Swimming endurance of haddock (*Melanogrammus aeglefinus* L.) at prolonged and sustained swimming speeds, and its role in their capture by towed fishing gears

Mike Breen, Jamie Dyson, Finbarr G. O'Neill, Emma Jones, and Michael Haigh

Breen, M., Dyson, J., O'Neill, F. G., Jones, E., and Haigh, M. Swimming endurance of haddock (*Melanogrammus aeglefinus* L.) at prolonged and sustained swimming speeds, and its role in their capture by towed fishing gears. — ICES Journal of Marine Science, 61: 1071−1079.

This paper describes an experiment to determine the swimming endurance of haddock (*Melanogrammus aeglefinus*) at prolonged swimming speeds. Fish were stimulated to swim in a circular path around an annular tank, using a moving light pattern to trigger the optomotor response. Individually tagged haddock (length range 16.0−40.2 cm) swam in groups over a range of speeds ($0.3-0.9 \, \text{m s}^{-1}$) and at a constant temperature ($9.85 \pm 0.07°\text{C}$). Endurance of individual fish was shown to be related to their swimming speed and length. However, there was also significant variation ($p < 0.05$) in the performance of fish of approximately equal length. Distinct behaviours and swimming gaits were also identified and associated with the performance of individual fish. The inverse-linear model is introduced, as an alternative to the log-linear model, for describing the relationship between swimming speed and endurance, and estimating maximum sustainable swimming speed (U_{ms}). Estimates of U_{ms} ranged from $0.38 \pm 0.03 \, \text{m s}^{-1}$ and 3.16 ± 0.02 BL s^{-1} (for a 16.0-cm fish) to $0.62 \pm 0.04 \, \text{m s}^{-1}$ and $1.51 \pm 0.07 \, \text{BL s}^{-1}$ (for a 42.0-cm fish). U_{ms} represents an important threshold in the behavioural physiology of fish, marking the upper limit of aerobic swimming. The relevance of these results and U_{ms} to the fish capture process is discussed.

M. Breen, F. G. O'Neill, and E. Jones: Fisheries Research Services, Marine Laboratory, PO Box 101, Aberdeen, Scotland, UK. J. Dyson and M. Haigh: Aberdeen University, Zoology Department, Tillydrone Road, Aberdeen, Scotland, UK. Correspondence to M. Breen: tel: +44 1224 295474; e-mail: m.breen@marlab.ac.uk.

Introduction

Endurance in fish generally decreases with increasing swimming speed (Videler and Wardle, 1991). The range of swimming speeds used by fish has been broadly categorized into "sustained", "prolonged", and "burst" swimming; and at each of these speeds different muscle types are recruited to power the swimming gait (Webb, 1994). "Sustained" swimming uses only red myotomal muscle, while the faster "prolonged" swimming employs progressively more white myotomal muscle to supplement the power provided by the red muscle. This progressive recruitment of different muscle types, with their differing functional properties, explains the reduction in endurance with increasing speed and is comprehensively reviewed

in Webb (1994), Videler (1993), and Coughlin (2002). The boundary between "sustained" and "prolonged" swimming speeds is defined as the "maximum sustainable swimming speed" (U_{ms}). It represents an important threshold in the behavioural physiology of fish, marking the upper limit of aerobic swimming.

The importance of swimming endurance in the fish capture process, in particular during the herding of fish by the otter boards and in the mouth of the trawlnet, is well understood (Wardle, 1993; Engås, 1994; Godø, 1994). However, little consideration has been given to the swimming capabilities of fish entering the trawl following this potentially exhausting process. It is likely that many of these fish will only be capable of swimming at or below their maximum sustainable speed (U_{ms}), as respiratory

substrates in the white muscles are depleted (Webb, 1994; Coughlin, 2002). In many fisheries, discarding is reduced by allowing undersized and non-target species to escape via the codend meshes, or through some other selective device. A limit on swimming capability will therefore have implications for the effectiveness of these selective devices, where fish require a positive swimming action to escape.

This paper describes an experiment to investigate the endurance of haddock, of different sizes, over a range of swimming speeds ("sustained" and "prolonged"). Haddock are a demersal gadoid species that swim predominantly using "body and caudal fin" (BCF) gaits (Webb, 1994), particularly when interacting with towed fishing gears. In this experiment, their swimming endurance was measured at different speeds (0.3−0.9 m s^{-1}) and a constant temperature (9.85 $\pm$ 0.07°C) in a large annular tank. The technique has a number of advantages over flume tanks: the fish swim through a static water mass; the dimensions of the tank are such that fish can be studied in groups; and the swimming stimuli are comparable to those encountered by fish interacting with towed fishing gears.

The relationship between endurance and swimming speed has previously been described using a log-linear function,

$$\log_{10} t = mU + c \tag{1}$$

where t is endurance time (minutes), U is the swimming speed (m s^{-1} or body lengths per second (BL s^{-1})) and m and c are the linear coefficient and intercept, respectively (Videler, 1993). In this study, an alternative model was used where the data were described using an inverse-linear relationship:

$$\frac{1}{t} = mU + c \tag{2}$$

This model better represents the current understanding of the limiting capacity of anaerobic metabolism at prolonged swimming speeds (Webb, 1994). As swimming speed decreases, endurance tends to an asymptote (to infinity) at the speed at which white muscle recruitment ceases. The asymptote in this relationship provides a parameter-based estimate of the maximum sustainable swimming speed (U_{ms}):

$$U_{ms} = \frac{-c}{m} \tag{3}$$

Previous methods for estimating U_{ms} have been limited by the need to define a maximum endurance time (usually restricted to the maximum observation period), which could result in values for U_{ms} being overestimated. For example, direct measurement (He and Wardle, 1988; Xu *et al.*, 1994), extrapolation from regression analysis (Peake *et al.*, 1995), probit analysis (Brett, 1967, 1982; Bernatchez and Dobson, 1985) and failure analysis (Winger *et al.*, 1999, 2000).

In this paper, the inverse-linear model is fitted to haddock endurance data and the maximum sustainable swimming speed (U_{ms}) for each fish is estimated. The importance of individual variation and the effect of length on U_{ms} are described. Finally, the relevance of these results, in particular the magnitude of U_{ms}, to the fish capture process and selective properties of towed fishing gears is discussed.

Methods

Specimen collection and tagging

Haddock were captured locally by handline or trawl in shallow water ($<$ 50 m). Prior to beginning the experiment, all fish were anaesthetized in 0.0075% methanosulfonate salt solution (MS222), weighed, measured (total body length), and tagged. Each fish was identifiable from a unique combination of luminescent polymer strips (elastomer) injected subdermally on the dorsal side. The fish were allowed to recover and acclimatize to captive conditions in the aquarium for at least 3 days before commencing pre-experimental training.

Apparatus

A circular swimming channel was constructed within an annular tank (originally described by He and Wardle, 1988) using fabric-covered barriers. The channel was approximately 1 m wide with a mean radius of 3.97 m and median circumference of 24.97 m. A gantry arm, pivoted at the tank's centre, rotated around the tank at a controlled speed (Figure 1). The fish were stimulated to swim primarily through an optomotor response (Arnold, 1974) to a moving light pattern projected from the gantry arm onto the channel walls. To ensure there were no contradictory visual references, the experiment was conducted in low light conditions (2.5 $\times$ 10^{-4} lux). The swimming speed was controlled by adjusting the speed of the gantry arm, and was estimated to be the product of the angular velocity and the median circumference of the swimming channel.

When not in the swimming channel, fish were kept in four holding pens in the centre of the annular tank. Access to the swimming channel prior to each experimental swim was through a gate in the inner barrier (Figure 1). This ensured that the fish experienced no significant changes in environmental conditions and minimal physical contact prior to each swim. Key environmental parameters were maintained at an approximately constant level throughout the experiment to ensure consistent replication of swimming performance (water temperature 9.85 $\pm$ 0.07°C, air temperature 12.97 $\pm$ 0.41°C, and oxygen saturation 97.4 $\pm$ 0.6%). They were each measured before and after each swim: water and air temperature using a temperature probe (RS 427-461) and/or mercury thermometer; oxygen saturation with an Oxyguard MkIII oxygen meter; and
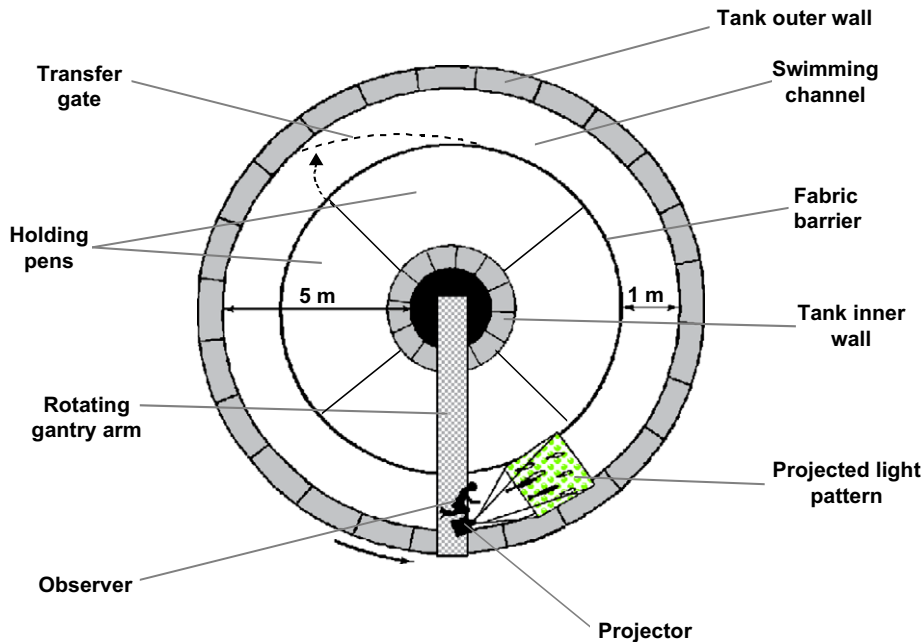
Figure 1. A plan view of the annular tank and gantry arm, with moving light pattern (adapted from He and Wardle, 1988) (not to scale).

atmospheric pressure using a Griffin and George mercury barometer.

Measuring swimming endurance

Haddock were divided into five different groups of similar-sized individuals in order to minimize length-based variability in endurance times within each. Prior to any experimentation, the fish in each group were "trained" by swimming them at slow speeds (< 1.5 BL s^{-1}) in the swimming channel for short periods of time (30–45 min) up to twice a day. To reinforce the optomotor response, any fish failing to stay within or ahead of the light pattern was herded back by an observer, stationed on the gantry, using a long wooden paddle. Physical contact with the fish was avoided, the paddle being used to induce a pressure wave behind the fish to stimulate the caudal reflex. As well as reinforcing the optomotor response, training served to acclimatize fish to the inevitable stressors associated with the experimental conditions and therefore minimize the variation in endurance due to experimentally induced secondary stressors.

The endurance trials consisted of separate swims over a range of set speeds from 0.3209 to 0.9055 m s^{-1}. During each trial, the fish swam at a constant velocity until all individuals became fatigued and were removed, or had swum for at least 200 min. At the start of each swim, the gantry speed was set relatively low (~ 2 BL s^{-1}) and gradually increased to the target speed over a 3 min period. The stimuli to swim were the same as those used during the training swims: optomotor response in association with the

moving light pattern and the caudal reflex, when necessary. Continuous observation was maintained by both the observer on the gantry and the controller at the tank side and general and individual behaviour noted. Fish were sometimes unable or refused to swim ahead of the gantry; this was referred to as an "escape". The time of each escape was recorded and the individual identified by the controller using a blue lamp to illuminate the elastomer tags. On rejoining the shoal, once the gantry had completed a revolution of the tank, the escapee was tracked to ensure it completed at least one complete revolution while swimming in the light pattern. If it failed to do so, this was noted as a "consecutive escape". The fish was considered to be "fatigued" after five consecutive escapes. At this point it was removed by net from the swimming channel, identified again for confirmation, and transferred to one of the central holding pens.

Following each endurance swim, the fish were rested for a minimum of 36 h, during which time they were fed to satiation. The speed of each successive swim was increased by a small increment (~ 0.025–0.05 m s^{-1}) until all fish in the group had recorded endurance times of < 30 min. Once this had been achieved, the fish were rested for 24 h and then removed for weighing and measuring. This process was continued for each subsequent set of swims, with the aim of providing three replicate swims at each speed.

Data analysis

The inverse-linear model, Equation (2), was fitted to the endurance data using a generalized linear regression

(McCullagh and Nelder, 1989) with Genstat 5.0 software (Payne, 1993). The residuals were assumed to be normally distributed, the link function was set at identity, and the dispersion parameter (φ) was estimated. During the fitting of the model, the inverse transformation resulted in a systematic increase in variance in the transformed data with decreasing endurance times, and hence higher swimming speeds. This was accounted for by weighting the transformed data (at each speed) with respect to the inverse of their variance.

The relative performance of individual fish within each group was assessed by including in the model an additional factor for each fish, along with its interaction with speed. Likewise, to test the independence of repeat measurements at the same swimming speed for each fish, a repeat factor was included in each individual model. However, the repeat factor proved insignificant in all cases ($p < 0.05$) and independence within the data was assumed.

Not all recorded endurance data were included in the analysis. Firstly, endurance times were excluded where the experiment was terminated (i.e. after 200 min) before the fish reached an appropriate end-point (i.e. fatigue). These are generally referred to as censored data (Winger et al., 2000). Also excluded were data when the fish had clearly under-performed on a particular run, but only at speeds below the fastest observed censored speed for that fish.

Results

Swimming behaviour

The haddock swam in a loose shoal in or ahead of the projected light pattern. Most followed a gently curved path, which approximated about the median line in the channel. Some fish, however, adopted a shorter path, swimming close to the inner wall, and generally close to the bottom of the swimming channel. Others, particularly larger individuals, swam with their bodies tilted laterally about the central longitudinal axis, typically with the dorsal side towards the inner wall of the swimming channel (e.g. fish 7 and 54). Occasionally, some fish were observed swimming at or close to the surface of the swimming channel. Where this behaviour was habitual (e.g. fish 18), endurance times may have been reduced because of increases in drag (Hertel, 1966).

A fish's behaviour at, or close to, the experimental end-point varied between two general types: "fatigued" and "unwilling". A "fatigued" fish would reach the end-point with five consecutive escapes in quick succession. These fish were easily caught in the hand-net and made no excessive movement during the transfer to the holding pens. In comparison, an "unwilling" fish would exhibit numerous non-consecutive "escapes" before eventually reaching the end-point of five consecutive escapes. On removal, these fish were often more difficult to catch, exhibiting some capacity for burst swimming speeds, suggesting they were not truly "fatigued". No relationship between the form of end-point behaviour and swimming performance was apparent.

Swimming endurance

A total of 216 non-censored endurance observations were obtained from 22 haddock. A further 18 fish were withdrawn from the experiment due to death or injury. Of these, nine died within 24 h of a swimming trial and were thought to have succumbed to post-exhaustion stresses (Wood et al., 1983). There was a significant ($p < 0.05$) inverse relationship between endurance time and swimming speeds for all fish (Table 1, Figure 2). The day-to-day performance of some fish varied considerably at the same speed. In general, the inverse-linear model had a superior fit to the observed data than the log-linear model, as can be seen in Figure 2. In most cases the log-linear model significantly underestimates performance at lower speeds, while overestimating performance at intermediate speeds.

Estimates of maximum sustainable swimming speed (U_{ms})

Estimates of the maximum sustainable swimming speed (U_{ms}) were modified to provide values for the fish swimming in a straight line (U_{ms}^s) (He and Wardle, 1988) (Table 1, Figure 3). The effect of the curved swimming path clearly increases with size, but appears to have a negligible impact upon the smallest fish (< 20 cm). There was a significant relationship ($p < 0.001$) between U_{ms} (and U_{ms}^s) and length, in terms of both absolute speed (m s^{-1}) (Figure 3a) and relative speed (BL s^{-1}) (Figure 3b). It is clear that the relative influence of length, with respect to U_{ms} (and U_{ms}^s), decreases with increasing length. In particular, at absolute swimming speeds there was almost a 50% increase in U_{ms} (and U_{ms}^s) between haddock of ~ 15 cm and ~ 25 cm, while the difference in U_{ms} (and U_{ms}^s) for fish of ~ 25 cm and ~ 45 cm was negligible.

Variation in endurance between fish of the same length

For all groups, except group B, the performance of individuals within the same group, and therefore of approximately the same length, varied significantly ($p < 0.001$) with respect to both absolute (m s^{-1}) and relative (BL s^{-1}) swimming speeds (Figure 4). For group B, significant differences ($p < 0.001$) in endurance were only seen with respect to relative swimming speeds (BL s^{-1}). In group C, fish no. 18 clearly under-performed in comparison to the other fish (Figure 4c). It habitually swam at or close to the surface of the swimming channel and is likely to have experienced an increased drag (Hertel, 1966). As this was unrepresentative of natural swimming conditions and likely

Table 1. Summary of inverse-linear model and estimates of maximum sustainable swimming speed for individual fish.

Details of individual fish				Inverse-linear model parameter estimates					Estimates of maximum sustainable swimming speed		
Number	Group	Length (cm)	Weight (g)	c	Speed (m s^{-1})	n	R^2	P	U_{ms} (m s^{-1})	95% CI* (m s^{-1})	U_{ms}^s (m s^{-1})
1	A	31.3	301.9	−0.156	0.284	15	49.5	0.002	0.548	0.034	0.579
3	A	31.3	354.1	−0.149	0.253	11	90.1	<0.001	0.590	0.011	0.627
5	A	30.6	314.6	−0.236	0.394	11	66.8	0.001	0.599	0.009	0.633
7	A	31.6	344.4	−0.155	0.262	11	95.9	<0.001	0.592	0.006	0.628
2	B	32.3	325.5	−0.315	0.553	10	64.0	0.003	0.570	0.015	0.603
9	B	33.6	411.0	−0.165	0.269	9	80.4	<0.001	0.614	0.026	0.655
10	B	32.6	390.5	−0.164	0.300	4	87.5	0.042	0.546	0.065	0.582
11	B	37.5	565.9	−0.096	0.174	10	70.5	0.001	0.552	0.049	0.597
18	C	23.3	142.2	−0.486	1.128	9	44.6	0.030	0.431	0.043	0.446
19	C	23.3	141.8	−0.132	0.239	14	82.8	<0.001	0.552	0.027	0.572
20	C	24.6	166.0	−0.134	0.225	8	77.0	0.003	0.594	0.029	0.618
21	C	25.5	178.1	−0.084	0.147	7	81.0	0.004	0.572	0.052	0.596
22	C	25.5	203.9	−0.104	0.203	14	48.4	0.003	0.515	0.024	0.538
23	D	16.0	40.2	−0.213	0.536	12	55.4	0.003	0.397	0.048	0.403
24	D	16.3	39.9	−0.120	0.300	14	92.1	<0.001	0.400	0.031	0.406
25	D	18.3	53.3	−0.110	0.258	14	97.5	<0.001	0.428	0.005	0.436
27	D	17.8	52.3	−0.263	0.476	6	69.9	0.003	0.553	0.020	0.563
30	D	16.0	44.2	−0.407	1.063	8	82.1	0.001	0.383	0.026	0.390
31	D	18.8	68.1	−0.162	0.324	9	82.5	<0.001	0.500	0.034	0.511
49	G	42.2	954.3	−0.059	0.101	6	70.9	0.022	0.585	0.066	0.637
54	G	38.7	842.3	−0.072	0.116	6	77.7	0.013	0.624	0.044	0.676
56	G	40.8	787.2	−0.202	0.335	8	93.0	<0.001	0.603	0.026	0.652

*Confidence interval (95%) for U_{ms} estimate.

to have affected its performance, data from fish 18 were excluded from any comparative analysis.

Discussion

The inverse-linear model showed a better fit to the observed endurance estimates than the log-linear model. Furthermore, it has a sounder theoretical basis and enables a parameter-based estimate (Equation 3) of maximum sustainable swimming speed (U_{ms}). A disadvantage of this model, which is shared with the log-linear model, is that censored data cannot be included in the data set. The failure analysis of Winger *et al.* (1999, 2000) does not have this limitation; however, it still requires the fixing of an arbitrary maximum endurance time to estimate U_{ms}. A model that uses both censored and uncensored data, but retains a functional description of endurance of the type defined here for speeds greater than U_{ms}, would be useful future research.

The importance of size, in particular length, in determining swimming performance of fish with respect to speed and endurance is well documented (Beamish, 1978; Blake, 1983; Videler, 1993). In general, an increase in size, for fish of the same species, means that fewer tail-beats are required to cover the same distance (Videler and Wardle, 1991). Hence, at the same absolute speed (m s^{-1}), larger fish will have longer endurance times and higher U_{ms}. Although this effect was shown for haddock in this study (Figure 4a), its relative influence is negligible among fish of greater than 25-cm length. Moreover, in terms of relative speed (BL s^{-1}), smaller haddock had the better endurance times and U_{ms} (Figure 4b). That is, tail-beat for tail-beat, smaller fish appear to have a more efficient swimming gait. This has also been seen in other species (e.g. sockeye salmon (Brett, 1965) and saithe (He and Wardle, 1988)) and has been attributed to the increase in hydrodynamic drag from the increase in body size, which outweighs the advantages of increased metabolic scope and swimming musculature (Brett, 1965).

It was demonstrated that significant differences in endurance at prolonged speeds exist between fish of comparable length. There are a number of possible sources of physiological and morphological variation that could explain this variation. Morphologically, the relationship between weight and length will inevitably include considerable variation among individuals (Coull *et al.*, 1989). This variation will also reflect the relative amount of swimming muscle available to provide propulsive power, which could directly affect swimming performance (Bainbridge, 1960).
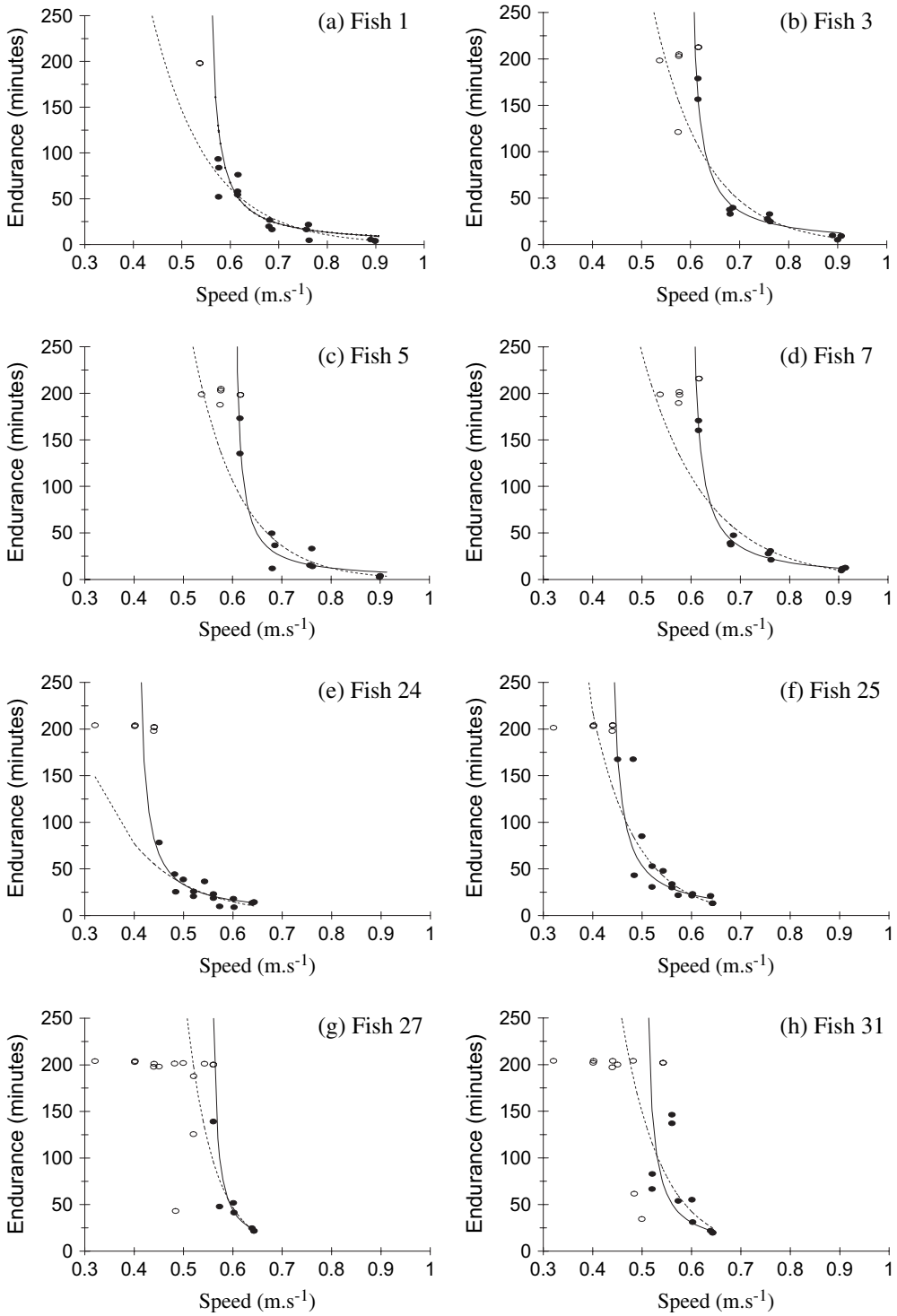
Figure 2. (a–h) The relationship between endurance and swimming speed (m s^{-1}), examples for individual fish. Measured values of endurance are shown as closed circles (●); censored data as open circles (○); fitted inverse-linear model as a continuous line; and the fitted log-linear model as a broken line.
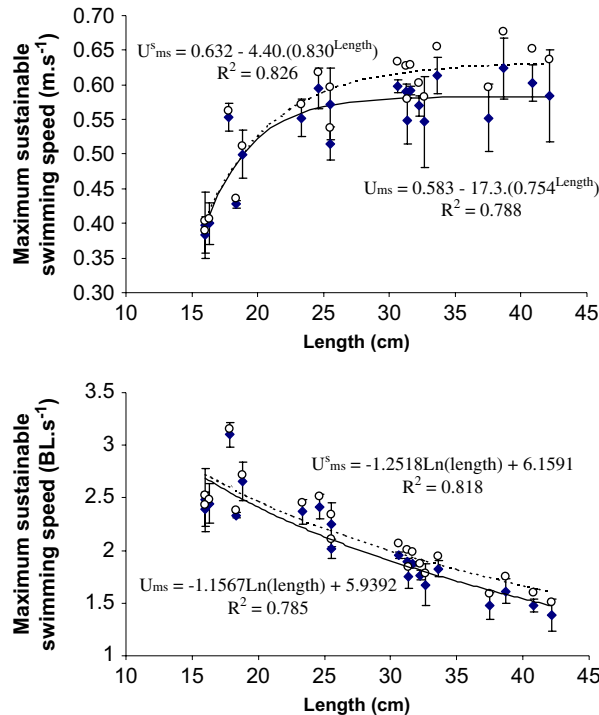
Figure 3. The relationship between maximum sustainable swimming speed and length: (a) at absolute speeds (m s^{-1}) and (b) at relative speeds (BL s^{-1}). Estimates of maximum sustainable swimming speed: in a curved path (U_{ms}) are shown as solid diamonds with 95% confidence interval (T-bars) and the fitted curve as a continuous line; and along a straight path (U^s_{ms}) as open circles and the fitted curve as a broken line.

These small but significant differences in body shape between individuals will produce subtle changes in the drag experienced by each fish (Webb, 1974), which may influence their swimming performance. The energy reserves stored in the swimming muscle cells are likely to vary between individuals and the efficiency of the catabolic pathways utilizing these substrates may also vary. A recent study on cod (*Gadus morhua*) demonstrated that swimming endurance was significantly (p = 0.02) affected by condition (K_w), with starved fish swimming for only 30% of the time (and distance) of well-fed fish (Martinez *et al.*, 2003). However, no significant relationship was found between the physical condition (K_w) of the individual fish in this study and their relative performance. Finally, the qualitative description of the swimming behaviour and gaits of fish in this study suggested considerable differences from fish to fish, which may also explain some of the observed individual variability in swimming performance.

The estimates of U_{ms} in haddock obtained from this experiment ranged from 0.38 ± 0.03 m s^{-1} and 3.16 ± 0.02 BL s^{-1} (for a 16.0-cm fish) to 0.62 ± 0.04 m s^{-1} and 1.51 ± 0.07 BL s^{-1} (for a 42.0-cm fish). These values are less than estimates by Chandler (1967), who observed that haddock of 35.2–38.0 cm could swim continuously for 240 min at 0.89 m s^{-1} in 10.5°C water temperature.

However, these estimates were obtained using a flume tunnel for which the key stimulus to swim was an electrified grid downcurrent of the fish. This suggests that the strength of stimuli to swim may have an influence on endurance. When compared to estimates from a comparable methodology, haddock do not perform as well as other gadoids. He and Wardle (1988) estimated U_{ms} of 2.1–2.6 BL s^{-1} (0.74–0.91 m s^{-1}) for 35-cm cod (*Gadus morhua*) and 3.4 BL s^{-1} (0.85 m s^{-1}) for a 25-cm saithe (*Pollachius virens*), based on a maximum endurance time of 200 min.

This study can provide no empirical data on endurance of haddock at prolonged swimming speeds equivalent to the operational speeds of demersal trawls (∼1.0–2.0 m s^{-1}). However, the experiment did demonstrate that fish up to ∼40 cm in length could not sustain a swimming speed of ∼0.9 m s^{-1} for more than 15 min. It is generally assumed that fish entering the main body of the trawl only do so because they are too fatigued to maintain position in the mouth of the net (Wardle, 1993; Engås, 1994). Whether the individual fish is physiologically exhausted, or not, is debatable. This study has demonstrated that seemingly "fatigued" fish may have sufficient energy reserves to undertake short periods of prolonged or burst swimming. However, if it is assumed that a fish is driven to utilize most, if not all, respiratory substrates in its white myotomal muscles during the initial capture phase at the mouth of the
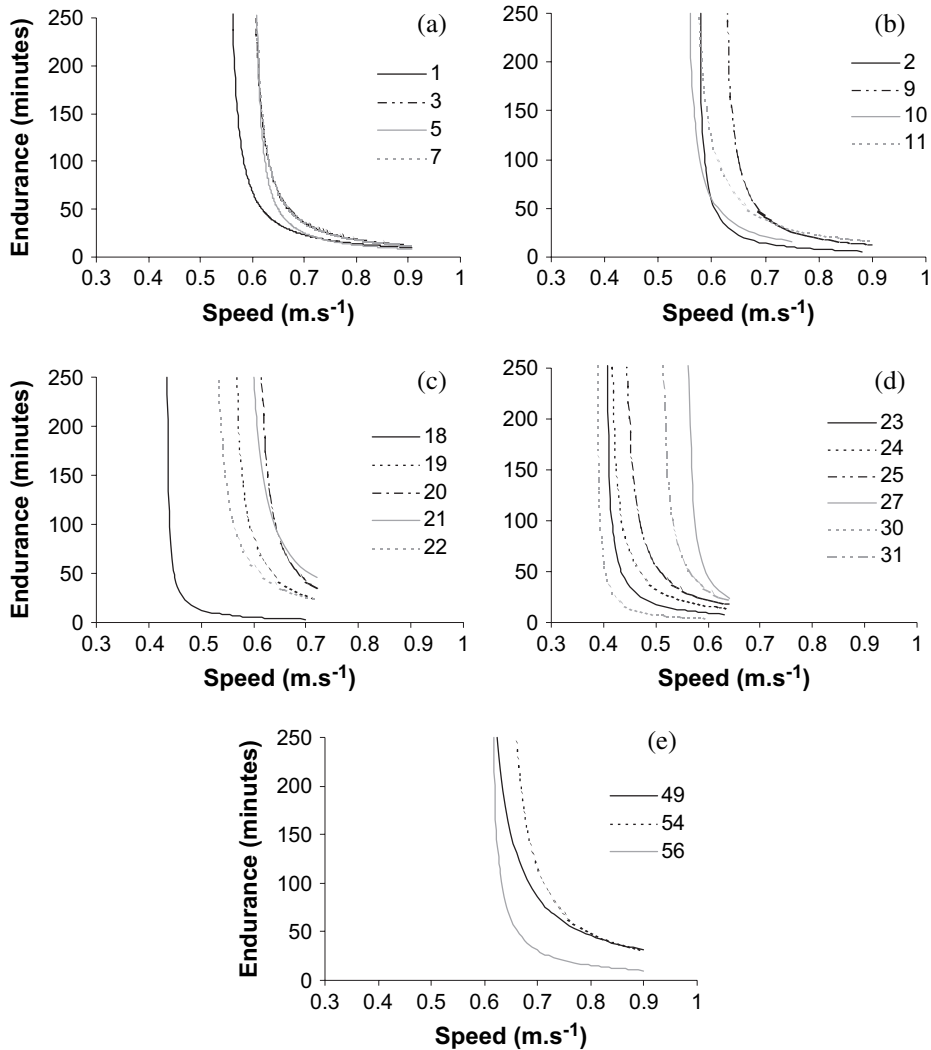
Figure 4. (a–e) The relationship between swimming endurance and absolute speed (m s^{-1}) for individual fish (numbered) within groups of approximately equal length. (a) Group A, mean length 31.2 cm; (b) group B, mean length 34.0 cm; (c) group C, mean length 24.4 cm; (d) group D, mean length 17.2 cm; and (e) group G, mean length 40.6 cm.

net, then once it enters the net it will be dependent upon the power provided by its red myotomal muscles alone. As such, the fish will be limited to swimming at speeds of less than or equal to its maximum sustainable swimming speed (U$_{ms}$). This reduced swimming ability will have consequences for the effectiveness of selective devices that require a positive swimming action from the fish. In this study, the U$_{ms}$^{s} for a 30-cm fish was estimated as ~ 0.62 m s^{-1}. If the water flow past a selective device (e.g. square mesh panels (e.g. Madsen *et al.*, 1999)) was in excess of this, fish of this size and less would be unlikely to generate enough propulsive force to swim against this current and make an effective escape through an open mesh in the netting. A recent study of the selectivity of square mesh panels (Zuur *et al.*, 2001) demonstrated that small

haddock (<30 cm) had a reduced probability of contacting the netting of the square mesh panel, suggesting that this process may be occurring. Clearly, greater consideration must be given to the future design of such selective devices, to ensure that non-target fish are physically capable of making an active escape.

Finally, in this experiment some haddock died after participating in the swimming trials. Post-swimming mortality has been seen in other studies (Black, 1958; Beamish, 1966) and it is likely that these fish died as a result of post-exhaustion physiological stresses (Wood *et al.*, 1983). If this is true, a fish's swimming ability may not only determine its likelihood of capture by a towed fishing gear, but could also influence its survivability even if it escapes. Post-escape mortality in haddock has been

observed (Sangster *et al.*, 1996) and any failure to account for this, or understand its causes, could underestimate fishing mortality in exploited stocks (Breen and Cook, 2002).

Acknowledgements

References

Arnold, G. P. 1974. Rheotropism in fishes. Biology Review, 49: 515−576.

Bainbridge, R. 1960. Swimming and stamina in three fish. Journal of Experimental Biology, 37: 129−153.

Beamish, F. W. H. 1966. Muscular fatigue and mortality in haddock *(Melanogrammus aeglefinus)* caught by otter trawl. Journal of the Fisheries Research Board of Canada, 23: 1507−1521.

Beamish, F. W. H. 1978. Swimming capacity. *In* Fish Physiology, VII: Locomotion, pp. 101−187. Ed. by W. S. Hoar, and D. J. Randall. Academic Press, New York and London. 576 pp.

Bernatchez, L., and Dobson, J. J. 1985. Influence of temperature and current speed on the swimming capacity of Lake Whitefish (*Coregonus clupeaformis*) and Cisco (*C. artedii*). Canadian Journal of Fisheries and Aquatic Sciences, 42: 1522−1529.

Black, E. C. 1958. Hyperactivity as a lethal factor in fish. Journal of the Fisheries Research Board of Canada, 15: 573−586.

Blake, R. W. 1983. Fish Locomotion. Cambridge University Press, Cambridge. 208 pp.

Breen, M., and Cook, R. 2002. Inclusion of discard and escape mortality estimates in stock assessment models and its likely impact on fisheries management. ICES CM 2002/V: 27. 15 pp.

Brett, J. R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada, 23: 1491−1501.

Brett, J. R. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. Journal of the Fisheries Research Board of Canada, 24: 1731−1741.

Brett, J. R. 1982. The swimming speed of adult pink salmon, *Oncorhynchus gorbusca*, at 20°C and a comparison with sockeye salmon, *O. nerka*. Canadian Technical Report of Fisheries and Aquatic Sciences, 1143. 37 pp.

Chandler, R. A. 1967. Swimming endurance of haddock. Fisheries Research Board of Canada, Manuscript Report Series, 930. 14 pp.

Coughlin, D. J. 2002. Aerobic muscle function during steady swimming in fish. Fish and Fisheries, 3: 63−78.

Coull, K. A., Jermyn, A. S., Newton, A. W., Henderson, G. I., and Hall, W. B. 1989. Length/weight relationships for 88 species of fish encountered in the North East Atlantic. Scottish Fisheries Research Report, 43, 1989, 81 pp.

Engås, A. 1994. The effects of trawl performance and behaviour on the catching efficiency of demersal sampling trawls. *In* Marine Fish Behaviour in Capture and Abundance Estimation, pp. 45−65. Ed. by A. Fernö, and S. Olsen. Fishing News Books, Oxford. 221 pp.

Godø, O. R. 1994. Factors affecting the reliability of groundfish abundance estimates from bottom trawl surveys. *In* Marine Fish Behaviour in Capture and Abundance Estimation, pp. 166−195. Ed. by A. Fernö, and S. Olsen. Fishing News Books, Oxford. 221 pp.

He, P., and Wardle, C. S. 1988. Endurance at intermediate swimming speeds of Atlantic mackerel, *Scomber scombrus* L., herring, *Clupea harengus* L., and saithe, *Pollachius virens* L.. Journal of Fish Biology, 33: 255−266.

Hertel, H. 1966. Structure, Form, Function. Reinhold Publishing Company. 251 pp.

McCullagh, P., and Nelder, J. A. 1989. Generalised Linear Models (2nd edn). Chapman and Hall, London. 511 pp.

Madsen, N., Moth-Poulsen, T., Holst, R., and Wileman, D. A. 1999. Selectivity experiments with escape windows in the North Sea Nephrops trawl fishery. Fisheries Research, 42: 167−181.

Martinez, M., Guderley, H., Dutil, J-D., Winger, P., He, P., and Walsh, S. J. 2003. Condition, prolonged swimming performance and muscle metabolic capacities of cod (*Gadus morhua*). Journal of Experimental Biology, 206: 503−511.

Payne, R. W. 1993. Genstat 5 Release 3 Reference Manual. Clarendon Press, Oxford. 796 pp.

Peake, S., Beamish, F. W. H., McKinley, R. S., Katpodis, C., and Scuton, D. A. 1995. Swimming performance of lake sturgeon, *Acipenser fulvescens*. Canadian Technical Report of Fisheries and Aquatic Sciences, 2063. 36 pp.

Sangster, G. I., Lehmann, K. M., and Breen, M. 1996. Commercial fishing experiments to assess the survival of haddock and whiting after escape from four sizes of diamond mesh cod-ends. Fisheries Research, 25: 323−346.

Videler, J. J. 1993. Fish Swimming. Chapman and Hall, London. 260 pp.

Videler, J. J., and Wardle, C. S. 1991. Fish swimming stride by stride: speed limits and endurance. Reviews in Fish Biology and Fisheries, 1: 23−40.

Wardle, C. S. 1993. Fish behaviour and fishing gear. *In* The Behaviour of Teleost Fishes, 2nd edn, pp. 609−641. Ed. by T. J. Pitcher. Chapman and Hall, London. 715 pp.

Webb, P. W. 1974. Hydrodynamics and energetics of fish propulsion. Bulletin of the Fisheries Research Board of Canada, 190. 158 pp.

Webb, P. W. 1994. Exercise performance of fish. Comparative Vertebrate Exercise Physiology: Phyletic Adaptations, Advances in Veterinary Science and Comparative Medicine, 38(B): 1−49.

Winger, P. D., He, P., and Walsh, S. J. 1999. Swimming endurance of American plaice (*Hippoglossoides platessoides*) and its role in fish capture. ICES Journal of Marine Science, 56: 252−265.

Winger, P. D., He, P., and Walsh, S. J. 2000. Factors affecting the swimming endurance and mortality of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 57: 1200−1207.

Wood, C. M., Turner, J. D., and Graham, M. S. 1983. Why do fish die after severe exercise? Journal of Fish Biology, 22: 189−201.

Xu, G., Shirai, T., and Arimoto, T. 1994. Endurance and muscle lactic acid of swimming jack mackerel. Fisheries Science, 60: 657−659.

Zuur, G., Fryer, R. J., Ferro, R. S. T., and Tokai, T. 2001. Modelling the size selectivities of a trawl codend and an associated square mesh panel. ICES Journal of Marine Science, 58: 657−671.