Prey capture in the chain pickerel, *Esox niger*: correlations between feeding and locomotor behavior

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The predatory behavior of the chain pickerel *Esox niger* was studied by high-speed cinematography to correlate patterns of jaw bone movement with locomotor patterns. Pattern B strikes were initiated at significantly shorter distances from the prey, had higher acceleration rates, and the velocity of mouth opening and suspensorial abduction was greater than for pattern A strikes. No difference was found in the excursion amplitudes of jaw movements between pattern A and pattern B strikes. Significant differences were found between midwater and corner strikes in the amplitude of mouth opening and hyoid depression: both were smaller in corner attacks and suction velocity was higher. Both velocity and amplitude of each mechanical unit in the head can be varied depending on the locomotor pattern and the position of the prey.

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Le comportement prédateur du brochet maillé *Esox niger* a été étudié par cinématographie à haute vitesse afin d'établir la corrélation entre les mouvements de la mâchoire et les patterns locomoteurs. Les attaques de type B sont déclenchées plus près de la proie et ont des vitesses d'accélération plus grandes que les attaques de type A; la vitesse d'ouverture de la bouche et celle de l'abduction des muscles suspenseurs sont également supérieures. L'amplitude des mouvements de la mâchoire est la même au cours des attaques A et des attaques B. Il existe des différences significatives d'amplitude d'ouverture de la bouche et de dépression de l'hyoïde entre les attaques de coin et les attaques en eau libre: l'amplitude est plus faible lors des attaques de coin et la vitesse de succion est supérieure. La vitesse et l'amplitude de chaque unité mécanique de la tête peuvent varier en fonction des patterns locomoteurs et en fonction de la position de la proie.

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Introduction

Following the early use of cinematography by Marey (1895) and the classification of the propulsive movements in fish by Breeder (1926) a large body of literature has accumulated on locomotion in fishes (Gray 1933; Gero 1952; Bainbridge 1958, 1962; Lighthill 1969; Weihs 1973; Webb 1975, 1978, 1979; Webb and Skadsen 1980). In the same light, since the studies of Alexander (1966, 1967) the mechanics of feeding in fishes has been the topic of a number of investigations using electromyography and cinematography (Ballintijn *et al.* 1972; Elshoud-Oldenhave and Osse 1976; Lauder 1979, 1980; Lauder and Liem 1980; Liem 1978, 1979; Osse 1969). No study, however, has analyzed both locomotor patterns and jaw movements and how they interact during prey capture. In this paper we analyze correlations between the locomotor patterns used during rapid strikes at prey items by the pickerel *Esox niger*, and the timing and magnitude of jaw movements.

The fast-start locomotor pattern studied in this paper was noted originally by Hoogland *et al.* (1956) and described by Webb (1976) as "S starts." During stage 1 of an S start, the body of the fish quickly bends from a stretched-straight position into an S shape. During the propulsive stroke of an S start the body of the fish bends from this S shape into an opposite S shape where continued propulsion or braking takes place.

S starts may be divided into two distinct types. Webb and Skadsen (1980) describe "pattern A" starts or strikes as the characteristic S start, beginning from a straight body posture and progressing through stages one and two. In a second type of S start the preliminary stroke is deleted and the fast start begins at stage 2 after the fish assumes a full S posture. This was called a "pattern B" start by Webb and Skadsen (1980).

The objectives of this study are (1) to quantitatively describe the jaw kinematics of *Esox*, and (2) to correlate patterns of jaw bone movement with the locomotor categories defined by Webb and Skadsen (1980).

Materials and methods

Fish

Three chain pickerel, *Esox niger* Lesueur (216 mm,

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TABLE 1. Descriptive statistics for body kinematics of pattern A and pattern B midwater strikes. Data are lumped for all three fish. Mean values are shown followed by the number of observations and standard deviation in parentheses. NS = not significant at the 0.05 level

Type of strike	Peak rate of lateral displacement of anal fin (body lengths/s)	Peak rate of propagation of body wave (body lengths/s)	Peak lateral displacement of anal fin (body lengths)	Time taken to reach peak wave amplitude (s)
Pattern A catch	10.21 (16, 2.60)	11.47 (15, 3.23)	0.156 (14, 0.057)	0.074 (14, 0.027)
Pattern A miss	9.36 (7, 2.75)	12.62 (6, 2.06)	0.175 (6, 0.058)	0.074 (7, 0.012)
Pattern A combined	9.95 (23, 2.62)	11.80 (21, 2.94)	0.162 (20, 0.056)	0.074 (21, 0.030)
Pattern B catch	9.25 (7, 2.75)	11.72 (7, 1.59)	0.196 (7, 0.017)	0.50 (7, 0.215)
t-test				
Pattern A catch vs. pattern B catch	NS	NS	NS	$P < 0.005$
Pattern A combined vs. pattern B catch	NS	NS	NS	$P < 0.005$
Pattern A miss vs. pattern A catch	NS	NS	NS	NS

227 mm, and 273 mm fork length), were seined from Pope's Pond in Milton, Massachusetts. The fish were kept in 60-L (60 cm × 30 cm × 40 cm), 40-L (50 cm × 25 cm × 30 cm), and 90-L (90 cm × 30 cm × 40 cm) tanks respectively and acclimated to laboratory water and temperature (21°C) for over a month. All individuals were fed goldfish (*Carassius auratus*) obtained from a local bait shop, and shiners (*Notemigonus chrysoleucas*) seined from Pope's Pond or obtained from a local bait shop. Food was withheld for up to 1 week prior to an experiment.

Cinematography

High-speed cinematography was used to examine the strike of pickerel as described by Lauder (1980, 1981) and Liem (1978). A mirror was placed in each tank at a 45° angle providing a ventral view of the fish which was photographed with the lateral view. Single prey (out of water) were introduced by hand from above the tank. More than 40 strikes were analyzed frame by frame; jaw movements were measured directly from projection on a screen, whereas body kinematics were measured from tracings of the body taken in each frame. Due to the orientation of the pickerel with respect to the plane of the film in the camera and with respect to the mirror, it was not always possible to measure all kinematic parameters in each strike. As a result the sample sizes vary somewhat. Kinematic data were compared using a two-sample Student's *t*-test.

Results

Midwater strikes

Table 1 shows the maximum rate of lateral displacement of the anal fin, the maximum rate at which the body wave is propagated down the length of the fish, and the maximum lateral displacement of the anal fin averaged for all pattern A and pattern B midwater strikes. There is no significant difference in any of these three parameters between pattern A and pattern B strikes, nor is there a significant difference between successful and unsuccessful pattern A strikes. By definition pattern B strikes omit stage 1 and the fish slowly bends into an S posture; as expected, pattern B strikes take significantly more time to reach maximum body amplitude during adoption of the strike posture.

Pattern A strikes were initiated at greater distances from the prey than pattern B strikes (Table 2), and the difference is still significant if pattern A catches and misses are combined. The difference in initiation distances for successful and unsuccessful pattern A strikes is not significant. More time does elapse from first mouth opening to reaching the prey in unsuccessful strikes than in successful strikes, and this suggests that a major cause of failure is opening the mouth too soon. Nyberg (1971) found this to be true in bass.

Table 3 shows data on the velocity and acceleration of the pickerel for pattern A and pattern B midwater strikes. Peak velocity is just significantly greater for successful pattern A strikes than for pattern B strikes. Velocity in the first frame of mouth opening is significantly greater for all pattern A strikes than for pattern B strikes. The average velocity from first forward movement to reaching the prey is significantly greater in pattern A strikes than in pattern B strikes, and on average, acceleration was positive for the first 41 ms in pattern B strikes ($n = 7$, SD = 14), and was positive for the first 82 ms in pattern A strikes ($n = 23$, SD = 38). The difference is significant ($P < 0.01$).

There is no significant difference in peak mouth opening, peak hyoid depression, peak opercular dilation, and peak suspensory abduction between pattern A

TABLE 2. Descriptive statistics of strike initiation distance, the timing of mouth opening, and time taken to reach the prey for pattern A and pattern B midwater strikes. Data are lumped for all fish. Mean values are shown followed by the number of observations and standard deviation in parentheses

Type of strike	Distance to prey at first forward movement (body lengths of *Esox*)	Distance to prey at first mouth opening (body lengths of *Esox*)	Distance moved at first mouth opening (body lengths of *Esox*)	Distance moved during mouth opening (body lengths of *Esox*)	Distance moved at peak mouth opening (body lengths of *Esox*)	Time elapsed from first movement to reaching the prey (s)	Time elapsed from first mouth opening to reaching the prey (s)
Pattern A catch	0.367 (16, 0.208)	0.279 (16, 0.108)	0.107 (16, 0.133)	0.306 (16, 0.098)	0.385 (16, 0.148)	0.092 (16, 0.044)	0.059 (16, 0.011)
Pattern A miss	0.370 (7, 0.194)	0.350 (7, 0.174)	0.028 (7, 0.039)	0.250 (7, 0.077)	0.280 (7, 0.106)	0.114 (6, 0.042)	0.105 (6, 0.020)
Pattern A combined	0.368 (23, 0.199)	0.300 (23, 0.132)	0.083 (23, 0.119)	0.289 (23, 0.094)	0.353 (23, 0.140)	0.098 (22, 0.043)	0.072 (22, 0.025)
Pattern B catch	0.138 (7, 0.078)	0.135 (7, 0.078)	0.007 (7, 0.008)	0.171 (7, 0.070)	0.179 (7, 0.071)	0.051 (7, 0.018)	0.057 (7, 0.023)
t-test							
Pattern A catch vs. pattern B catch	$P < 0.01$	$P < 0.005$	$P < 0.05$	$P < 0.005$	$P < 0.005$	$P < 0.025$	NS
Pattern A combined vs. pattern B catch	$P < 0.005$	$P < 0.005$	NS	$P < 0.005$	$P < 0.005$	$P < 0.025$	NS
Pattern A catch vs. pattern A miss	NS	NS	NS	NS	NS	NS	$P < 0.05$

TABLE 3. Descriptive statistics for velocities and accelerations of pattern A and pattern B midwater strikes. Data are lumped for all fish. Mean values are shown above the number of observations and standard deviation in parentheses. Velocities are in body lengths of *Esox*/s. Accelerations are in body lengths of *Esox*/s^2

Type of strike	Peak velocity	Velocity in frame of first mouth opening	Average velocity from first forward movement to reaching the prey	Average acceleration in first 50 ms of strike	Average acceleration from first forward movement to reaching the prey
Pattern A catch	9.05 (16, 2.58)	2.82 (16, 1.86)	3.96 (16, 0.955)	81.0 (16, 26.0)	77.2 (16, 33.5)
Pattern A miss	7.43 (7, 2.12)	1.10 (7, 1.36)	3.77 (6, 1.17)	89.4 (7, 46.3)	39.6 (6, 32.3)
Pattern A combined	8.56 (23, 2.52)	2.29 (23, 1.88)	3.91 (22, 0.99)	83.0 (23, 32.0)	66.9 (22, 36.7)
Pattern B catch	6.95 (7, 1.97)	0.83 (7, 0.85)	2.73 (7, 0.13)	121.0 (7, 37.0)	80.1 (7, 53.5)
t-test					
Pattern A catch vs. pattern B catch	$P < 0.05$	$P < 0.01$	$P < 0.05$	$P < 0.005$	NS
Pattern A combined vs. pattern B catch	NS	$P < 0.05$	$P < 0.025$	$P < 0.01$	NS
Pattern A catch vs. pattern A miss	NS	$P < 0.025$	NS	NS	$P < 0.025$

TABLE 4. Descriptive statistics for the time taken for the mechanical units of the jaw to reach maximum displacement in pattern A and pattern B midwater strikes. Data are lumped for all three fish. Mean values are given followed by the number of observations and standard deviation in parentheses. Time is in seconds

Type of strike	Time elapsed in mouth opening	Time elapsed in hyoid depression	Time elapsed in opercular dilation	Time elapsed in suspensory abduction
Pattern A catch	0.067 (16, 0.013)	0.054 (14, 0.012)	0.090 (10, 0.020)	0.087 (7, 0.017)
Pattern A miss	0.067 (7, 0.018)	0.057 (7, 0.016)	0.110 (4, 0.030)	0.120 (4, 0.038)
Pattern A combined	0.067 (23, 0.014)	0.055 (21, 0.014)	0.097 (14, 0.025)	0.099 (11, 0.030)
Pattern B catch	0.055 (7, 0.012)	0.051 (7, 0.021)	0.080 (4, 0.014)	0.053 (2, 0.011)
t-test				
Pattern A catch vs. pattern B catch	$P < 0.05$	NS	NS	$P < 0.05$
Pattern A combined vs. pattern B catch	$P < 0.05$	NS	NS	$P < 0.05$
Pattern A catch vs. pattern A miss	NS	NS	NS	$P < 0.05$

and pattern B strikes ($P > 0.05$). There is also no significant difference between the two types of strikes in the time taken to reach maximum displacement of the hyoid or opercular series (see Fig. 1). Less time is taken to abduct the suspensorium and to open the mouth in pattern B strikes than in pattern A strikes (Table 4). There was no significant difference beween pattern A ($\underline{X} = 1.26$ body lengths/s, SD = 0.796) and pattern B ($X = 1.60$ body lengths/s, SD = 0.876) strikes in suction speed ($P > 0.10$), the velocity at which prey entered the mouth.

Corner strikes

As the prey frequently swam to the corners of the tank after being introduced, a number of strikes were recorded there.

The mouth is opened significantly further and the hyoid is depressed significantly further in midwater strikes than in corner strikes. The time taken to reach these peak displacements is significantly greater in the midwater strikes than in corner strikes (Table 5, Fig. 1). The speed at which the prey were sucked into the mouth was significantly higher than the suction speed of midwater strikes (Table 5), although there is no significant difference between midwater and corner strikes in initiation distance, in the distance moved by the time the mouth begins to open, or in the velocity of *Esox* when the mouth begins to open.

Discussion

Other studies have shown that a variety of fishes can modify the pattern of jaw movements used during feeding according to the nature and location of the prey (Elshoud-Oldenhave and Osse 1976; Lauder 1981; Liem

1978, 1979). It has been suggested by Liem (1978) that piscivorous cichlids possess a repertoire of two patterns of prey capture and that each one represents a stereotyped motor pattern. One pattern is recruited for agile prey, which are difficult to catch, whereas the second pattern correlates with sluggish prey. The results of this study have shown that *Esox niger* also possesses a repertoire of at least two patterns of jaw movement.

During encounters with prey in the corners of the tank, the pickerel consistently reduced the opening of the mouth and the degree to which hyoid depression occurred. This pattern of jaw movement represents a distinctly different motor output from that of midwater feedings.

Nyberg (1971) found a similar behavior in largemouth bass, which reduced the opening of the mouth when striking at prey on the bottom. He explained that if the rate of change of orobranchial chamber volume is constant, a smaller mouth opening would result in water entering at a higher velocity. This was found to be true for *Esox*, as the speed with which the prey were sucked into the mouth was higher in corner strikes than midwater feedings.

It is likely that the hyoid plays a major role in modulating the suction speed in corner strikes as hyoid depression is relatively independent of mandibular depression. A smaller mouth opening did not result in a proportionally smaller hyoid depression (Fig. 1) in corner strikes, and the volume of the orobranchial chamber was thus not reduced as much as mouth opening. This results in higher suction velocities in corner strikes.

The pattern of jaw movements typical of corner attacks does not appear to be linked with a particular
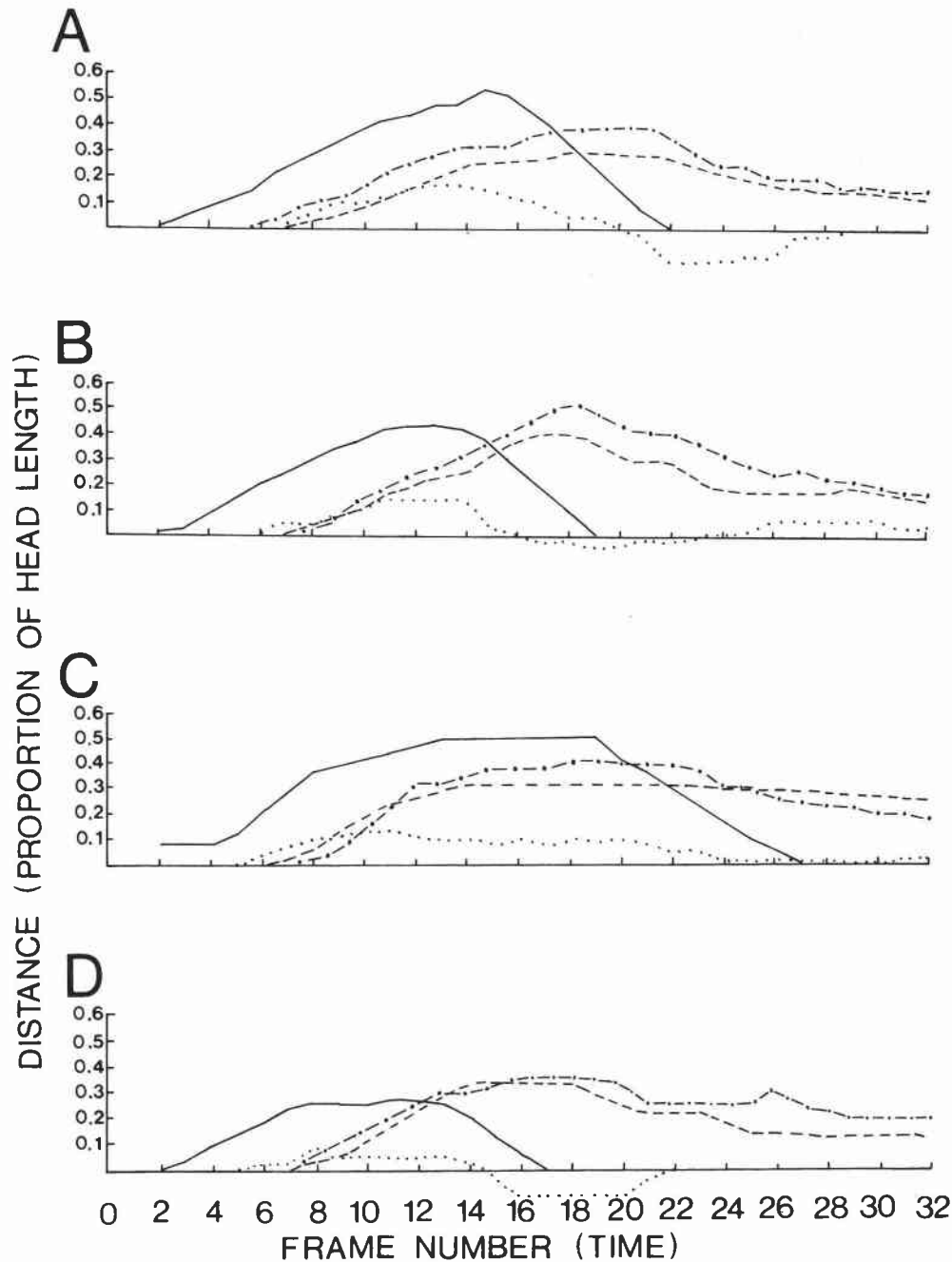
FIG. 1. Graphic representation of mouth opening (—), opercular dilation (–·–), suspensory abduction (- - -), and hyoid depression (····), expressed as a proportion of head length, versus time. (A, B) Two midwater pattern A strikes; (C) a pattern B midwater strike; (D) a pattern A strike in the corner. Note the reduction in mouth opening and hyoid depression in the corner strike. Time between successive frames is 0.005 s.

locomotor pattern as both pattern A and pattern B starts were employed in corner strikes. Although only one pattern B start was observed in a corner attack, mouth

opening and hyoid depression were well within the range of values for the entire sample of corner strikes.

In strikes that took place in the middle of the tank, two

TABLE 5. Descriptive statistics for midwater and corner strikes. Only pattern A strikes are included. Data are lumped for all three fish. Mean values are shown above the number of observations and standard deviation in parentheses. HL = head lengths of *Esox*. Suction speeds are in body lengths of *Esox*/s

Position in tank	Peak mouth opening (HL)	Time elapsed during mouth opening (s)	Peak hyoid depression(HL)	Time elapsed during hyoid depression (s)	Suction speed (body lengths/s)
Midwater	0.430 (16, 0.120)	0.067 (16, 0.013)	0.134 (14, 0.031)	0.054 (14, 0.021)	1.26 (8, 0.786)
Corner	0.231 (11, 0.062)	0.046 (11, 0.010)	0.097 (6, 0.026)	0.031 (6, 0.002)	3.21 (7, 1.62)
t-test	$P < 0.005$	$P < 0.005$	$P < 0.025$	$P < 0.005$	$P < 0.01$

distinct patterns of jaw movement were observed. The results show that the mouth is opened and the suspensorium is abducted more rapidly in pattern B strikes than in pattern A strikes.

The concept of a central nervous system oscillator that produces a highly sterotyped motor output to the jaw muscles has been a fundamental element of recent explanations of the dynamics of prey capture in fishes (Liem 1978; Nyberg 1971). In general, the "oscillator hypothesis" holds that the motor activity observed during feeding is not subject to peripheral modification during the strike and that successive feeding events are highly similar in the relative timing and magnitude of bone movements. This hypothesis has subsequently been expanded to encompass the result that many fishes appear to have more than one pattern of motor output (Lauder 1981; Liem 1978, 1980), although each distinct component of the total repertoire of feeding outputs is still held to be the result of a nonmodifiable neural oscillator.

No explicit tests have been conducted of the assumption of nonmodifiability. Lauder (1981) adduced preliminary evidence to show that certain kinematic components of the strike were independent of each other and could be modified depending on the type and position of the prey. The data presented here for *Esox* corroborate this suggestion and reveal that both the magnitude and velocity of jaw movements may be regulated independently. During midwater strikes, the velocity of suspensory abduction and mouth opening differ significantly between pattern A and pattern B strikes but the magnitudes of excursion and both the magnitude and velocity of other bone movements remain constant. However, when corner strikes are compared with midwater strikes, it is the magnitude and velocity of both mouth opening and hyoid depression which differ. The data show that movement magnitudes and velocities are not tightly coupled and organized into one or two distinctly different preprogrammed patterns that are elicited during feeding. Rather, the data indicate the existence of a large number of independent movement and velocity parameters that are combined in a statistically predictable manner in different feeding situations.

The concept of a "neural oscillator" evoking a fixed preprogrammed motor output is thus useful only in a trivial sense. The variability within each statistically defined pattern of jaw bone movement indicates that the number of discrete observable patterns may be limited only by our ability to present different feeding situations to the predator.

Acknowledgements

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