMETRY

The activity transmitters used (EMG*i*, Lotek Engineering) consisted of an epoxy-coated transmitter package with a pair of electrodes and a single antenna (Beddow & McKinley, 1998). Nine-carat gold electrodes measuring 7 mm were affixed to the end of the electrode wires. The electrodes detect the electromyographic activity within the axial red muscle, which then charge a capacitor. When capacitance has been reached, a pulse is emitted from the transmitter. This signal provides information on integrated electrical activity (EMG*i*), rather than data on individual muscle contractions.

The signal recorded by the receiver is an EMG*i* pulse interval (ms), which is related inversely to muscular activity. As muscle activity increases, the muscle EMGs increase, charging the capacitor more rapidly, thus decreasing the interval between pulses. The tags measured 51 mm in length and 13 mm in diameter, and weighed 18·0 g in air. Transmitters broadcast at distinct frequencies within an operating band of 148–150 MHz. Other studies have also implanted EMG*i* transmitters in centrarchid species (Demers *et al.*, 1996; Bunt, 1999) and found no ill effects of long-term transmitter implantation.

SURGICAL PROCEDURE (LABORATORY AND FIELD)

Fish were anaesthetized using a 60 ppm induction bath of clove oil and ethanol. Fish lost equilibrium after several minutes and then were measured (L_T, mm) and weighed (g) before being placed ventral side up in a V-shaped acrylic trough lined with neoprene on a surgery table. A maintenance dose of anaesthetic (30 ppm) in oxygenated water irrigated the gills continuously.

Surgical procedure was similar to that of Kaseloo *et al*. (1992). A 3-cm incision was made on the ventral surface, just posterior to the pectoral girdle. Electrodes were positioned 10 mm apart, in the red axial musculature below the lateral line using 16½ g rods. Electrode placement was standardized at the anterior portion of the dorsal fin (Beddow & McKinley, 1999). Then a plunger secured the electrodes in the muscle, allowing the rods to be removed. Then the transmitter was inserted through the incision and pushed anteriorly into the body cavity. A 16½ g hypodermic needle was pushed through the body cavity wall using the shielded needle technique, and the antenna wire was passed though to the outside. The incision was closed using four independent braided silk sutures (2/0 Ethicon). A small amount of cyanoacrylate glue (Vet-Bond, 3M Inc.) was applied to the sutures to increase the abrasion resistance. The entire procedure lasted <5 min and fish recovered quickly when returned to fresh oxygenated water. Fish used for laboratory calibrations were transported to the University of Waterloo wet laboratory facilities 2 weeks prior to the experiment and acclimated at 18 ± 1° C (Sephton & Driedzic, 1991). For laboratory calibrations, fish were returned to the holding tank following surgery to recover for 5 days.

LABORATORY CALIBRATION OF MUSCLE ACTIVITY TO SWIMMING SPEED

Calibrations were performed in a 120-l Blazka-type respirometer. The dimensions and details of this swimming chamber were described in detail by Booth *et al*. (1997) and are represented schematically in Thorstad *et al*. (1997). Fish were loaded in the swim chamber and allowed to acclimate for 15 min (Peake *et al*., 1997) to the no flow conditions (velocity=0). The swim chamber was operated on flow through for each calibration, providing fish with fresh oxygenated water. Water velocity was increased in a constant stepwise progression in increments of 50 rpm (representing *c*. 10 cm s^{-1}). Fish were swum at each interval for 5 min during which time EMG*i* signals were collected. One observer recorded behaviour of the fish while another recorded EMG*i* values using a dictaphone during periods of constant swimming. A minimum of 30 signals were collected at each increment. Signals were also collected for the last 5 min of the acclimation period when the fish was immobile and in a resting state. Fish were considered fatigued when they could no longer maintain position in the chamber and were forced against the rear blocking screen twice. At this point, fish were removed from the chamber and killed with an overdose of the clove oil/euganol mixture (150 ppm) and post-mortems were conducted to examine electrode placement.

To apply the laboratory calibrations to data collected on different fish in the field, EMG*i* values were standardized. EMG*i* transmitters produce different baseline pulse intervals depending on electrode placement and unique thresholds within electronic components. All baseline or resting values were standardized and an activity index I_A defined as follows:

$$I_A = (1 - (\text{EMG}i \text{ value for speed } X/\text{resting EMG}i \text{ value}))*100$$

This index rises from 0 at resting, increasing as pulse interval decreases with rising fish activity.

FIELD EMG*i*

Fish implanted with EMG*i* transmitters in the laboratory were also angled from the study site. The same surgical procedure performed in the laboratory was used in the field. The only modifications involved holding the fish in 100-l coolers after surgery and obtaining resting EMG*i* values at this time. The procedure for obtaining resting levels was the same as outlined above. Fish were released at the site of capture within 1 h and were permitted to recover for 5 days prior to initiating monitoring. Field measurements were collected using a mobile EMG*i* receiver over a 15-day period from 24 June. When

TABLE I. Vital statistics and mobility estimates of smallmouth bass from mark-recapture

Variable	Weight (g)	Total length (mm)	Time between mark-recapture (days)	Gross movement (m)	Mean daily movement (m)
Mean ± S.E.	565·44 ± 34·39	312·44 ± 6·39	19·41 ± 3·41	281·67 ± 32·12	47·50 ± 12·48
Median	575	310	8	300	17·86
95% CI	—	—	12·5–26·4	216·2–347·2	30·0–43·6
Min./max.	335/1135	274/425	2/51	0/525	0/212·5

water temperatures in the forebay were similar (18 ± 1° C) to those in the laboratory calibration procedure. EMG*i* signals were collected and averaged over 30-min intervals (Briggs & Post, 1997*a*,*b*) prior to being summed to provide daily estimates of activity. Then the results from the field study were applied to the laboratory model to estimate mean daily movement. Data were $\log_{10}$ transformed prior to one-way analysis of variance. Tukey–Kramer HSD *post hoc* tests were used to test for pairwise differences (Day & Quinn, 1989). Values reported are means ± 1 S.E. and tests were deemed significant at $\alpha = 0{\cdot}05$.

RESULTS

MARK-RECAPTURE

A total of 967 smallmouth bass (310·9 ± 2·2 mm; 574·3 ± 10·5 g) was captured and marked. Between 20 May and 4 August 1998, 41 smallmouth bass (312·4 ± 6·4 mm; 565·4 ± 34·4 g) representing 4·23% of all marked fish were recaptured (Table I). Mean total lengths ($t = 1{\cdot}967$, $P = 0{\cdot}83$) and weights ($t = 1{\cdot}968$, $P = 0{\cdot}82$) did not differ significantly between the marked population and recaptured individuals. The mean time between mark and recapture was 19·4 ± 3·4 days. The mean gross movement between mark and recapture was 281·7 ± 32·1 m, and the mean daily movement was 47·5 ± 12·5 m.

Number of days between mark and recapture, gross movement and mean daily movement were not correlated significantly with total length or weight of the fish. However, the positive correlation between weight and the number of days between mark and recapture was only marginally non-significant ($r = 0{\cdot}37$, $P = 0{\cdot}05$). The mean daily movement was correlated negatively with time between mark and recapture ($r = -0{\cdot}58$, $P = 0{\cdot}002$) (Fig. 2) and was correlated positively with gross movement ($r = 0{\cdot}47$, $P = 0{\cdot}014$). There was no significant correlation between the time between mark and recapture and gross movement ($r = -0{\cdot}12$, $P = 0{\cdot}558$).

FIXED CONVENTIONAL TELEMETRY

Sixteen smallmouth bass (318·9 ± 5·0 mm; 747·5 ± 38·0 g) were monitored for an average of 36·8 ± 3·2 days (Table II). The mean gross movement was 3018·8 ± 449·7 m, and the mean daily movement 77·1 ± 10·6 m. A total of 4145 discrete locational signals was recorded for radiotagged fish.

Correlation analysis revealed that the number of days fish were tracked and gross movement were not affected significantly by total length or weight of the fish. However, there was a significant negative, and marginally non-significant

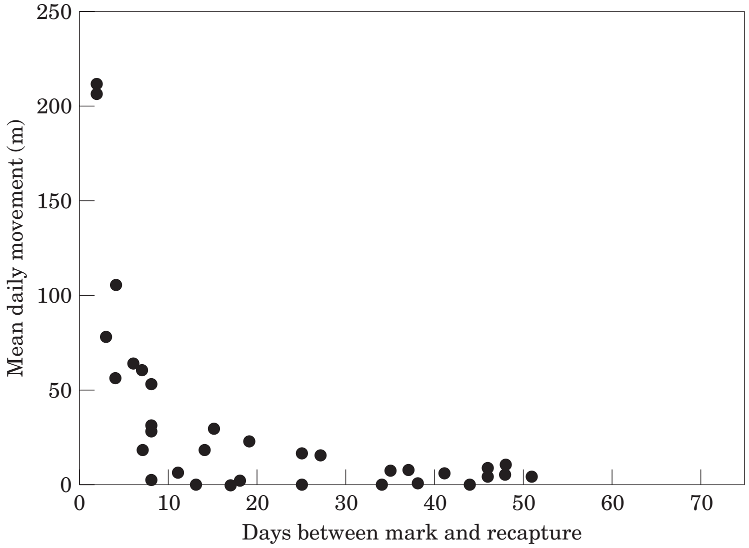

FIG. 2. Mean daily movement of smallmouth bass marked with anchor tags and the duration between mark and recapture. The curve generated by the data is similar to a power relationship with the maximum detectable movement depending on the number of days the fish are at large.

TABLE II. Vital statistics and mobility estimates of smallmouth bass from fixed locational telemetry

Variable	Weight (g)	Total length (mm)	Time tracked (d)	Gross movement (m)	Mean daily movement (m)
Mean ± S.E.	747·50 ± 37·97	318·88 ± 4·95	36·75 ± 3·23	3018·75 ± 449·71	77·11 ± 10·57
Median	712	316	42·5	3075	82·97
95% CI	—	—	30·0–43·6	2061·2–3974·8	54·5–99·7
Min./max.	555/1030	274/425	6/47	75/6150	4·69/155·35

negative correlation between average daily movement and both weight ($r = -0{\cdot}53$, $P = 0{\cdot}037$) and total length ($r = -0{\cdot}49$, $P = 0{\cdot}057$), respectively. Mean daily movement and number of days tracked were both correlated significantly and positively with gross movement ($r = 0{\cdot}80$, $P < 0{\cdot}001$ and $r = 0{\cdot}75$, $P < 0{\cdot}001$, respectively).

LABORATORY CALIBRATIONS

There was no mortality following the surgical implantation of transmitters. Postmortem examinations revealed that the gold electrodes were positioned in the narrow band of red muscle that runs along the lateral line, *c*. 7 mm apart, within 2 mm of the skin, at 0·4 body lengths. All six fish swam for at least six intervals, with the highest interval achieved being nine. Individual linear regressions for each fish were all significant and highly correlated ($r^2 = 0{\cdot}89$–$0{\cdot}99$, P's $< 0{\cdot}001$). A linear regression through the origin described the relationship

TABLE III. Vital statistics and mobility estimates of smallmouth bass from activity (EMG*i*) telemetry

Variable	Weight (g)	Total length (mm)	Mean daily movement (m)
Mean ± S.E.	1291·25 ± 131·96	383·75 ± 12·03	27 408·04 ± 4085·05
Median	1237·5	379	28 053·04
95% CI	—	—	17 795–37 020
Min./max.	1065/1625	362/415	16 809/36 716

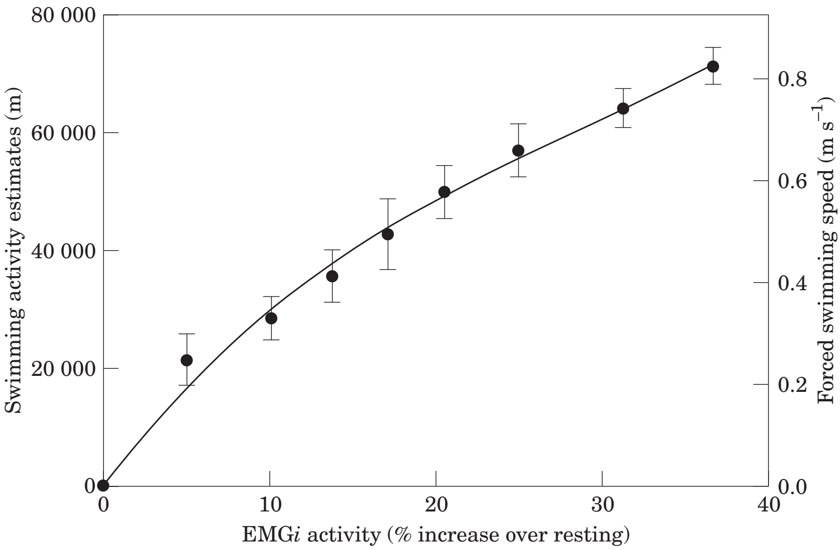

FIG. 3. Relationship between swimming speeds, mean daily movement rate and activity index for smallmouth bass (n=6). Third order polynomial regression through the origin described the relationship between forced swimming speed (y=m day^{-1}) and the activity index (I_A). When all individuals were pooled the relationship was described by the equation ($y=1{\cdot}01768\ I_A^3-85{\cdot}98895\ I_A^2+3751{\cdot}50960\ I_A$; $r^2=0{\cdot}99$, $P<0{\cdot}001$).

between forced swimming speed (y=m day^{-1}) and standardized EMG*i* signals when all individuals were pooled ($F=358{\cdot}576$, d.f.=42, $r^2=0{\cdot}90$, $P<0{\cdot}001$), but the relationship was described better by a third-order polynomial regression through the origin ($y=1{\cdot}01768\ I_A^3-85.98895\ I_A^2+3751{\cdot}50960\ I_A$; $r^2=0{\cdot}99$, $P<0{\cdot}001$; Fig. 3).

FIELD EMG*i*

Individuals implanted with EMG*i* transmitters (n=4) were monitored for 15 days (Table III). One was recaptured by angling after the study (August 1998). The incision had healed completely and there was no evidence that the transmitter had any negative effects on fish behaviour. Because EMG*i* telemetry records information on muscular activity and not specific locations, maximum total displacement within the forebay could not be determined. Instead, the

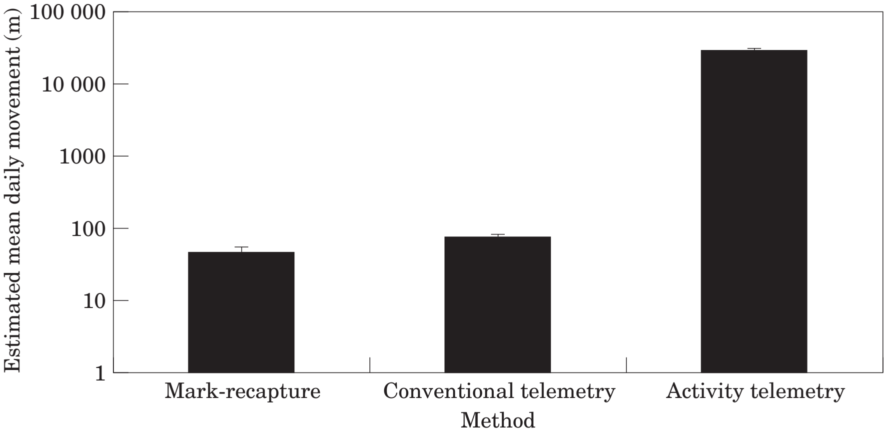

FIG. 4. Comparison of mean (±S.E.) smallmouth bass activity and mobility estimates derived using mark-recapture, continuously monitored fixed telemetry and EMG*i* activity. Data are presented in a $\log_{10}$ scale.

polynomial regression equation generated in the laboratory was used to estimate the mean daily movements of the fish. EMG*i*'s above resting values for field individuals (calculated using the same formula as in the laboratory) when applied to the activity index, estimated that mean daily movement for all fish combined was $27\,408 \pm 4085$ m. No significant correlation existed between average daily movement and total length or weight.

COMPARISON OF TECHNIQUES

Significant differences existed between all of the methods (ANOVA $F = 59{\cdot}1$; $P < 0{\cdot}001$) (Fig. 4). Estimates derived using activity telemetry exceeded those obtained using either mark/recapture or conventional telemetry by more than 100 times. Mark-recapture resulted in significantly lower mean mobility estimates than conventional telemetry methods ($F = 59{\cdot}1$; $P = 0{\cdot}017$).

DISCUSSION

Both mark-recapture and continuously monitored radio transmitters underestimated significantly mobility and activity estimates of smallmouth bass in a confined lentic environment relative to estimates derived using activity transmitters. The latter suggested that activity levels were several orders of magnitude greater than those detected using the other two techniques. Such drastic underestimates of activity would contribute to errors in energetics modelling.

Early mobility estimates derived from mark-recapture studies of lotic fishes suggested that most fish exhibited restricted movement (Funk, 1955; Gerking, 1959). Data from recent telemetry studies and from several reappraisals of salmonid literature suggest that the notion of restricted movement was largely an artifact of sampling methodologies (Gowan *et al.*, 1994). Intrinsic differences in the effectiveness of the techniques, and sampling biases contributed error to the mobility estimates. In a stream or river, fish can move upstream or downstream until they reach an impassible barrier. In large lentic systems, fish may also swim long linear distances, usually bounded only by physical or environmental barriers. In these systems, it is these barriers that usually set the boundaries for study areas. These boundaries also set limits on displacement. Fish can move only from one extreme barrier to the other. In the present study, fish were restricted similarly, but restrictions were more pronounced than in many other systems.

The longest linear distance in the forebay (675 m) and inability to recapture fish on the same day that they were tagged determined the maximal detectable displacement. This intrinsic strong negative power relationship between number of days between mark and recapture and the calculation of movement per unit time is an inherent bias in mark-recapture studies. In any mark-recapture study, the maximal observable distance would be that between the two most distant aspects of the system, assuming that one of the sites was where the fish was marked and the other where it was recaptured. In the present study, ability to detect and estimate movement using mark-recapture decreased substantially for every day that a fish was at large. Therefore the mark-recapture estimates do not represent true activity costs of free swimming smallmouth bass.

The fixed telemetry system detected greater mobility than would be possible using conventional manual tracking. Typically, conventional manual tracking involves following individual fish continuously for periods of time and then determining how long it took the fish to move the given distance (Gerber & Haynes, 1988; Bevelhimer, 1995). These methods have yielded daily movement rates for smallmouth bass of 1243 m in Melton Hill Reservoir, Tennessee (Bevelhimer, 1995) and *c*. 700 m in Lake Ontario (Gerber & Haynes, 1995). Ney (1993) acknowledged that telemetric observations must be considered underestimates of average velocity since fish rarely travel in straight lines between points. The continuously monitored system as well as coded tags minimized scan times and ensured that ability to detect movement was maximized (Cooke *et al*., 2000). Even with this technological advantage, it was impossible to discriminate between the localized movements that were logged on the receiving systems. To improve precision, numerous antennae with reduced sensitivity would be required to pinpoint position, especially in three dimensions. Thus, conventional telemetry is useful for documenting range of movements, but may not be effective for establishing total movements or activity for studies of energetics.

Potential underestimates of smallmouth bass mobility and activity were identified first by Hinch & Collins (1991). They placed videography equipment adjacent to two nesting male smallmouth bass in Lake Opeongo, Ontario. Tail beat frequencies were related to the cost of swimming in place to those of non-guarding swimming to provide a daily mobility estimate of 28 800 m. The present EMG*i* estimates suggest that the free swimming adult smallmouth bass, when not nesting, were expending a similar amount of energy as nest guarding fish in Lake Opeongo (Hinch & Collins, 1991). It is possible that present activity estimates were influenced by searching behaviour resulting from the confined nature of the site and additional estimates in open systems will be helpful in developing these relationships.

Demers *et al*. (1996) explored EMG*i* activity of smallmouth bass in Ranger Lake, Ontario. Maximum movement rates occurred with variable but near baseline EMG*i* pulse rates. Conversely, elevated EMG*i* activity occurred while smallmouth bass were apparently stationary. In the same study, similar but more pronounced patterns of limited movements, accompanied by elevated EMG*i* data were collected from largemouth bass *Micropterus salmoides* (Lacépède). Based on these results, the authors concluded that EMG*i* activity at temporal and spatial scales was too minute to be detected by conventional tracking, may account for significant proportions of daily activity (Demers *et al.*, 1996). Smallmouth bass in the present study showed similar heightened EMG*i* activity while remaining in discrete areas within the forebay. Therefore, activity parameters from energetics models should incorporate data derived from activity telemetry studies that estimate muscular activity of free-swimming fish more realistically. As new data on fish activity becomes available, they should be incorporated into existing energetics models to account for activity and resultant energetic expenditure that may not be associated with changes in location.

Activity estimates from both Hinch & Collins (1991) videography data and present EMG*i* data are much higher than the daily mobility estimate of 4320 m derived from a largemouth bass bioenergetics model (Rice, 1981; Rice *et al.*, 1983; Rice & Cochran, 1984). Hinch & Collins (1991) calculated a 60% increase in respiration in the model when their mobility value was used rather than 4320 m day^{-1} (5 cm s^{-1}) (Rice, 1981; Rice *et al.*, 1983). Rice & Cochran (1984) indicated that adjusting the swimming speed by 50% above and below the 5 cm s^{-1} model value resulted in a 7% decrease or increase in final mass respectively. Although Hinch & Collins (1991) illustrated the potential shortcomings of the 5 cm s^{-1} value, they were unable to provide activity estimates for free-swimming, non-nesting smallmouth bass. Present results permit this direct comparison in free-swimming fish, and can be used to improve swimming speed values in the model.

To illustrate the effect of activity estimates on energy requirements, a series of simulations of fish consumption and growth were conducted using Fish Bioenergetics 3·0 for Windows (UW Sea Grant, 1997). Estimates differed substantially depending on which of the three activity estimate were used. The amount of fish was estimated that must be consumed for a 1000-g largemouth bass (Rice *et al.*, 1983) (due to model constraints with smallmouth bass) to maintain its bodyweight at 18° C for 30 days. The activity multiplier of the respiration model 1, which regards swimming speed as a constant (Rice *et al.*, 1983) was changed to reflect the three present estimated activity levels. The activity estimate from mark-recapture was 0·055 cm s^{-1} and the model provided a consumption estimate of 151·7 g of prey (fish). Using conventional telemetry, the activity estimate was 0·089 cm s^{-1} and the consumption estimate 152·8 g. However, activity telemetry yielded an activity estimate of 31·7 cm s^{-1} and the model predicted consumption would increase by 37% to 209·7 g of prey to maintain body mass. Growth estimates were affected similarly by activity estimates. If total consumption was set at 150 g for a 1000-g largemouth bass, activity estimates derived from mark-recapture would result in a fish weighing 1022·2 g after 30 days at 18° C. Similarly, using activity estimates from conventional telemetry, a 1000-g largemouth bass would also weigh 1022·2 g after 30 days. In contrast, using rates from activity telemetry, the largemouth bass would lose weight from 1000 g to 986·0 g after 30 days. These simulations illustrate the importance of localized activity in the daily energy budget of bass. Many authors including Rice *et al.* (1983) used 5 cm s^{-1} in their energy models for largemouth bass, a value that is probably low based upon the work of Hinch & Collins (1991) and this study. Variation in activity estimates produces significant differences in the outcome of energetic models, and must be considered when energy budgets of free-swimming bass are investigated.

Recent reviews of bioenergetic model accuracy suggest these models overestimate food consumption (Wahl & Stein, 1991; Ney, 1993; Chipps *et al*., 2000). However, for species such as largemouth bass (Whitledge & Hayward, 1997) and yellow perch *Perca flavescens* (Mitchill) (Boisclair & Leggett, 1989*d*) the models can result in underestimates. Errors have been associated with seasonal metabolic rates (Wahl & Stein, 1991), effects of feeding and growth rates (Chipps *et al*., 2000), and activity (Kerr, 1982; Boisclair & Leggett, 1989*d*). Present results suggest inaccuracy in estimates of activity rates of natural populations are probably an important source of these errors for some species.

This study has compared directly movement rates estimated from mark-recapture, location tracking and activity telemetry. Each technique allows for determinations of a range of movements. However, only activity telemetry permitted quantification of fine scale, perhaps stationary activity. Estimates derived from mark-recapture and conventional telemetry are unable to provide representative data on fish activity. The study highlighted the need to reevaluate how activity and mobility estimates are derived, with implications for bioenergetics. It is recommended that work continue towards the refinement of physiological telemetry devices that will permit the objective quantification of the *in situ* activity patterns of free-swimming fish. Additional advances in technology that incorporate several measures of activity and metabolic rate will be the most robust in the determination of the fate of ingested energy (Ney, 1993). Fisheries management decisions and aquaculture production planning are both becoming dependent upon bioenergetics modelling. Accurate and reliable estimates of the input parameters, and in particular, of the activity component, will be essential to the success of these tools.

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