

## Swimming endurance of American plaice (*Hippoglossoides platessoides*) and its role in fish capture

P. D. Winger, P. He, and S. J. Walsh



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The swimming capability of fish plays an important role in determining the selectivity and efficiency of capture by mobile bottom-trawl fishing gears. The authors test the hypotheses that the swimming endurance of American plaice (*Hippoglossoides platessoides*) is independent of fish size and water temperature. Using a swimming flume, swimming endurance was examined across a range of fish sizes (14–44 cm) and water temperatures (–0.2 to 9.7°C). All trials were conducted at a swimming speed of 0.30 ms<sup>-1</sup>. This is comparable to the swimming speeds required by flatfish during herding by bottom-trawl sweeps. The data were analysed using failure time (survival) analysis, a more robust statistical technique for endurance-type data. The advantage of this technique over traditional regression analyses is that censored observations can be included in the analysis. An important distinction, however, is that the dependent variable being modelled was not endurance *per se*, but the instantaneous rate of exhaustion, or hazard rate at a given time *t*. The results showed that both fish length and water temperature had a negative effect on the endurance hazard rate. This is equivalent to an increase in the probability of American plaice achieving a given endurance with increasing fish length and water temperature. This was sufficient evidence to reject the null hypotheses that the swimming endurance of American plaice is independent of these variables. Probability curves for the distances the fish would be capable of swimming were calculated for different fish sizes and water temperatures. The findings suggest that the herding efficiency of American plaice by bottom-trawl sweeps may be largely size- and temperature-dependent.

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Key words: American plaice, flatfish, swimming endurance, fish size, temperature, otter trawl, selectivity, failure time analysis.

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### Introduction

A fish's ability to avoid capture by bottom-trawl fishing gear is thought to be related to its swimming capability, including its maximum swimming speed, manoeuvrability, and swimming endurance. Several intrinsic factors such as fish size, age, physiological condition, and extrinsic factors such as ambient light intensity and ocean-bottom temperature can affect swimming capability and hence capture success (e.g. Parrish *et al.*, 1964; Beamish, 1969; Hemmings, 1969; Wardle, 1983, 1993; Glass and Wardle, 1989; He, 1991, 1993; Walsh, 1991; Walsh and Hickey, 1993). These

factors have a direct bearing on the efficiency and selectivity of mobile sampling gears used to estimate abundance and size composition of commercial finfish resources (Walsh, 1997).

The average proportion of fish that are effectively captured per unit of fishing effort is defined as the *catchability* of a fishing gear (Gunderson, 1993). Godø (1994) and Walsh (1996) have described three zones during the fish capture process in which fish behaviour can influence otter trawl catchability (Figure 1). Here, we are primarily interested in fish behaviour in Zone 2. Fish located in this zone will initially lie within one of three sub-zones, either directly in the trawl path itself, or

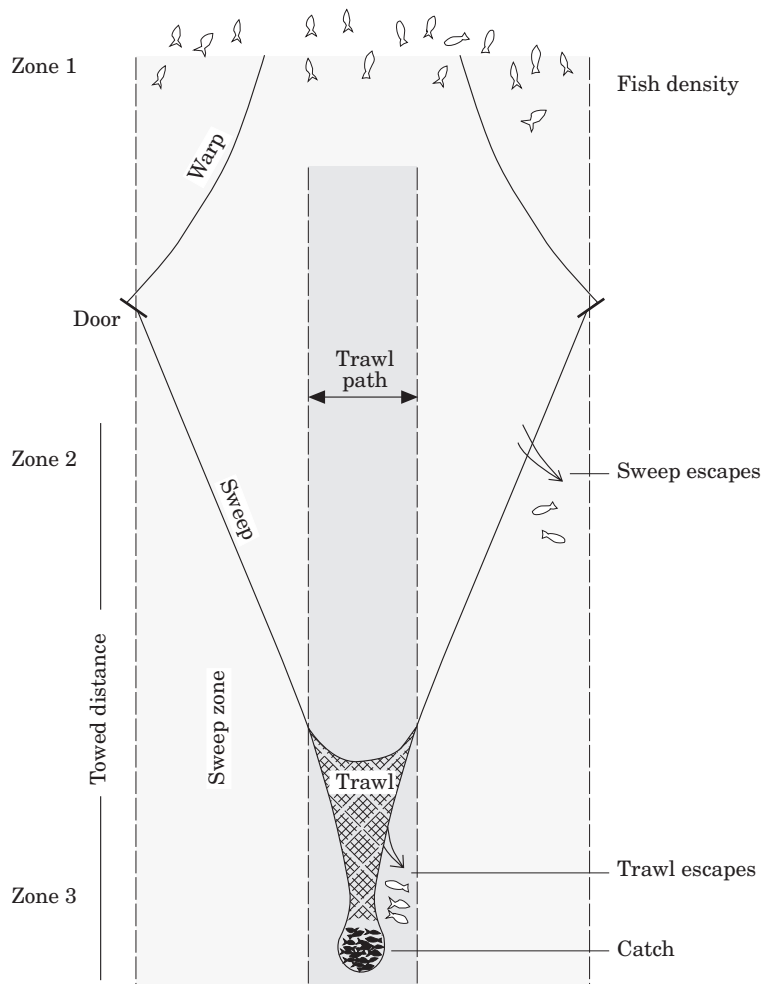


Figure 1. Schematic drawing of an otter trawl illustrating the three catching zones of influence in the fish capture process. Fish which initially lie in the two sweep zones (Zone 2) must first be herded into the trawl path in order to become available for capture by the trawl net. (Adapted from Godø, 1994.)

in one of the two sweep zones between the wings and trawl doors. The trawl path is defined as the area swept between the wing-ends of the trawl net. Fish located in this zone are directly available for capture by the trawl net. However, fish which initially lie in the two sweep zones must first be herded into the trawl path in order to become available for capture. This herding behaviour can be induced after direct or near contact with the doors, sweeps, and sand clouds. Here, we use the term sweeps to categorically include trawl bridles, sweep lines, and ground warps. The efficiency and selectivity of this herding process is dependent on trawl geometry, fish behaviour, and the swimming capability of the target species. For example, comparative studies manipulating the sweep lengths of survey trawls have demonstrated species- and size-dependent herding efficiency in gadoids and flatfish (e.g. Engås and Godø, 1989; Andrew *et al.*, 1991; Somerton and Munro, 1996). These differences

could be a potential source of error in estimating population abundance and size composition.

Several studies have investigated the behaviour of flatfish species in response to otter trawls (Beamish, 1969; High, 1969; Main and Sangster, 1981; Walsh and Hickey, 1993; Bublitz, 1996). Direct video observations have shown that flatfish lying in the sweep zones react to the approaching sweeps by swimming toward the trawl path in a direction  $90^\circ$  away from the sweeps (Main and Sangster, 1981). For herding to be effective, flatfish must swim at a speed equal to or greater than the herding speed of the advancing sweeps and have sufficient endurance to reach the trawl path. The distance required to swim is dependent on: (1) sweep angle (i.e. angle of attack of the sweep to the direction of tow); (2) the position along the sweep where the fish initially encounter the gear; and (3) the angle of avoidance in which the fish choose to swim (for review see Foster

*et al.*, 1981). Fundamental to understanding the effect of herding efficiency on size composition and catch rates are the effects of fish size and ocean bottom temperature on swimming capability.

The swimming endurance of demersal fish has been shown to be species-, size-, and temperature-dependent in laboratory studies (Beamish, 1966; He and Wardle, 1988; He, 1991). Of these, only one previously known study has directly investigated the swimming endurance of flatfish (Beamish, 1966). In that study, winter flounder (*Pleuronectes americanus*) in the size range of 19–23 cm were tested at temperatures of 5.0, 8.0, 11.0, and 14.0°C and at swimming speeds ranging from 0.75 to 1.35 ms<sup>-1</sup>. Other quantitative data for flatfish of different sizes, at low temperatures and at low swimming speeds comparable to the herding speeds of otter trawls are still lacking.

Although empirical data have never been presented, it is generally assumed that the catchability of fish by otter trawls is greatly enhanced at low temperatures due to a reduction in swimming capability (e.g. Foster *et al.*, 1981; He, 1993; Engås, 1994; Smith and Page, 1996). In this study we investigate the swimming endurance of American plaice (*Hippoglossoides platessoides*), historically the most abundant and exploited flatfish by commercial mobile fishing gears in the Northwest Atlantic. Under laboratory conditions, we test the hypotheses that swimming endurance is independent of fish size and water temperature. All trials were conducted at a swimming speed of 0.30 ms<sup>-1</sup>. This is comparable to the swimming speeds required by flatfish during herding by bottom-trawl sweeps. The results are discussed in terms of the potential effects on the herding efficiency of survey trawls.

## Materials and methods

### Specimens

American plaice were captured with a bottom trawl on the Grand Bank of Newfoundland. The fish were transported to the Ocean Sciences Centre of Memorial University of Newfoundland for tank adaptation and endurance testing. The fish were kept in a 2.0 × 2.0 × 0.5 m fiberglass tank with a continuous supply of coastal seawater. The indoor aquarium lighting was operated using an outdoor light sensor thereby synchronizing the photoperiod with seasonal changes in day length. The fish were fed chopped Atlantic herring (*Clupea harengus*) once a week to satiation. All fish were starved for a minimum period of 48 h prior to endurance testing and only fish that appeared in good condition were used. A minimum period of 3 weeks was permitted for tank adaptation before endurance testing. Fish size was recorded as the total fish length, measured to the nearest cm. Endurance trials were carried out using

plaice ranging in length from 14 to 44 cm ( $\bar{x}$  = 30.8 cm; s.d. = 6.9).

### Apparatus

The swimming flume used in this study is described previously by He (1991). Additional modification of the existing chamber dimensions were necessary, however, in order to encourage plaice to swim in this apparatus. A reduced chamber size of 1.80 × 0.50 × 0.26 m (length × width × depth) was found to be the most effective at encouraging swimming behaviour in plaice. At water depths greater than 0.26 m, the plaice tended to either turn around frequently or flare-up perpendicular to the direction of water flow. The floor of the chamber was also equipped with a continuously moving belt. The belt moved at the same speed and in the same direction as the water flow. The moving floor served several purposes: (1) preventing negatively buoyant fish, such as plaice, from settling on the floor of the chamber; (2) simulating ground passing under a swimming fish as it would appear in the ocean; and (3) maintaining uniformity of flow near the floor of the chamber thus preventing fish from taking advantage of reduced flow in that area. A floating plexiglass cover positioned on the water surface prevented plaice from swimming near the surface and protruding their snout out of the water. The cover also reduced surface turbulence and improved the uniformity of flow within the swimming chamber.

Pairs of electrodes were installed in the downstream end of the swimming chamber in order to encourage plaice to swim against the water flow until exhausted. A pulsing electrical stimulus (2 Hz) was continuously applied across the electrodes with peak voltage of approximately 8 V (DC voltage).

A Hi-8 video camera was installed for the monitoring and recording of plaice swimming activities. The camera was positioned horizontally with a field of view through the large plexiglass observation window along the side of the flume.

The swimming flume was operated on a flow-through basis with a continuous supply of coastal seawater. Auxiliary holding tanks were established near the flume for additional acclimation and recovery of the fish. Measures of water temperature, dissolved oxygen content, and oxygen saturation were recorded for all swimming trials using a portable digital meter (Model UK-2000, Central Kagaku Corp.). Calibration of flow speeds was conducted using a Seba mini-current meter (Model 486, Geneq Inc.).

### Endurance trials

Endurance trials were carried out over a period of 16 weeks during the months of February through June of 1997. Seasonal changes in the ambient temperature of

the incoming seawater supply during this period provided the opportunity to test for natural temperature-dependent effects on swimming endurance. Trials were conducted at temperatures ranging from  $-0.2$  to  $9.7^{\circ}\text{C}$  ( $\bar{x}=3.4^{\circ}\text{C}$ ,  $\text{s.d.}=2.8$ ).

A standardized routine was developed for testing the endurance of plaice. This began by haphazardly choosing an individual fish from one of the holding tanks and placing it into the swimming chamber of the flume. Most fish tended to immediately settle onto the chamber floor (stationary), often orienting against the direction of water flow. A minimum period of 10 min was provided for acclimation at a water flow of  $0.10\text{ ms}^{-1}$  before endurance testing. Close observation of the fish suggested that longer periods of acclimation were not necessary. Following the acclimation period, the electrodes were activated and the floor belt and water flow speeds were gradually increased until they reached the target speed of  $0.30\text{ ms}^{-1}$ . All trials were conducted at an ambient light level of approximately 3.1 lux.

Endurance was defined as the period of time a fish was able to swim at  $0.30\text{ ms}^{-1}$  before becoming exhausted. A fish was considered exhausted when it was unable to lift-off the downstream electrodes after a duration of 10 s. Prodding techniques used in similar studies (e.g. Beamish, 1966; Taylor and McPhail, 1985) were not used in order to avoid the possibility of subjectively biasing the results. In cases where endurance exceeded 200 min, the trials were terminated and the data were treated as *censored* observations (see Analysis). In these cases, exhaustion was not observed and the total time to fatigue was therefore not known. Data of this nature are common among endurance studies (Brett, 1964, 1967; Beamish, 1966; He and Wardle, 1988; He, 1991) in which fish (under certain conditions) fail to exhaust within an appreciable period of time and the experimenter must eventually terminate the trial. The 200 min cutoff period used in this study was chosen *a priori* and is consistent with the methodology of He and Wardle (1988) and He (1991).

Given the limited numbers of fish and tank space available, endurance testing of the same fish a number of times was necessary for suitable replication. The experimental fish were not individually identifiable and hence within- and between-individual differences in swimming endurance could not be assessed. The fish were selected from the holding tanks haphazardly without replacement in order to optimize the recovery period before retesting. The minimum recovery period was generally 1 week and it was estimated that the maximum number of trials for any given fish did not exceed four.

## Analysis

Measures of swimming endurance are by definition classified as *time-to-event* data. Modelling this type of

data as a function of one or more independent variables has traditionally been done using regression analysis (for reviews see Beamish, 1978; Videler, 1993). The disadvantage of this technique, however, is that it cannot accommodate censored observations. As a result, previous endurance studies have typically excluded censored swimming trials from their analyses entirely or simply discussed them in a qualitative manner (e.g. Brett, 1964, 1967; Beamish, 1966; He and Wardle, 1988; He, 1991). It is argued here that endurance data cannot be appropriately modelled if censored observations are excluded from the analysis. Excluding this portion of the data set could potentially bias the analysis and conclusions. Clearly, the appropriate method of analysis must accommodate both the uncensored observations as well as the censored observations.

Statistical analysis of the data was conducted using failure time analysis, also known as survival analysis. Unlike regression analysis, this technique is designed specifically for time-to-event data (see discussions by: Muenchow, 1986; Lee, 1992; Smith *et al.*, 1994; Marubini and Valsecchi, 1995). This type of data is unique for several reasons: (1) the distribution of failure (endurance) times are often skewed or far from normal; (2) failure time is a non-negative random variable assuming values in the interval from zero to  $T$ ; and (3) the data set often contains censored observations. Perhaps the primary advantage of this technique over traditional regression analysis is that it can accommodate censored observations. Therefore, even fish which did not exhaust within 200 min, in the current study, can be included in this type of analysis.

The purpose of failure time analysis is to model the underlying distribution of failure time ( $T$ ) and to assess the dependence of  $T$  on independent predictor variables. The probability distribution of  $T$  can be specified several ways, although two are particularly useful in failure time analysis. This includes the *survivorship* function and the *hazard* function. The survivorship function,  $S(t)$ , is the probability that an individual survives (i.e. has endurance) longer than time  $t$ . It can also be interpreted as the proportion of individuals still surviving (or swimming) at time  $t$ . By comparison, the hazard function,  $h(t)$ , is the conditional failure rate or instantaneous failure rate at time  $t$ . It is a measure of the proneness to failure (i.e. exhaustion) as a function of the independent predictor variables.

In the current study, the distribution of endurance time ( $T$ ) for plaice was modelled using the Cox Proportional Hazards Model (Cox, 1972; Cox and Oakes, 1984). This is a semi-generalized linear model analogous to multiple regression analysis. An important distinction, however, is that the dependent variable being modelled is not endurance *per se*, but the instantaneous rate of exhaustion, or *hazard rate* at time  $t$ . The

hazard function is expressed as a function of time ( $t$ ) and one or more independent predictor variables. The general form of the hazard function is given by:

$$h(t) = h_0(t) e^{\beta X} \quad (1)$$

where  $\beta X$  represents the regression function,  $\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_p X_p$ , and  $h_0(t)$  is the time dependent baseline hazard function. In this model, the independent variables ( $X_i$ ) act multiplicatively on the hazard function. The regression coefficients ( $\beta_i$ ) are derived using the method of partial likelihood (Kalbfleisch and Prentice, 1980). If the regression coefficients ( $\beta_i$ ) are all equal to zero (i.e. the independent variables have no effect on endurance), then the exponent term  $e^{\beta X}$  equals one, and the hazard function  $h(t)$  is equal to the baseline hazard function  $h_0(t)$ . If the coefficients are different from zero, then  $e^{\beta X}$  is positive and the hazard function is some multiple of the baseline hazard function. The model is referred to as a *proportional hazards* model since the hazards remain in the same proportion for all  $t$  for any given set of values of the independent variables.

The proportional hazards model for plaice endurance was developed using forward stepwise variable selection analogous to multiple regression analysis. The order of entry of the variables into the model was based on their level of significance of the Score statistic (Norušis, 1994). Criteria for removal from the model was based on a variable's level of contribution to the reduction of the log likelihood value for the model (likelihood ratio test; Lee, 1992). All independent variables were treated as continuous variables. Diagnostic methods for the examination of the data set were conducted by investigating the DfBeta plots and partial residual plots. The assumption of proportional hazards (between individuals across time) was checked by plotting the log of the negative of the log of the cumulative survival function against swimming endurance (Norušis, 1994), also known as log-minus-log plots. All analyses were carried out using SPSS version 6.1.

Post-analysis of the video recordings was conducted in order to determine which swimming trials should be excluded from the statistical analysis. Trial results were excluded on the basis of two criteria: (1) if the fish was unable to achieve the target swimming speed of  $0.30 \text{ ms}^{-1}$ ; or (2) if once achieving the target swimming speed, the fish then sat on the chamber floor at the downstream end and ceased swimming. In trials where the latter was observed, these fish were not considered exhausted, just uncooperative for reasons unknown, and did not fit the established exhaustion criteria.

## Results

A total of 228 swimming trials were completed during the 16-week experiment. Of these, 98 trials were classi-

Table 1. Descriptive statistics for 98 successful swimming endurance trials for American plaice (*Hippoglossoides platessoides*) at different water temperatures.

Temperature	No. of fish	Length range (cm)	Mean length (s.d.)
-0.2–1.9°C	38	18–44	32.05 (6.14) cm
2.0–3.9°C	26	14–41	28.81 (8.00) cm
4.0–5.9°C	9	22–38	31.00 (4.92) cm
6.0–7.9°C	17	17–40	29.17 (7.97) cm
8.0–9.9°C	8	29–42	33.88 (4.67) cm

fied as successful (Table 1), in which 88 plaice swam to exhaustion and 10 plaice were censored after exceeding an endurance of 200 min. The remainder of the trials were unsuccessful and were therefore excluded from the analysis. In these trials, the fish either: (1) failed to reach the target swimming speed of  $0.30 \text{ ms}^{-1}$ ; or (2) once achieving the target swimming speed, sat on the chamber floor at the downstream end and refused to swim. Uncooperative behaviour did not appear to be a function of fish length, water temperature, or the duration of acclimation in the swimming chamber.

Swimming endurance was found to increase with increasing fish length and water temperature (Figures 2 and 3). For plaice between 15 and 20 cm in length, the average endurance was 1.5 min (s.d.=1.2) at temperatures from 0.0 to 2.0°C, rising slightly to 2.6 min (s.d.=1.2) at temperatures from 6.0 to 8.0°C. By comparison, larger plaice between 35 and 40 cm in length had an average endurance of 36.5 min (s.d.=29.9) at temperatures from 0.0 to 2.0°C, rising to 76.3 min (s.d.=47.1) at temperatures from 6.0 to 8.0°C. Only the larger fish were found to have endurance greater than 200 min ( $\bar{x}$ =35.8 cm, s.d.=5.1) and were observed on different occasions at water temperatures ranging from 0.3 to 9.7°C. Small fish (<25 cm) typically showed a burst-and-glide swimming strategy and were usually observed struggling to swim away from the downstream end of the flume. Larger fish (>25 cm) had greater swimming capability and tended to use either a steady cruising or a swim-and-settle strategy. The latter behaviour was characterized by repeatedly swimming toward the upstream end of the chamber followed by settling on the moving floor and riding back to the downstream end. Some variability in endurance is suspected to have occurred due to between-individual differences in swimming strategy. Many of the fish were observed switching to a burst-and-glide swimming strategy when nearing exhaustion.

The results of the failure time analysis (Table 2) indicate that both fish length and water temperature had a significant effect ( $p < 0.0001$ ,  $p = 0.0116$ ) on the endurance hazard rate. Fish length provided the greatest

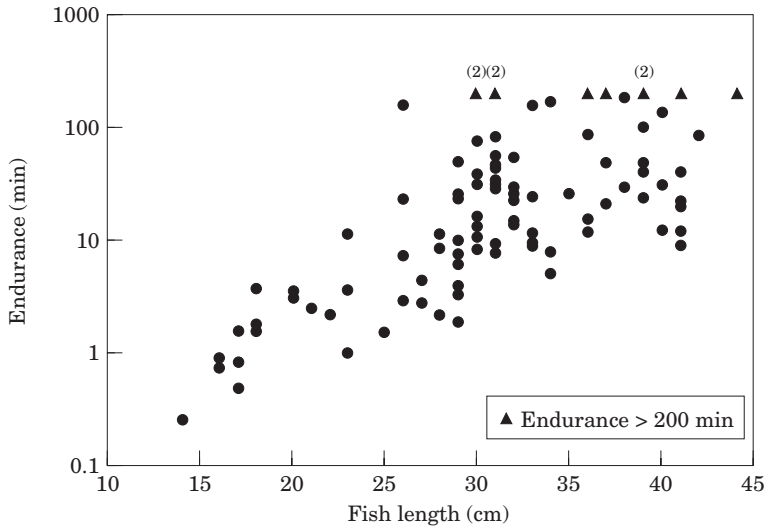


Figure 2. Logarithm of endurance (min) of American plaice (*Hippoglossoides platessoides*) plotted against fish length (cm). Values in parentheses represent the number of fish (>1) still swimming at the end of the 200 min test period.

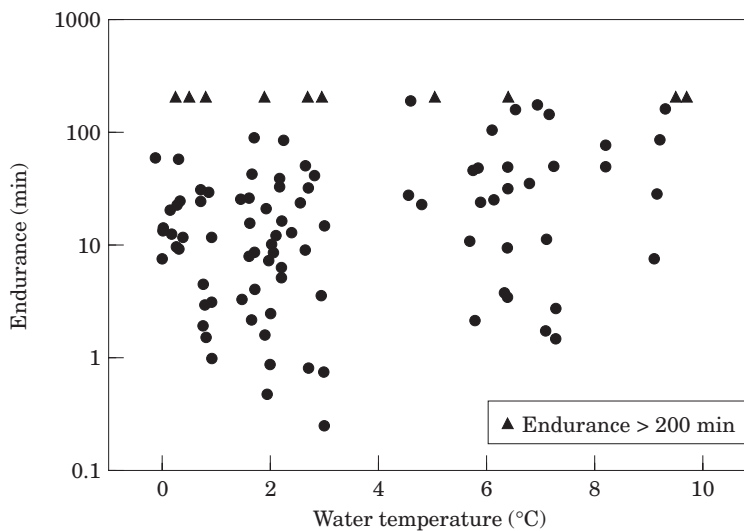


Figure 3. Logarithm of endurance (min) of American plaice (*Hippoglossoides platessoides*) plotted against water temperature (°C).

reduction in the log likelihood statistic followed by water temperature. The interaction term for fish length and water temperature was not statistically significant ( $p > 0.05$ ) and was not included in the model. The negative regression coefficients for fish length and water temperature indicates that given the baseline rate of failure, the hazard rate for an individual fish is decreased with increasing fish length and water temperature. This decline in the hazard rate is equivalent to an increase in the endurance probability. In other words, the probability of a fish exceeding a given endurance is increased with increasing fish length and water temperature.

No obvious trends were found in the partial residual plots or DfBeta plots. Figure 4 shows the DfBeta statistics for fish length and water temperature plotted for each swimming endurance trial. The DfBeta statistic is an estimate of the change in the regression coefficient with and without the swimming trial included in the analysis. Most of the values are shown to fall in a narrow horizontal band around zero. However, three potentially influential endurance times were noted, including: (1) a 26 cm plaice which demonstrated an endurance time of 163 min at 6.6°C; and (2) both a 30 and 31 cm plaice which exceeded an endurance of

Table 2. Failure time analysis of the swimming endurance of American plaice (*Hippoglossoides platessoides*) using the Cox proportional hazards model. Variables were entered into the regression model using forward stepwise selection. The significance of the variables were tested on the basis of their reduction of the log likelihood value for the model. The likelihood-ratio test statistic ( $\chi^2$ ) is defined as  $-2(\log \text{likelihood before variable added} - \log \text{likelihood after variable added})$ .

Variables in the model		Coefficient (s.e.)	Log likelihood of model	$\chi^2$ Value	d.f.	p-value
Step number	Variable					
0	—	—	− 339.468	—	—	—
1	Fish length (cm)	− 0.169 (0.025)	− 313.468	52.002	1	<0.0001
2	Temperature (°C)	− 0.095 (0.038)	− 310.282	6.371	1	0.0116
		Global $\chi^2$	d.f.	p-value		
		55.977	2	<0.0001		
Variables not in the model		Score	d.f.	p-value		
Variable						
Fish length $\times$ temperature		0.006	1	0.937		

200 min despite the relatively low temperatures of 0.5 and 0.8°C, respectively. While these endurance times were high compared to other fish of the same length and temperature, there was no biological or technical reason for eliminating them from the analysis. It was concluded that the endurance times for plaice resulted in a good fit of the Cox proportional hazards model.

Estimates of endurance probability,  $S(t)$ , were calculated from the predicted endurance hazard rates,  $h(t)$ , and some examples of probability curves for different fish lengths and water temperatures are illustrated in Figure 5a–d. From these figures it is evident that the probability of exceeding a given endurance increases rapidly with increasing fish length and water temperature. For example, at 0.0°C the probability that plaice has endurance greater than 10 min is near 0% for 15 cm fish, 18% for 25 cm fish, 73% for 35 cm fish, and 94% for 45 cm fish. By comparison, an increase in water temperature is shown to improve the probability of 15 cm fish achieving an endurance of 2 min from 21% at 0.0°C to 52% at 9.0°C.

Dissolved oxygen content within the flume remained high throughout the experiment. The mean concentration was  $11.8 \text{ mg O}_2\text{l}^{-1}$  (s.d.=1.3) with the percent of dissolved oxygen saturation never falling below 83.5%. The mean concentration for the censored endurance trials ( $\bar{x}=11.6 \text{ mg O}_2\text{l}^{-1}$ , s.d.=1.5) was not statistically different (two-tailed t-test,  $p=0.604$ ) from the mean concentration for trials where endurance was less than 200 min ( $\bar{x}=11.9 \text{ mg O}_2\text{l}^{-1}$ , s.d.=1.3).

## Discussion

### Swimming flume designs

Encouraging flatfish to swim in flumes has achieved only moderate success in previous studies (Beamish, 1966;

Priede and Holliday, 1980; Duthie, 1982). Compared with roundfish species, flatfish tend to exhibit: (1) greater disorientation in the presence of a water current; and (2) the tendency to settle onto the chamber floor and cease swimming. The latter has proven to be a major obstacle in the investigation of flatfish swimming capabilities. Using a horizontal Blažka-type respirometer, Beamish (1966) reported that winter flounder could not be induced to swim, i.e. lift off bottom, at speeds less than  $0.75 \text{ ms}^{-1}$ . Detailed behavioural observations of North Sea plaice (*Pleuronectes platessa*) have further shown that flatfish species are behaviourally adapted to counteract hydrodynamic lift and maintain station on the chamber floor (Arnold, 1969). This problem was later addressed by Priede and Holliday (1980) who developed a tilting Brett-type respirometer to test the critical swimming speeds ( $U_{\text{crit}}$ ) and oxygen consumption of North Sea plaice. In that study, the chamber was tilted forward at an angle of approximately 60°, forcing the fish to slip off the bottom and swim in a downhill direction. While this design encouraged flatfish to swim at slower speeds, it was found to reduce the power (energy) requirement for swimming and therefore bias estimates of oxygen consumption. Priede and Holliday (1980) also reported that many of their fish never performed satisfactorily, often facing in the wrong direction or becoming disoriented when the flow speed was increased. Similar difficulties using the same apparatus were also found by Duthie (1982) in his studies of critical swimming speeds ( $U_{\text{crit}}$ ) and oxygen consumption in European flounder (*Platichthys flesus*), common dab (*Limanda limanda*), and lemon sole (*Microstomus kitt*).

In this study, an alternative flume design was used for encouraging flatfish to swim under laboratory conditions. The use of a moving belt as the floor of the swimming chamber was sufficient stimulus to induce American plaice to swim continuously at slow speeds

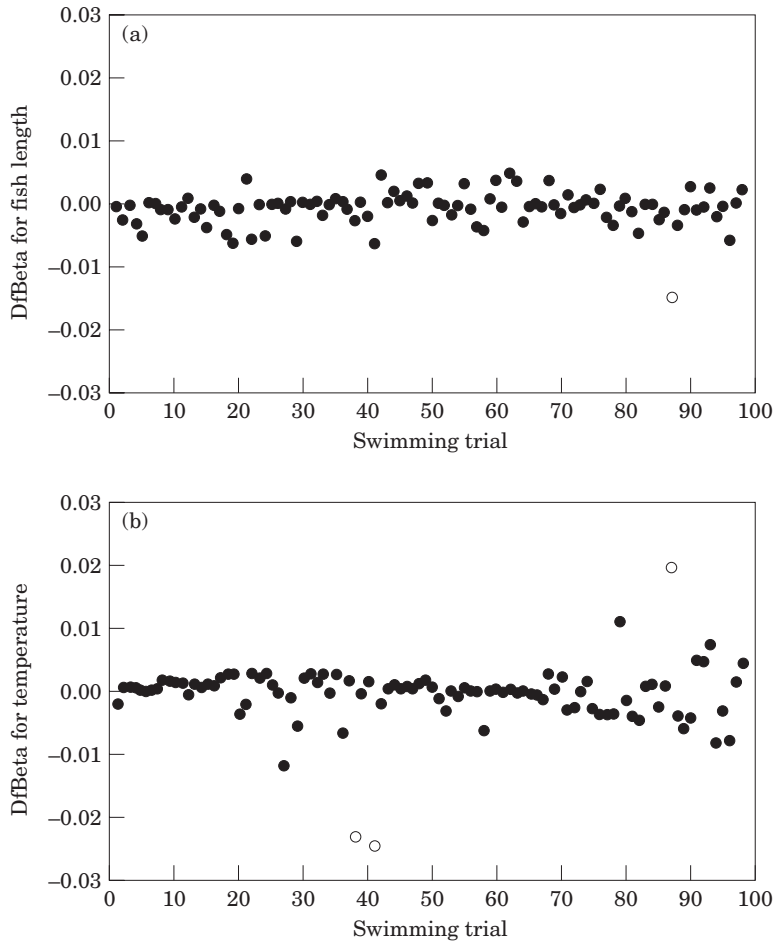


Figure 4. DfBeta statistics for (a) fish length and (b) water temperature plotted for each swimming endurance trial of American plaice (*Hippoglossoides platessoides*). The DfBeta statistic is an estimate of the change in the regression coefficient with and without the swimming trial included in the analysis. Open circles represent potentially influential endurance times.

until exhaustion. The energetic bias due to swimming downhill (Priede and Holliday, 1980; Duthie, 1982) and the use of high flow speeds to induce swimming (Beamish, 1966) were thus eliminated in this flume design.

### Swimming endurance

The results of the failure time analysis revealed that both fish length and water temperature had a significant effect on the endurance hazard rate. This is sufficient evidence to reject the null hypotheses that the endurance of American plaice is independent of these variables. This study marks the first systematic attempt to investigate factors affecting the endurance of this species. The only previously known study which has directly investigated the endurance of flatfish was by Beamish (1966). In that study, winter flounder (19–23 cm) were tested at temperatures of 5.0, 8.0, 11.0, and 14.0°C and at swimming

speeds ranging from 0.75 to 1.35  $\text{ms}^{-1}$ . While the author did observe increased levels of endurance at 14.0°C, no appreciable difference in swimming endurance was found across the lower temperature treatments. The primary literature on the swimming performance of other flatfish species is limited to only a few studies. Much of this research has been directed toward measuring maximum or critical swimming speeds ( $U_{\text{crit}}$ ) with little attention to swimming endurance at fixed speeds. Blaxter and Dickson (1959) observed an increasing trend in the maximum swimming speeds of North Sea plaice with increasing water temperature and fish length. For this same species, Priede and Holliday (1980) reported an increasing trend in  $U_{\text{crit}}$  values with increasing temperature. Similar findings were also found for European flounder, but could not be demonstrated for common dab or lemon sole (Duthie, 1982).

It should be noted that the effect of water temperature found in this study was not supported in our preliminary



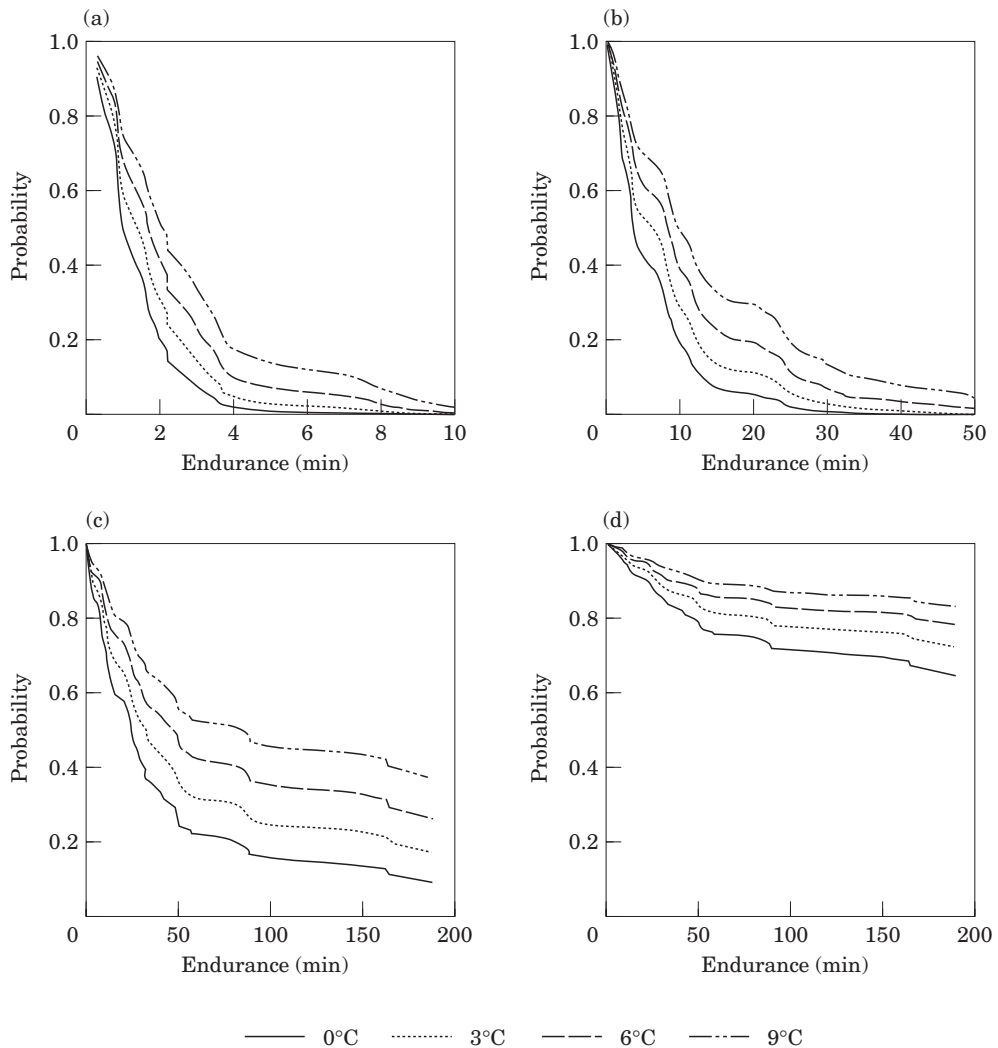


Figure 5. Estimated probability curves for the swimming endurance of American plaice (*Hippoglossoides platessoides*) at different water temperatures for fish lengths (a) 15 cm, (b) 25 cm, (c) 35 cm, and (d) 45 cm.

analysis of the data (Winger *et al.*, 1997). This difference is suspected to be the result of: (1) our choice of statistical technique; and (2) the subset of endurance trials examined. In the preliminary analysis, the data were modelled using multiple regression analysis rather than failure time analysis. As a result, the censored observations in which swimming endurance exceeded 200 min could not be included in that analysis. Secondly, the selection of suitable endurance trials for the current analysis (see Analysis) also benefitted from the post-video observation of the trials. This tool was not used in selecting trials in the preliminary analysis. Further investigation should be directed toward the statistical comparison of multiple regression analysis and failure time analysis for the modelling of endurance-type data.

The finding that swimming endurance was length-dependent suggests that different sizes of fish were operating within different levels of their individual swimming capability. Depending on the fish size, relative swimming speeds ranged from 0.7 to 2.1 body lengths per second ( $\text{BL s}^{-1}$ ). Clearly, smaller fish were disadvantaged compared to their larger counterparts when swimming at a fixed speed of  $0.30 \text{ ms}^{-1}$ . This is represented by the negative regression coefficient for fish length, indicating that a reduction in fish size corresponds with an increase in the hazard rate, or risk of exhaustion. Length-dependent swimming capability is well documented (e.g. Bainbridge, 1960; Brett, 1965; Brett and Glass, 1973; Taylor and McPhail, 1985; He and Wardle, 1988), though little is known about the interaction between fish size and choice of swimming

strategy. This is particularly true for negatively-buoyant fish such as flatfish. Theoretical calculations by [Priede and Holliday \(1980\)](#) and [Duthie \(1982\)](#) of the cost of swimming (in mg O<sub>2</sub> consumed per unit distance travelled) have suggested that it would be uneconomical for flatfish to swim at speeds below 0.60 BL s<sup>-1</sup>. Both of these studies also reported that the theoretically most optimal swimming speeds should be closely correlated with U<sub>crit</sub> values for flatfish species. The studies concluded that the aerobic scope of certain flatfish species may be insufficient to allow them to swim at what is theoretically their most optimal swimming speeds. As a result, both papers have speculated that, over long distances, flatfish may adopt anaerobic swimming strategies such as bursting followed by periods of rest to counter balance the accrued oxygen debt. The findings from this study have shown that American plaice are capable of employing different combinations of swimming strategies and that the ability to employ certain strategies appears to be somewhat dependent on fish length. Further studies should be directed toward examining the interaction between fish size and swimming strategy. Video analysis of flatfish swimming kinematics, in particular, has been largely unexplored and would prove valuable to the understanding of flatfish swimming energetics.

Photoperiod has been shown to influence the swimming capability of fish. [Kolok \(1991\)](#) reported a significant reduction in the U<sub>crit</sub> values of juvenile largemouth bass (*Micropterus salmoides*) at 5.0 and 10.0°C when kept at seasonally inappropriate photoperiods. Given that the current study was designed to take advantage of seasonal changes in the ambient seawater temperature, choosing a constant photoperiod seemed inappropriate. Instead, by maintaining the plaice under conditions of ambient photoperiod combined with ambient seawater temperature, it is assumed that the fish received the natural cues associated with seasonal change. Little is known about the effect of photoperiod on the swimming capability of marine fish.

### Implications for otter trawl catchability

The estimation and modelling of the herding efficiency of otter trawl sweeps has been the subject of much research (e.g. [Foster, 1969](#); [Hemmings, 1969](#); [Harden Jones et al., 1977](#); [Foster et al., 1981](#); [Engås and Godø, 1989](#); [Andrew et al., 1991](#); [Dickson, 1993a, 1993b](#); [Ramm and Xiao, 1995](#); [Somerton and Munro, 1996](#)). Unfortunately, little empirical data exist on the herding efficiency of flatfish species. Direct video observations have shown that flatfish are typically herded into the trawl path after direct or near contact with the doors, sweeps, and sand clouds of the trawl ([Main and Sangster, 1981](#)). This behaviour has been modelled as an incremental process in which the flatfish (once disturbed

from the seafloor) swim toward the trawl path in a direction 90° away from the approaching sweeps ([Foster, 1969](#); [Hemmings, 1969](#); [Foster et al., 1981](#)). After swimming a distance of approximately 0.5–5.0 m, the fish settle onto the seafloor once again. Each time the sweeps approach, the flatfish repeat the behaviour and, progressively slip along the sweeps toward the mouth of the trawl.

General observations during the current study indicated that American plaice are capable of a number of swimming strategies, including steady cruising, swim-and-settle, and burst-and-glide. Direct video observations of flatfish behaviour in response to the groundropes of a Danish seine net have confirmed the use of such strategies during herding ([Hemmings, 1969, 1973](#); [Wardle, 1983](#)). By comparison, observations of flatfish behaviour in response to the sweeps of otter trawls have only reported the classical swim-and-settle strategy ([Main and Sangster, 1981](#)). In the current study, only the larger plaice (>25 cm) tended to have sufficient swimming capability to employ the steady cruising and swim-and-settle strategies. This suggests that smaller plaice (<25 cm) might be required to use the burst-and-glide strategy out of necessity during herding by otter trawl sweeps, even though direct observations of this strategy have not been reported. The importance of different swimming strategies on the herding efficiency of otter trawls has been stressed by [Hemmings \(1969\)](#) and [Foster \(1969\)](#). Both suggested that the energy reserves of fish may be expended either quickly or slowly depending on the “degree of motivation” of the fish. For example, highly motivated flatfish which initially encounter the sweep furthest from the wingtip may swim rapidly to their exhaustion and be subsequently overtaken near the middle of the sweep, whereas had they swum more slowly and steadily they might have successfully reached the trawl path. Empirical observations to support this hypothesis are still lacking. Direct measures of the reaction distance, angle of avoidance, swimming speed, and swimming strategy employed by flatfish in response to otter trawl sweeps remains poorly quantified.

For flatfish to be effectively herded, the fish must swim at a speed equal to or greater than the herding speed of the advancing sweeps and have sufficient endurance to reach the trawl path. The distance required to swim is dependent on: (1) sweep angle; (2) the position along the sweep where the fish initially encounter the gear; and (3) the angle of avoidance in which the fish choose to swim. While it is recognized that the angle of avoidance is probably quite variable between individual fish, for simplicity we will assume here that plaice swim on the average at an angle of 90° away from an approaching sweep. Given this assumption, the swimming speed and endurance required to successfully avoid the sweep and be herded into the trawl path can be roughly estimated.

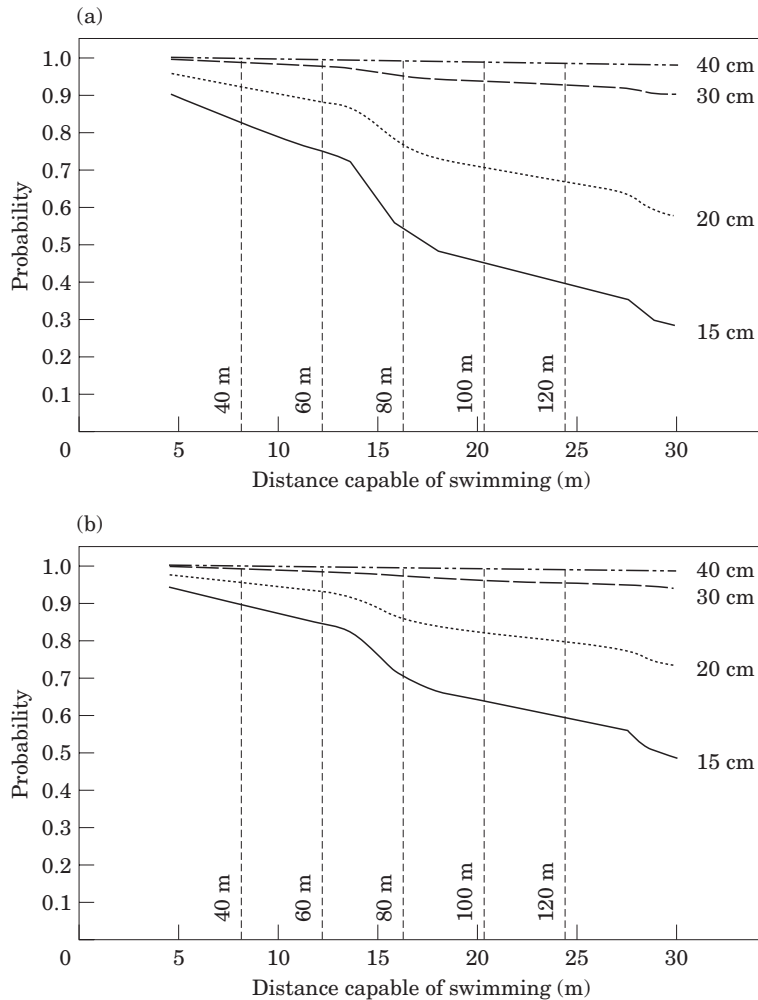


Figure 6. Estimated probability curves for the distances capable of swimming (at  $0.30 \text{ ms}^{-1}$ ) by American plaice (*Hippoglossoides platessoides*) of different fish lengths at (a)  $0^\circ\text{C}$  and (b)  $6^\circ\text{C}$ . Overlaid within the figures are vertical dashed lines representative of an otter trawl with a sweep angle of  $11.5^\circ$  and a forward towing speed ( $U_T$ ) of  $1.50 \text{ ms}^{-1}$  (i.e.  $U_H = 0.30 \text{ ms}^{-1}$ ). These lines indicate the distances that plaice would be required to swim in order to reach the trawl path after initially encountering the sweeps at distances of 40, 60, 80, 100, and 120 m from the wingtip. Corresponding probabilities of successfully reaching the trawl path can be read from the y-axis.

First, the swimming speed of the fish must be at least equal to or greater than the herding speed of the sweeps in order to avoid being overtaken by the gear. The herding speed of sweeps ( $U_H$ ) is defined as:

$$U_H = \sin\theta \cdot U_T \quad (2)$$

where  $\theta$  is the sweep angle and  $U_T$  is the forward towing speed of the trawl through the water. Second, the fish must also have sufficient endurance to reach the trawl path. Assuming an average angle of avoidance of  $90^\circ$  to the sweep, the distance required to swim to the trawl path ( $D_H$ ) is defined as:

$$D_H = \tan\theta \cdot D_W \quad (3)$$

where  $\theta$  is the sweep angle and  $D_W$  is the distance from the wingtip where the fish initially encounter the sweep. For example, Canadian research surveys conducted off the east coast of Newfoundland and Labrador use a Campelen 1800 shrimp trawl rigged with 40 m sweeps (McCallum and Walsh, 1995). Towing speed is standardized at  $1.50 \text{ ms}^{-1}$  and the upper bridle angles are known vary from  $7.4$  to  $22.6^\circ$  ( $\bar{x} = 19.2^\circ$ ,  $CV = 15\%$ ) over survey depths of 45–750 m (Walsh and McCallum, 1997). Assuming that the upper bridle angle is representative of the sweep angle (data not available), this would be equivalent to a range in  $U_H$  from  $0.19$  to  $0.58 \text{ ms}^{-1}$ . Depending on the distance from the wingtips where flatfish initially encounter the sweeps of this trawl,  $D_H$

will vary from zero up to a maximum of 13.9 m (using  $\theta=19.2^\circ$ ).

Since the sweep length and sweep angle cannot be optimal for the herding of all fish lengths across all bottom temperatures, it follows that the herding of plaice could be highly selective. If the results from the current study are representative of field conditions, then the herding efficiency of plaice (at  $0.30 \text{ ms}^{-1}$ ) may be both size- and temperature-dependent. At low temperatures small fish are expected to have a lower probability of sufficient endurance required to reach the trawl path. If this happens, these fish will suffer a greater likelihood of being overtaken by the sweeps and effectively escape from the gear. As fish length and water temperature increase, so should the probability of successfully swimming the required distance. Figure 6 shows the estimated probability curves for the distances that plaice of different fish lengths are capable of swimming (at  $0.30 \text{ ms}^{-1}$ ) at  $0.0$  and  $6.0^\circ\text{C}$ . The probability of exceeding a given swimming distance is shown to improve with increasing fish length and water temperature. Overlaid within the figure is an illustrative example of an otter trawl with a sweep angle of  $11.5^\circ$  and a forward towing speed ( $U_T$ ) of  $1.50 \text{ ms}^{-1}$  (i.e.  $U_H=0.30 \text{ ms}^{-1}$ ). The vertical dashed lines indicate the distances that plaice would be required to swim in order to reach the trawl path after initially encountering the sweeps at distances of 40, 60, 80, 100, and 120 m from the wingtip. The corresponding probabilities of successfully reaching the trawl path can be read from the y-axis. For example, at  $0.0^\circ\text{C}$  it is shown that 15 cm plaice will have roughly an 80% probability of reaching the trawl path if they initially encounter the sweep 40 m from the wingtip, compared to 40% probability at 120 m from the wingtip. At  $6.0^\circ\text{C}$ , these same fish will have nearly a 90% probability at 40 m and 60% probability at 120 m, respectively. Systematic size- and temperature-dependent vulnerability of this nature will largely affect the efficiency of the herding process during otter trawling. Any combination of long sweeps and large sweep angles should result in a reduction in the proportion of plaice effectively herded into the trawl path, especially smaller plaice at low bottom temperatures which encounter the sweeps far from the wingtips. However, given that endurance was tested only at  $0.30 \text{ ms}^{-1}$  in the current experiment, it is recognized that the herding efficiency of trawl sweeps can only be inferred under conditions where  $U_H$  approximates  $0.30 \text{ ms}^{-1}$ . Further laboratory studies should be directed toward examining the endurance of plaice across a range of swimming speeds comparable to the herding speeds of trawl sweeps, particularly in the range of  $0.20$ – $0.60 \text{ ms}^{-1}$ . This would provide the capability to estimate the herding efficiency of trawl sweeps across a wider range of gear performance as well as otter trawl designs.

Size- and temperature-dependent swimming endurance of American plaice may affect the selectivity and efficiency of bottom trawls used as survey instruments. Temporal and spatial changes in bottom temperature are expected to influence swimming capability and thus vulnerability to survey trawl capture. Systematic variation of this nature should result in a reduction in the levels of precision of the survey catch-at-age data and therefore increase the error in estimates of population abundance and size composition of plaice.

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