

Swimming speeds of marine fish in relation to fishing gears

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Swimming ability plays a vital role in the survival of fish in terms of catching a prey and escaping from a predator or a fishing gear. Knowledge of how fish swim and how well they can swim is very important in the design and operation of selective and energy-conserving commercial fishing gears, and in fisheries resource assessment through better understanding of selectivity and efficiency of survey trawls. This paper summarizes recent findings of swimming performance in marine fishes and discusses how a change in swimming ability due to biological and environmental conditions and how a change in trawl operation can influence the size selectivity of a trawl. Special attention is paid to commercially important species, including mackerel (*Scomber scombrus*), herring (*Clupea harengus*), cod (*Gadus morhua*), and saithe (*Pollachius virens*).

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Introduction

Many contributions have been made since the 1920s on how, and how well, fish swim (see Beamish, 1978; Videler and Wardle, 1991). However, our understanding of the swimming ability of commercial marine fishes and their swimming behaviour near fishing gears is very limited. Yet knowledge of fish behaviour has become increasingly important in present-day fisheries. Commercial fishing operations have come to such a stage that operators are required only to catch certain species of particular sizes, using specified fishing gears at the specified location and time. Fisheries scientists conducting survey fishing operations use the same fishing gear in a vast area, hoping for a constant and known efficiency and selective performance of the gear over space and time.

Fish swimming speeds have been reviewed by Blaxter (1969), Beamish (1978), and more recently by Videler and Wardle (1991), and underwater observations of fish behaviour near towed trawls by Wardle (1983, 1986, 1989). This paper summarizes recent findings concerning the swimming capacity of commercial marine fishes, combined with those from field observations of fish swimming near fishing gears, to explore the selectivity of a trawl codend and how it is affected by the way fish swim and their swimming ability.

Species mentioned in the text are bluefin tuna (*Thunnus thynnus* L.), cod, or Atlantic cod (*Gadus morhua*

L.), herring (*Clupea harengus* L.), jack mackerel (*Trachurus japonicus* (Temminck and Schlegel)), mackerel, or Atlantic mackerel (*Scomber scombrus* L.), Pacific mackerel (*Scomber japonicus* Houuttuyn), and saithe (*Pollachius virens* (L.)).

Swimming speeds: mackerel as an example

The Atlantic mackerel is by far the most completely studied fish species in respect to swimming performance. Here mackerel is taken as an example to define the swimming speeds of fish. Recorded swimming speeds of mackerel range from a minimum of 0.4 L s^{-1} (body lengths per second, 0.32 m specimen) to a maximum of 18 L s^{-1} (0.31 m specimen). Figure 1 summarizes swimming speeds, endurance, body attack angle, and the use of swimming muscles at different speeds.

The Atlantic mackerel has no swimbladder and is heavier than seawater, therefore it has to swim constantly in order to generate lift to keep itself from sinking. The minimum swimming speed (U_{\min}) of 0.4 L s^{-1} was recorded when the fish was swimming at a body attack angle of 27° (He and Wardle, 1986). Without body tilt, mackerel must swim at a minimum speed of 1 L s^{-1} . The preferred swimming speed (U_p) of mackerel was between 0.9 and 1.2 L s^{-1} when cruising around a 10 m diameter annular tank (He and Wardle, 1988). Mack-

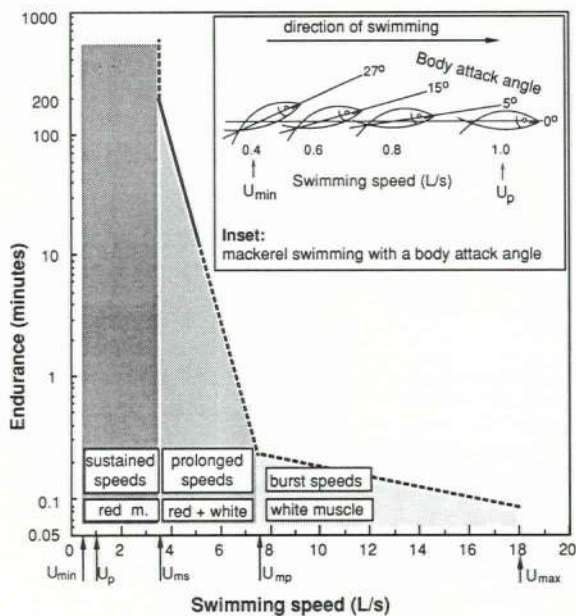


Figure 1. Swimming speeds (in body lengths per second) of the Atlantic mackerel (*Scomber scombrus* L.) from the lowest to the highest value recorded, plotted against endurance. Use of different types of muscles at different speed ranges is indicated. Inset: mackerel swimming with a body attack angle at speeds below U_p . See text for explanation.

erel swim at speeds below U_p only when space is restricted in a laboratory tank (He and Wardle, 1986) or when the light level is very low ($<10^{-6}$ lux) (Glass *et al.*, 1986). Many neutrally buoyant species can stop swimming; their minimum swimming speed is therefore equal to 0.

Mackerel can swim between 1 and 3.5 L s^{-1} indefinitely without leading to exhaustion (He and Wardle, 1988). This speed range is called the sustained swimming speeds, at which mackerel cruise voluntarily in large tanks and at sea, and during migration and feeding. When the swimming speed exceeds 3.5 L s^{-1} , limited endurance leads to exhaustion. This 3.5 L s^{-1} is called the maximum sustained swimming speed (U_{ms}). In practice, U_{ms} is the maximum swimming speed with an endurance equal to or greater than 200 min.

For swimming speeds greater than U_{ms} , the higher the speeds (U), the shorter the endurance (E). In mackerel, the relationship between E (in min) and U (in L s^{-1}) can be expressed in semi-log regression as (He and Wardle, 1988): $\text{Log}E = -0.96U \times 5.45$. The maximum swimming speed involving power from the red muscle may be predicted in the same way as Wardle (1975) did with the white muscle. The fastest red muscle contraction time is about twice that of the white muscle in mackerel (He *et al.*, 1990). These authors predicted that at swimming speeds above 7.5 L s^{-1} , the red muscle will become ineffective as an energy source for swimming, owing to simultaneous contraction of muscle on both sides. This

predicted 7.5 L s^{-1} swimming speed is called the maximum prolonged swimming speed (U_{mp}) and the range of speeds between U_{ms} and U_{mp} is called prolonged swimming speeds. The white muscle as well as the red muscle is used for swimming at the prolonged speeds.

Speeds beyond U_{mp} are called burst speeds, at which only the white muscle effectively contributes to the energy required for swimming. The white muscle operates anaerobically and its energy reserve can be depleted in a matter of seconds at burst speeds. The maximum swimming speed (U_{max}) of mackerel ever recorded is 18 L s^{-1} , which is very close to the predicted U_{max} from white muscle contraction time of 19 L s^{-1} at 12°C (Wardle and He, 1988).

The maximum sustained swimming speed

The maximum sustained swimming speed (U_{ms}) marks the upper limit of the sustained speeds (without leading to exhaustion) and the lower limit of the prolonged speeds (leading to exhaustion). It has been demonstrated by monitoring muscle activities in 0.15 m long jack mackerel that the red muscle only is used at swimming speeds up to U_{ms} of 6.2 L s^{-1} , while the white muscle joins in at speeds beyond U_{ms} (Xu, 1989).

The force generated from a muscle is related to the cross-sectional area of the muscle (Ikai and Fukunaga, 1968). It is thus not surprising that pelagic fish species possessing thick red muscle achieve a higher U_{ms} . For example, herring and saithe each of 0.25 m length have a maximum lateral red muscle cross-sectional area of 0.85

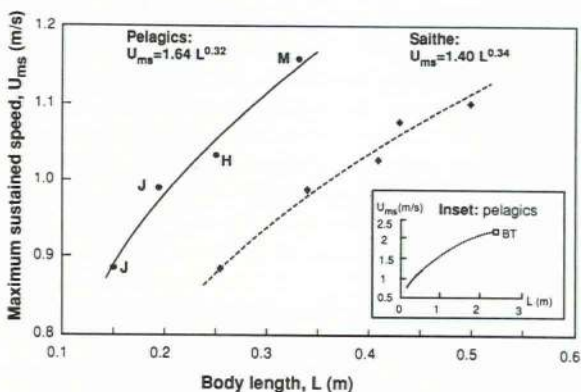


Figure 2. The maximum sustained swimming speed in relation to body length of pelagic species (solid curve) and demersal species (dashed curve). Letter symbols are: M – Atlantic mackerel, *Scomber scombrus*, 11.7°C , H – herring, *Clupea harengus*, 13.5°C (He and Wardle, 1988); and J – jack mackerel, *Trachurus japonicus*, 19°C (Xu, 1989). Solid diamonds: saithe, *Pollachius virens*, 14.4°C (He and Wardle, 1988). Inset: pelagic species; BT – bluetin tuna, *Thunnus thynnus*, of 2.44 m length with a predicted U_{ms} of 2.10 m s^{-1} (see text for explanation).

and 0.55 cm^2 respectively (He, 1986). Likewise, herring has a U_{ms} of 1.06 m s^{-1} compared with 0.89 m s^{-1} for saithe, both at around 14°C .

The maximum sustained swimming speed (U_{ms} , in m s^{-1}) increases with an increase in fish body length (L , in m) in both saithe and small pelagics (mackerel, herring, and jack mackerel) (Fig. 2), but U_{ms} is consistently lower in saithe. Bluefin tuna (pelagic species) can grow to more than 3 m in length. Bluefin tunas in farm cages with a mean length of 2.44 m swam at an average speed of 0.77 L s^{-1} or 1.88 m s^{-1} (Wardle *et al.*, 1989). Extrapolating the length to 2.44 m from the line for pelagic species, the predicted U_{ms} for 2.44 m tuna will be 2.10 m s^{-1} (Fig. 2: inset) or 0.86 L s^{-1} .

Endurance at prolonged swimming speeds

Endurance at prolonged swimming speeds has been measured by using the "fish wheel" (Bainbridge, 1960), swimming flumes (e.g. Beamish, 1966; He, 1991), a stationary annular tank (He and Wardle, 1988), and by observations at sea near fishing gears (Wardle, 1983). He and Wardle (1988) measured swimming speed and endurance of mackerel (see solid line Fig. 1), herring, and saithe in a 10 m diameter annular tank; it is particularly worth noting that these fish were induced to swim through still water by moving a projected visual pattern, imitating fish swimming in the mouth area of a towed trawl. Swimming at the same speed as the towed trawl at the mouth area is believed to be induced by moving netting panels. Measured endurance of commercial marine species is plotted against swimming speed in Figure 3. In all species swimming at prolonged speeds, endurance drops drastically as speed is increased.

Larger fish can swim longer at the same speed in m s^{-1} or they can swim faster at the same endurance. For example, a 0.50 m long saithe can swim for 30 min at 1.25 m s^{-1} , while a 0.25 m saithe can only swim for 2 min at the same speed of 1.25 m s^{-1} or can only swim at 0.95 m s^{-1} for the same endurance of 30 min (Fig. 3c). Pelagic species have a better endurance swimming ability. At 14°C , a herring of 0.25 cm can swim for over 15 min at 1.25 m s^{-1} , while a saithe of the same length can only sustain the same speed for 2 min.

Burst swimming speeds of marine fishes

Burst swimming speeds are difficult to measure, both in the laboratory and at sea. A large tank and a high-frame-rate camera with an accurate timer are essential equipment for recording high-speed movement. But the most difficult task is to make fish swim at their highest possible speed. A $10 \times 5.4 \times 1 \text{ m}$ deep tank and a cine camera capable of filming at a frame rate up to 500 frames per second were used in mackerel burst swimming speed measurements utilizing mackerel escape behaviour when released into the large tank (Wardle and He, 1988). With this arrangement, U_{max} of 18 L s^{-1} or 5.5 m s^{-1} was measured in a 0.31 m long mackerel.

The maximum swimming speed (U_{max}) increases with fish body length (L) and water temperature, and varies among fish species. Figure 4 shows measured U_{max} (in m s^{-1}) of commercial marine fishes plotted against L (in m) with temperature values indicated in the legend when available. Notice that most fish have a U_{max} between 10 and 20 L s^{-1} . U_{max} of those species falling below 10 L s^{-1} , such as saithe and Pacific mackerel, are probably higher than the plotted values. Notice that the swimming speed of herring (HR in Fig. 4) of 4.61 m s^{-1} or 17.1 L

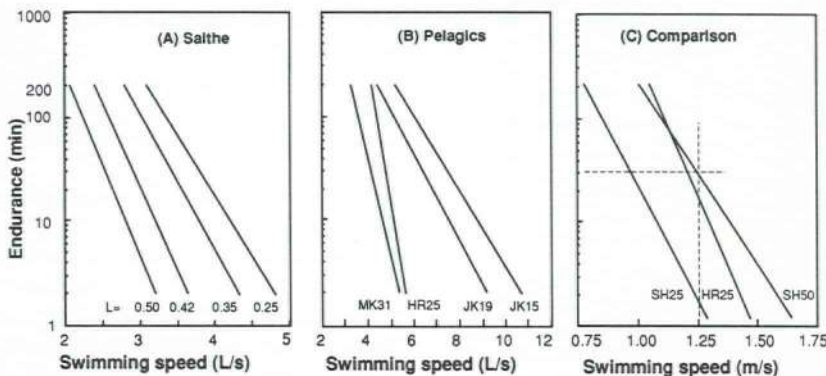


Figure 3. Swimming speed and endurance of marine fishes. (A) Demersal species: saithe, *Pollachius virens*, of different lengths (L , m) at 14.4°C (He and Wardle, 1988). (B) Pelagic species: MK31 – Atlantic mackerel, *Scomber scombrus*, 0.31 m long at 11.7°C , HR25 – herring, *Clupea harengus*, 0.25 m long at 13.5°C (He and Wardle, 1988), JK19 and JK15 – jack mackerel, *Trachurus japonicus*, 0.19 and 0.15 m long at 19°C (Xu, 1989). (C) Comparison of saithe (SH25) and herring (HR25), both 0.25 m long, and comparison of saithe 0.25 m (SH25) and 0.50 m (SH50) long. Dashed lines indicate endurance when swimming at 1.25 m s^{-1} (2.5 kt) and swimming speeds at endurance of 30 min for the three groups of fish. Pelagic species or larger fish have a better endurance swimming capability.

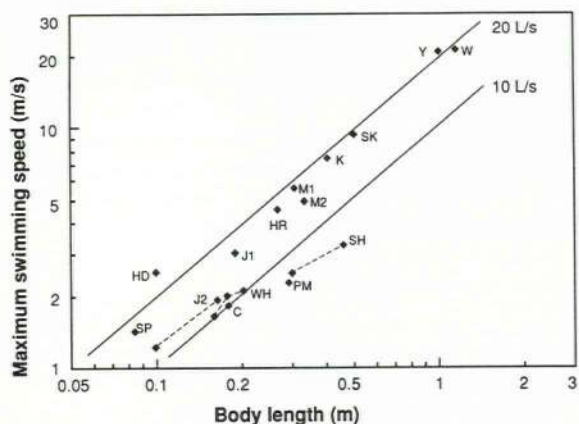


Figure 4. Maximum swimming speeds of marine fishes in relation to body length. Dashed lines link different lengths of the same species. Letter symbols, sources, and temperatures (when available) are: C – cod, *Gadus morhua*, 9.5–12°C (Blaxter and Dickson, 1959); HD – haddock, *Melanogrammus aeglefinus*, 12°C (Wardle, 1975); HR – herring, *Clupea harengus* (Misund, 1989); J1 – jack mackerel, *Trachurus japonicus*, 23°C (Xu, 1989); J2 – jack mackerel, *Trachurus symmetricus* (Hunter and Zweifel, 1971); K – kawakawa, *Euthunnus affinis*, 25°C (cited in Beamish, 1978); M1 – Atlantic mackerel, *Scomber scombrus*, 12°C (Wardle and He, 1988); M2 – Atlantic mackerel, *Scomber scombrus* (Zhou, 1985); PM – Pacific mackerel, *Scomber japonicus* (Hunter and Zweifel, 1971); SH – saithe, *Pollachius virens*, 10.8°C (He, 1986); SK – skipjack tuna, *Katsuwonus pelamis* (cited in Magnuson, 1978); SP – sprat, *Sprattus sprattus*, 12°C (Wardle, 1975); W – wahoo, *Acanthocybium solandrei*, >15°C (Walters and Fierstine, 1966); WH – whiting, *Gadus merlangus*, 9–13°C (Blaxter and Dickson, 1959); Y – yellowfin tuna, *Thunnus albacares* (Walters and Fierstine, 1966).

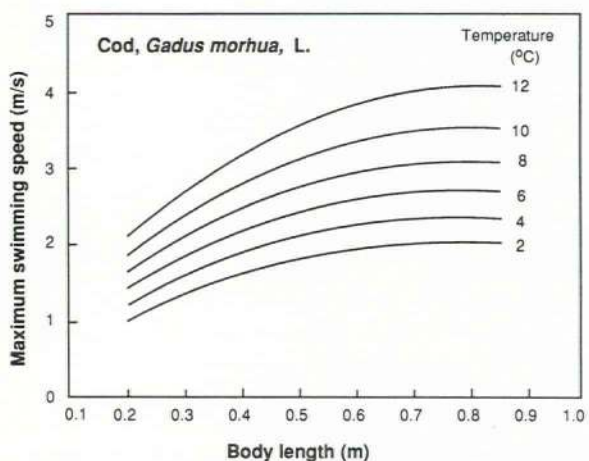


Figure 5. The maximum swimming speed of cod, *Gadus morhua*, in relation to body length and temperature as predicted from the measured muscle contraction time. Drawn from data given in Videler and Wardle (1991) with a stride length of 0.60 L.

s^{-1} is the speed of a herring school during purse seine operations measured by a scanning sonar sampled at 10 s intervals (Misund, 1989).

The maximum swimming speed can be predicted from the contraction time of the white muscle (which limits tail beat frequency, Wardle, 1975) and stride length (SL, distance travelled forward in one complete tail beat). Contraction time does not change among fish species, but varies with body length (Wardle, 1977), temperature (Wardle, 1980), and location of muscle along the body (Wardle, 1985). Stride length is species-specific; larger values are found in species with an efficient caudal fin and a low-drag streamlined body. The value of stride length varies between 0.60 and 1.04 L in marine fishes (Videler and Wardle, 1991). Scombroid fishes like mackerel and tuna have a well-streamlined body and a large caudal fin of high aspect ratio. For example, mackerel (SL=1.0 L, Wardle and He, 1988) will be able to swim 67% faster than cod (SL=0.60 L, Videler and Wardle, 1991) at the same tail beat frequency.

Effect of temperature on the swimming speeds of fish

All fish, except some large scombroids and large sharks, have a body temperature equal to the ambient water temperature which varies in time and space. Temperature has a profound impact on almost all aspects of fish physiology, including swimming performance.

There are no systematic, direct measurements of the maximum swimming speed at different temperatures. But measurements of white muscle contraction time indicate a higher maximum swimming speed in all species at higher temperatures. Figure 5 shows the maximum swimming speed of cod at temperatures between 2 and 12°C calculated from the measured muscle contraction time (Videler and Wardle, 1991). These same authors showed that fish can double their maximum swimming speed with a temperature increase of 10°C, i.e. a Q_{10} of 2. Higher temperature allows a higher maximum tail beat frequency (Wardle, 1980) and a higher power output from the white muscle (Johnston and Salamonski, 1984).

A reduction in temperature reduces swimming speed and endurance (Fig. 6). Typical temperatures for cod on the Newfoundland Grand Banks are between 0 and 5°C. Notice that a reduction in temperature from 5 to 0°C can cause a reduction in swimming speed from 1.05 $m s^{-1}$ to 0.65 $m s^{-1}$ for a swimming endurance of 30 min. Or if a fish has to swim at the same speed of 1 $m s^{-1}$ (e.g. at the mouth of a towed trawl), the fish will be exhausted in 2 min at 0°C compared with 50 min at 5°C.

U_{ms} decreases with a drop in water temperature, especially at lower temperatures (Fig. 7). U_{ms} of cod at 0.8°C is only 0.42 $m s^{-1}$ compared with 0.90 $m s^{-1}$ at 8°C (0.35–0.42 m cod), a reduction of 54%. This decrease of

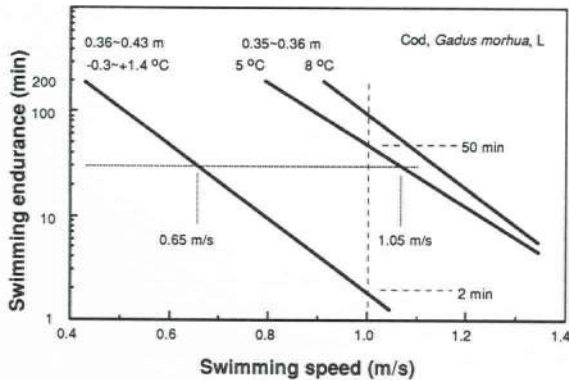


Figure 6. Swimming speed and endurance of cod, *Gadus morhua*, at different water temperatures from -0.3 to 8°C . Dotted lines indicate the swimming speed sustainable from an endurance of 30 min. Dashed lines indicate different endurance swimming at 1 m s^{-1} . Swimming speed and/or endurance decreases as temperature is reduced (redrawn from He, 1991).

U_{ms} in cod is comparable to a decrease in routine activity (by 75%), frequency of opercular movement (by 50%), feeding (by 58%), and growth rate (by 36%) for the same species when temperature is dropped from 8.3 to 0.6°C (Brown *et al.*, 1989), and in the maximum swimming speed (by 45%, see Fig. 5). Bottom and midwater temperature off Newfoundland can be as low as -1.8°C (He and Xu, 1992). Cod were observed by underwater video camera to swim around baited hooks at water temperatures as low as -1.2°C in fishing grounds, though the number of cod observed is very small compared with that at higher temperatures (He and Xu, 1992, unpublished). If the curve in Figure 7 is extended from $+0.8$ to -1.2°C , a predicted U_{ms} will only be 0.14 m s^{-1} (or 0.3 kt) for a 0.35 m long cod.

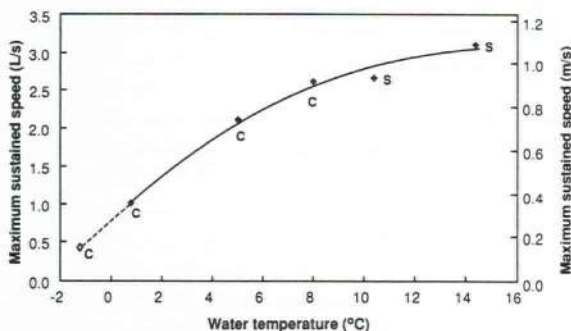


Figure 7. Effect of temperature on the maximum sustained swimming speed of Gadidae 0.34 to 0.36 m long. S – saithe, *Pollachius virens*, from He and Wardle (1988) and C – cod, *Gadus morhua*, from He (1991) and Beamish (1966). Solid symbols are measured data and the open symbol is the predicted value for the lowest temperature of -1.2°C as observed on the fishing grounds (He and Xu, 1992).

Differences in swimming speeds and endurance at different water temperatures influence the herding of fish by sweeps, the ability of fish to keep station with the trawl at the mouth area, and the escape of fish in the codend. All these temperature-related fish–trawl interactions can influence efficiency and selectivity of trawls. This is especially important when the trawl is used as a sampling tool for stock assessment.

Fish swimming and mesh selectivity of trawl codend

Selectivity of otter trawls occurs mainly in three areas: during herding by sweeps (or bridles); during swimming with the trawl at the mouth area; and mesh selection at the codend. All these are related to, among other things, the swimming behaviour and swimming capacity of fish. Herding by sweeps and exhaustion of fish at the mouth area in relation to swimming speed of fish have been discussed by Foster *et al.* (1981), and more recently by Wardle (1983, 1986, 1989). Codend selectivity is defined as the proportion of fish retained in the codend as catch, in relation to the total number of fish arrived at the codend prior to any escapement. Codend mesh size, mesh shape, and codend riggings are believed to affect the size selectivity of the codend (Robertson, 1989). However, the effect of towing speed and swimming ability of fish in relation to size selectivity in the codend has not been investigated. Here a model is developed to explore how the swimming ability of fish affects codend mesh selection.

It is assumed that a fish has escaped from the codend if the fish has swum a distance X_L (shoulder length) so that its shoulder $B1-B1'$ (the position of the maximum body height) moved to $B2-B2'$ in the time period when the mesh moved a distance of Mu_2-H (M is mesh size, u_2 the vertical hanging ratio and H the maximum body height) from the position of $A1-A1'$ to $A2-A2'$ (Fig. 8). Thus, the swimming speed required (U_r) to escape from the codend of a trawl towed at speed U_t is: $U_r = U_t K_x / (Mu_2 / L - K_h)$, where $K_x = X_L / L$, $K_h = H / L$. Whether a fish can escape from the codend is determined by the swimming speed required and the swimming speed achievable. As escape through the mesh occurs in a short time period, the maximum swimming speed is considered. From the above formulae, it can be seen that U_r is related to the size of mesh, fish length and body geometry (K_x and K_h), and the towing speed.

Swimming speeds required to escape from the codends of different mesh sizes towed at 3.5 knots (Fig. 9a) and from 130 mm mesh towed at different speeds (Fig. 9b) are calculated from the above formulae for cod (assuming $K_x=0.3$, and $K_h=0.2$). Plotted in the same graphs are the maximum swimming speed of cod at three different water temperatures from Figure 5. Those combinations of speed, length, and mesh size above the

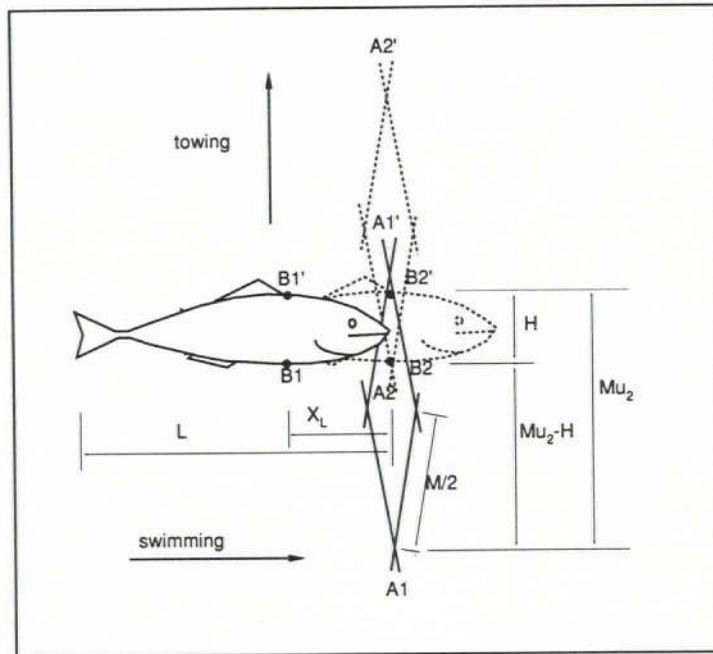


Figure 8. Schematic drawing of fish escapement through a codend mesh. Solid drawing is at time 1 and dashed drawing at time 2. B1-B1' (or B2-B2') is the shoulder position. X_L is the shoulder length and H the maximum body height. M is the mesh size ($M/2$ mesh bar length) and u_2 vertical hanging ratio. The swimming speed required for a fish to escape from the mesh is determined by whether the shoulder B1-B1' can move to B2-B2' just before the mesh moves from A1-A1' to A2-A2'.

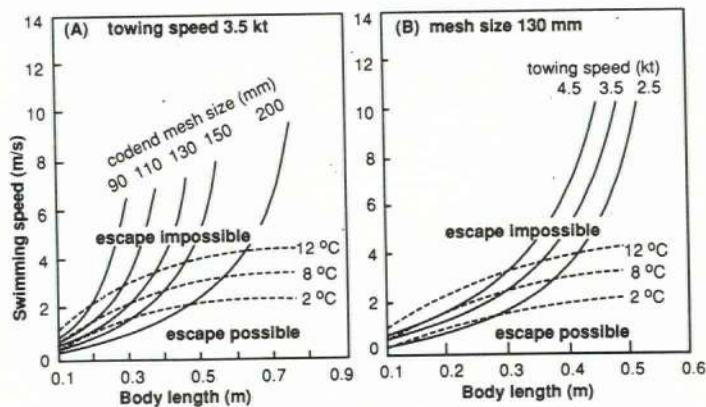


Figure 9. Swimming speed required (solid curves) to escape through the codend and the maximum swimming speed (dashed lines, from Fig. 5) of cod at different temperatures. (A) Different codend mesh sizes towed at 1.80 m s^{-1} (3.5 kt); (B) 130 mm codend mesh towed at different speeds. Those combinations of speed, length, and mesh size above the maximum speed line at a particular temperature indicate the area where escape is impossible.

maximum speed line at a particular temperature indicate the area where escape is impossible, and conversely. It can be seen that larger mesh sizes and slower towing speeds allow a wider range of fish to escape from the codend. Higher temperature increases swimming speed of fish and facilitates escape through codend meshes. For example, at 8°C , a 0.55 m cod will be able to escape a 200 mm mesh, while only fish equal to or less than 0.20 m

can escape a 110 mm mesh when towed at 3.5 knots (Fig. 9a). Slower towing speeds will allow larger fish to escape. At 8°C , a 0.35 m fish will be able to escape a 130 mm mesh towed at 2.5 knots, but only fish below 0.20 m can escape the same sized mesh towed at 4.5 knots (Fig. 9b). In the case of cod, when water temperature drops to around 0°C , almost no fish will be able to escape actively through any practical codend meshes.

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