

Quantitative Analysis of the Swimming Movements of Flatfish Reacting to the Ground Gear of Bottom Trawls

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Two typical responses have been documented for flatfish when they encounter the ground gear of bottom trawls: herding response and falling back response. These two responses were analyzed from video recordings of fish and were characterized by time sequences for four parameters: swimming speed, angular velocity, acceleration, and distance between the fish and the ground gear. When flatfish displayed the falling-back response, absolute values of the three swimming parameters and their deviations were significantly higher than those during the herding response. However, the swimming parameters were not dependent on the distance between the flatfish and the ground gear, regardless of which response occurred. The dominant periods for most of the movement parameters ranged from 2.0 to 3.7 s, except that no periodicity was observed for swimming speed or angular velocity during the falling-back response. However, variations in the four parameters during the falling -back response revealed greater irregularity in periodicity and higher amplitudes. This complex behavior is best described as a chaos phenomenon and is discussed as the building block for a model predicting the responses of flatfish to ground gear as part of the general understanding of the fish capture process.

Key words: Flatfish, Herding response, Falling -back response, Bottom trawl, Ground gear

Introduction

Underwater observations of flatfish behavior in relation to towed fishing gear (Hemmings, 1969; Main and Sangster, 1981; Wardle, 1983; Walsh and Hickey, 1993) have revealed that flatfish tend to swim relatively short distances once they have been stimulated to move; the fish are effectively herded by the bridles of the net and are driven towards the center of the ground rope bight. The flatfish react by swimming away from the gear at right angles whenever they are approached or touched by the ground ropes or bridles. Through repeated stimulus and response, the fish are progressively herded towards the mouth of the net, and in this zigzagging fashion, they are eventually arrived at the center of the ground rope.

Individual flatfish can maintain their position and match their swimming speed to the towing speed of the net while at the net mouth, showing an optomotor response, and generally remain close to the seabed. Field observations during trawl operations (Wardle, 1993) have revealed that the duration of optomotor response is no longer than several minutes. Most of the time, individual fish show erratic swimming responses involving irregular changes in their relative position and unpredictable movements (Kim and Wardle, 2003). Two alternative behaviour patterns involving these erratic movements in relation to the bridle or ground gear of towed fishing gear can be divided into two behaviours, defined as either the herding response or the escape response (i.e., falling

The fish will then typically rise over the ground gear and drop into the lower net panel or sometimes fall back under the bobbins (Glass and Wardle, 1989). The endurance during which individual fish can continue swimming ahead o the ground gear is dependent on fish size, temperature, and towing speed. However, there has been no quantitative analysis performed on the movements of flatfish in the trawl mouth, whether during herding or escapement, in relation to either the bridle or the ground gear (Bublitz, 1996; Somerton and Munro, 2001).

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back over the bridle or ground gear), and relating these two behaviors to towing time can provide an estimate of the herding or capture efficiency of the gear. Within this context, observations of these two behaviours of flatfish in trawl mouth were selected and the movement components were analyzed over time from field observations of bottom trawls.

Materials and Methods

The reactions of flatfish in relation to the bobbin ground gear of bottom trawls was analyzed from video tapes recorded by the Fisheries Research Services (FRS) Marine Laboratory, Aberdeen, UK, between 1980 and 1983. The recordings were made using a Hydroproducts RCH TC-125 SIT camera (minimum light 0.005 lx; angle of view: diagonal 46°, horizontal 38°, and vertical 25° with a 12.5-mm lens). The camera was either carried in a scuba divercontrolled, towed underwater vehicle (TUVII) or in a remotely controlled towed vehicle (RCTV; Main and Sangster, 1981; 1982b). All recordings were made using only natural daylight.

The swimming movements of flatfish were analyzed from recordings when the camera position and image clarity allowed parameter measurements. The analyzed recordings were as follows: nine scenes from FRV 'Mara' with a BT124Q trawl from 7-16 July 1980; two scenes from FRV 'Orcades' with a BT142 trawl from 26 May-2 June 1981; 38 scenes from FRV 'Clupea' with a BT130C trawl from 16 July-2 August 1982; and 19 scenes from FRV 'Clupea' with a BT130C trawl from 14 July-3 August 1983. The ground gear of the BT124Q (Main and Sangster, 1981) was constructed with 380-mm rubber bobbins (7.3 m), 90-mm rubber discs (3.05 m \times 2), and 12-mm alloy chains (6.25 m×2). The ground gear of the BT142 contained 75-mm rubber discs (11.22 m×3). The BT130C ground gear contained 450-mm double rubber bobbins (3.05 m×2), 150-mm rubber discs (6.85 m×2), and 16-mm alloy chains (7.5 m×2; Gal-braith, 1983). The nets were towed at 1.5 m/s (3 knots), and the wing end spreads were estimated as 8.5 m for the BT124Q, 10.3 m for the BT142, and 11.0 m for the BT130C.

The 68 scenes of flatfish reactions were analyzed frame by frame using the computer image -processing methods described by Kim and Wardle (2003). The accuracies of the real fish positions were estimated as ±1 cm per pixel from the Image Grabber Board (DT3851a-8, Data Translation Inc.; resolution was 512×512 pixels). Two distinct reactions were observed from the flatfish in the trawl mouth, which

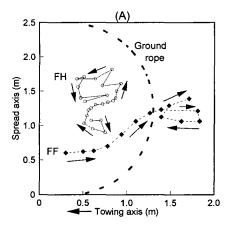
could be described as being herded in front of the ground gear (herding response) or falling back over the ground gear (falling-back response). For the faster moving falling-back response, the recordings of 36 flatfish were sampled for 162 s each, with frame intervals between 0.2 and 0.4 s. For the more stable herding responses involving slower movements or an optomotor response, the recordings of 32 flat-fish were sampled for 356 s each, with frame intervals between 0.5 and 1.0 s. The main species of flatfish observed were plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), and lemon sole (*Microstomus kitt*) with estimated body lengths of 20-30 cm (Main and Sangster, 1981).

The relative horizontal geometry of an individual's position was represented in relation to the trawl mouth, with the X-axis representing the towing direction and the Y-axis the spreading direction. The trawl geometry and net opening of the BT130C North Sea bottom trawl was measured during fishing operations using sonar (SIMRAD 300) mounted on the RCTV. For the other trawl gears, measured net openings during operations were obtained from published reports (Main and Sangster, 1982a; b).

In these field observations of the fish in relation to trawl, only one video camera was used, although the viewing positions and viewing directions of the camera changed. Therefore, known dimensions of reference objects, such as sphere bobbins, and the geometry of the ground gear were used to scale images and define horizontal position. The relative X-Z coordinates, which defined the position of individual fish, could then be calculated using the method of Kim and Wardle (2003). The swimming speed, acceleration, angular velocity, and the nearest distance to ground gear were also calculated in the same way as described by Kim and Wardle (2003). In addition, the time series analysis was carried out by a Fast Fourier Transform (FFT) algorithm using MATLAB software.

Results

While in front of the ground gear, most flatfish maintained their position with a steady swimming speed and head direction, in the so called optomotor response. However, two other erratic or panic behaviors were also observed and analyzed in this study, i.e., the herding response and the falling-back response. Examples of these two behavior patterns are shown in Fig. 1. An example of the herding response is shown by the swimming track of a flatfish (FH) in Fig. 1. The fish initially swam forward,



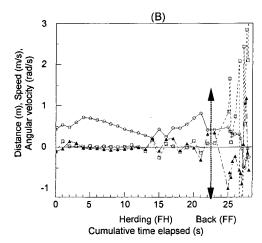


Fig. 1. Examples of the relative positions of individual flatfish (A) and the movement components (B) over time in the herding response (FH; time between each position is 1 s) and the falling-back response (FF; time between each position is 0.3 s). In (B), the open squares represent angular velocity, the filled triangles show relative swimming speed, and the open circles represent distance between the snout of the fish and the ground gear.

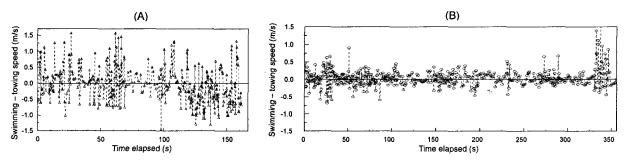


Fig. 2. Relative swimming speeds (swimming speed minus towing speed) of flatfish over time for 36 fish that displayed the falling-back response (A) and 32 fish that exhibited the herding response (B).

toward the front of the ground gear bight, and then turned and swam toward the back of the net. The fish continued swimming, creating a zigzagging path while being herded in front of the ground gear. The second fish track (FF in Fig. 1) shows the movements in the falling-back response. Here, the fish swam from the front of the ground gear toward the rear, rose up, dropped back down over the ground gear, moved just above the bottom panel of the net, and gradually dropped back down. The relative positions of the fish over time were analyzed; the estimated movement components such as relative swimming speed (swimming speed minus towing speed), angular velocity (i.e., changes in swimming direction), and the nearest distance to ground gear for both the herding and falling -back behavior patterns are shown in Fig. 1(B).

The relative swimming speeds of flatfish over time are shown in Fig. 2; swimming speeds were measured

for 36 individuals that performed the falling-back response (A) and 32 individuals that showed the herding response (B). The mean relative swimming speed ± standard deviation (S.D.) of flatfish was -0.05 ± 0.55 m/s (i.e., the absolute swimming speed was 1.45±0.55 m/s) during the falling-back response (n=413 measurements) and 0.04 ± 0.24 m/s (i.e., the absolute swimming speed was 1.54±0.24 m/s) during the herding response (n=565). The swimming speeds for both behavioral groups showed non-normal distributions. A negative value for the relative swimming speed indicates a speed slower than the towing speed of the ground gear and an S.D. greater than the mean value indicates a higher variation. Consequently, the relative swimming speeds were significantly different between the herding and falling -back responses (Student's t-test or variance F-test in summarized Table 1).

The angular velocities of flatfish over time are

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Parameter	Behavior	Mean \pm S.D.	X ² -test	Period	t-test & F-test
Relative swimming speed (m/s)	Herding	0.040 ± 0.236	52.89	3.44	t = -16.87* (p<0.001)
	Falling back	-0.053 ± 0.557	10.26	N/A	F = 284.73* (p<0.001)
Angular velocity (rad/s)	Herding	-0.008 ± 0.425	198.88	2.99	t = -11.04* (p<0.001)
	Falling back	0.848 ± 3.368	399.07*	N/A	F = 121.90* (p<0.001)
Acceleration of swimming speed (m/s ²)	Herding	0.012 ± 0.617	276.70	2.05	t = -11.77* (p<0.001)
	Falling back	-0.111 ± 2.071	144.04	3.65	F = 138.49* (p<0.001)
Acceleration of angular velocity (rad/s²)	Herding	0.048 ± 1.407	364.57*	2.99	t = -11.77* (p<0.001)
	Falling back	1.739 ± 16.184	417.74*	2.03	F = 138.57* (p<0.001)

Table 1. Results of statistical comparisons between the herding (n=514 measurements) and the falling -back responses (n=413) of flatfish in reaction to ground gear

^{*}indicates statistically significant values.

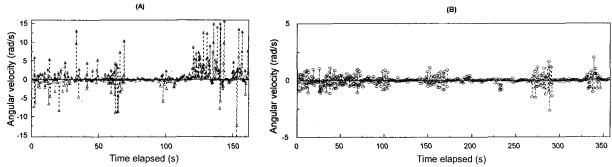


Fig. 3. Angular velocities of flatfish over time. Measurements were taken for 36 fish that showed the falling-back response (A) (n=413 measurements) and 32 fish that showed the herding response (B) (n=565).

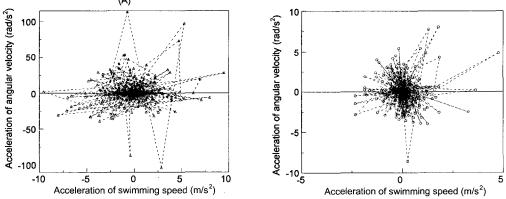


Fig. 4. Acceleration in swimming speed versus acceleration in angular velocity during both the falling-back response (A) and the herding response (B) of flatfish.

shown in Fig. 3. Angular velocities were recorded for 36 fish that exhibited the falling -back response (A) (n=413; measurements were taken throughout a 162-s period) and for 32 fish that displayed the herding response (B) (n=565; measurements were taken throughout a 356-s period). Positive values of angular velocity represent right (clockwise) turns by fish, and negative values represent left (counter-clockwise) turns. The mean angular velocity during the falling-back response $(0.85\pm3.37 \text{ rad/s})$ was significantly higher than during the herding response $(-0.01\pm0.43 \text{ rad/s})$ by Student's t-test and variance F-test). The

frequency distribution of angular velocities during the falling -back response followed a normal distribution, while the frequency distribution during the herding response was non-normal (Chisquare test; Table 1).

The relationship between the acceleration in swimming speed and the acceleration in angular velocity over time is shown in Fig. 4 for both the falling -back response (A) and the herding response (B). Values close to zero in Fig. 4 indicate that the fish is showing the optomotor response; swimming speed is stable and close to the towing speed of the net and the fish is maintaining a constant swimming

direction that is parallel to the towing direction. The mean acceleration of the relative swimming speed during the falling-back response was -0.11 ± 2.07 m/s², compared to 0.01 ± 0.62 m/s² during the herding response. The mean acceleration of the angular velocity was 1.74±16.18 rad/s² during the falling-back response and 0.05±1.41 rad/s² during the herding response. The frequency distributions of acceleration in angular velocity for both behavioral responses were normal, while the distributions of acceleration in relative swimming speed for behavioral responses were non-normal, as shown in Table 1. Both the acceleration in swimming speed and the acceleration in angular velocity were significantly higher during the falling-back response than during the herding response, a pattern consistent with the results for relative swimming speed and angular velocity.

The relationships between the nearest distance from a flatfish to the ground gear and relative swimming speed and angular velocity are shown in Figs. 5 and 6, repsectively. The frequency distribution of the distance between the fish and the ground gear during the herding response was relatively concentrated between 0 and 1.5 m, while the same distribution was dispersed between -1 and 2.5 m for the falling-back response. However, the correlation coefficients for the four plots were very low (p<0.1), and there were no significant relationships between the distance to the ground gear and either the relative swiming speed or the angular velocity during either falling back response or herding response.

The periodicity spectra based on time series analyses (FFT method of MATLAB) for relative swimming speed during the falling-back response and the herding response are shown in Fig. 7. The period distribution from the given time series data of relative swimming speed during the falling -back response of flatfish (Fig. 7A) showed no dominant period and had a wide spectrum. Similarly, the period distribution of herding flatfish (Fig. 7B) revealed a wide spectrum, although there was a dominant period when the maximum spectrum was 3.5 s.

The periodicity spectra for acceleration of relative swimming speed during the falling -back response

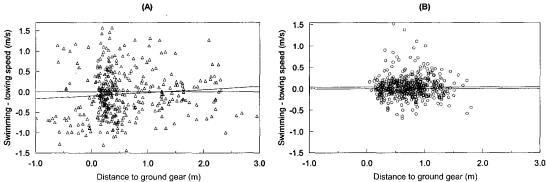


Fig. 5. Nearest distance from the fish to the ground gear versus relative swimming speed for the falling-back response (A) and the herding response (B) of flatfish.

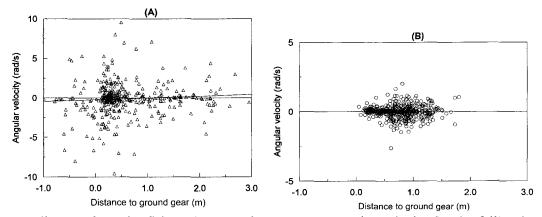


Fig. 6. Nearest distance from the fish to the ground gear versus angular velocity for the falling-back response (A) and the herding response (B) of flatfish.

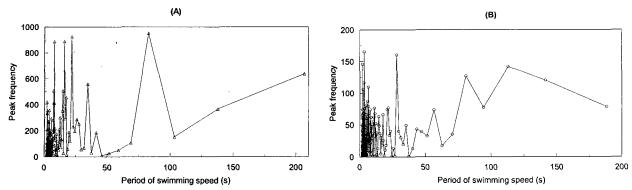


Fig. 7. Periodicity spectrum based on time series analysis for the relative swimming speed of flatfish during the falling-back response (A) and the herding response (B).

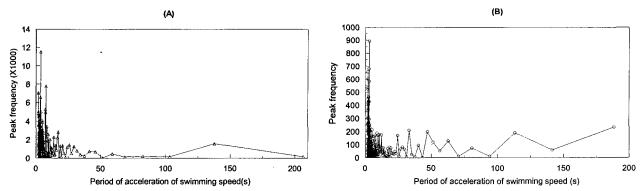


Fig. 8. Periodicity spectrum by time series analysis for the acceleration of relative swimming speed of flatfish during the falling-back response (A) and the herding response (B). The dominant period for acceleration of relative swimming speed was 3.7 s during falling back and 2.1 s during herding.

(with a dominant period of 3.7 s) and during the herding response (with a dominant period of 2.1 s) are shown in Fig. 8 and summarized in Table 1. However, the periodicity of movement parameters, such as relative swimming speed, angular velocity, and their accelerations, showed several peaks representing several dominant periods with irregular variations.

Discussion

Flatfish swimming exhibits complex and chaotic characteristics when broken down into relative swimming speed, angular velocity, accelerations, and the nearest distance to ground gear, during either the falling-back or herding responses elicited by the ground gear of trawls. The characteristics of these flatfish movements are very similar to those of haddock during the same trawl-induced herding and falling-back responses (Kim and Wardle, 2003).

The range in variation of relative swimming speed for flatfish during the erratic falling-back response

was ± 1.5 m/s, comparable to the variation in the relative swimming speed of haddock. The variation range of angular velocity for flatfish during the erratic falling -back response was ±15 rad/s, which was higher than during the herding response. We found no relationship between the nearest distance to the ground gear and relative swimming speed or angular velocity, which is also consistent with haddock reactions (Kim and Wardle, 2003). The maximum swiming speed for flatfish at the trawl mouth was 3 m/s (relative swimming speed 1.5 m/s plus towing speed 1.5 m/s), which was estimated to be 10 body lengths (BL)/s for a flatfish 30 cm long, while the burst speed for 14-cm flatfish was reported to be 12 BL/s (Webb, 1981). The maximum angular velocity of flatfish was 15 rad/s; this means that flatfish can switch from facing forward to facing backwards in 0.2 s ($180^{\circ} = \pi$ rad for 0.2 s=15.7 rad/s). This maximum value for angular velocity is a useful metric to express the limit for relative changes in fish tracks during fish captures (Kim and Wardle, 2003).

The ranges of acceleration in relative swiming speed and angular velocity during the falling-back response were $\pm 10 \text{ m/s}^2$ and $\pm 100 \text{ rad/s}^2$, respectively, which were higher than during the herding response. These values for flatfish are below or equal to the measured range of the fast startle response of fish (Eaton et al., 1977). The dominant period of maximum peaks in the spectrum of movement components for flatfish in front of ground gear ranged from 2 to 3.7 s, with the exception of relative swimming speed and angular velocity during the falling-back response. However, there were several peaks that created a dominant period during the periodicity analysis, which represent irregular changes in swimming movements. Therefore, even in the stable optomotor response of flatfish swimming, the movement parameters can be varied alternatively within a certain period of time. Furthermore, during erratic panic responses, the movement parameters may also vary irregularly with a complex periodicity, as in other chaotic phenomena, but they do not seem to vary randomly.

The distribution of the distance to the ground gear during the herding response of flatfish is concentrated between 0 and 1.5 m, whereas it is widely scattered between ± 1 m, when above the ground rope, and 2.5 m, when ahead of the ground rope, during the fallingback response, with a peak mode near the ground rope 0-0.5 m as observed by Main and Sangster (1981). Bublitz (1996) observed two distinct behavior patterns for flatfish that were described as rapid escape and slow avoidance behaviors. These two behaviors can be employed when the fish fall back over the ground gear and enter the trawl mouth. No relationship was found between body length and herding time, but the entry sequences between these two behavior patterns were found to depend on distance. However, our study focused on measuring the variations of movement components during the falling-back behavior as precisely as possible, with short time intervals, and included no such division within this behavior pattern.

The endurances during which flatfish can remain ahead of the net, before falling back into the trawl mouth, is no more than 60 s at a towing speed of 1.5 m/s (Main and Sangster, 1981; Winger et al., 1999). Generally, flatfish rise up and fall back over the ground rope when they reach a fatigued state (Wardle, 1983). The swimming stamina varies with swimming speeds above the maximum sustainable swiming speed (Videler and Wardle, 1991) and can be predicted for flatfish of different lengths using a model

of the swimming limits (Kim and Wardle, 1997). Therefore, the proportion of fish entering the trawl (Bublitz, 1996; Winger et al., 2004) or fishing efficiency (Fuwa, 1989; Tanaka et al., 1991; Ramm and Xiao, 1995; Somerton and Munro, 2001; Weinberg et al., 2002) can be affected by swimming performance of individual flatfish and distributions of flatfish (Gibson, 1997), given fishing conditions and the responses of flatfish during decision-making (Lemke and Ryer, 2006).

The reactions of flatfish in the trawl mouth show a complex combination of swimming movements. At one moment a fish might employ an optomotor response and then begin an erratic response, or switch between the herding and falling-back responses. In any particular situation, these choices reflect a combination of the details of the stimulus and the specific abilities of each individual. The stimuli from the fishing gear can be predicted using parameters such as light level, visibility range, and visual contrast (Kim and Wardle, 1998) and then related to the visual sensitivity of the fish eye, as modeled by Kim (1998), and water flow (Kim, 1997). Flatfish endurance through changing swimming speed can be estimated by a model of swimming ability limits (Kim and Wardle, 1997).

The decision-making process that leads to displaying either the herding or falling -back responses of flatfish has been depicted in a summary diagram of alternative reactions of fish in the mouth of trawl (Kim and Wardle, 2003). Therefore, our results indicate that movement parameters can be used to define the characteristics of two key behavior patterns in the response of flatfish to ground gear. Furthermore, a predictive model for the response of flatfish in the mouth of trawls could be established and improved by the application of some form of chaos theory and neural networks based on a previous model by Kim and Wardle (2005).

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References

Bublitz, C.G. 1996. Quantitative evaluation of flatfish behaviour during capture by trawl gear. Fish. Res., 25,

- 293-304.
- Eaton, R.C., R.A. Bombardierii and D.L. Meyer. 1977. The Mauthner initiated startle responses in teleost fish. J. Exp. Biol., 66, 65-81.
- Fuwa, S. 1989. Fish herding model by ground ropes considering reaction of fish. Nippon Suisan Gakkaishi, 55, 1767-1771.
- Galbraith, R.D. 1983. The Marine Laboratory fourpanel trawl. Scot. Fish. Info. Pamphlet, 8, 1-21.
- Gibson, R.N. 1997. Behaviour and the distribution of flatfishes. J. Sea Res., 37, 241-256.
- Glass, C.W. and C.S. Wardle. 1989. Comparison of the reactions of fish to a trawl gear, at high and low light intensities. Fish. Res., 23, 165-174.
- Hemmings, C.C. 1969. Observations on the behaviour of fish during capture by the Danish seine nets, and their relation to herding by trawl bridles. Proceedings of the FAO Conference, Bergen, 19-27 Oct. 1967. FAO Fish. Reports, 62, 645-655.
- Kim, Y-H. 1997. Modelling relative water flow and its sensitivity of fish in a towed fishing gear. Bull. Kor. Soc. Fish. Tech., 33, 226-233.
- Kim, Y-H. 1998. Modelling on contrast threshold and minimum resolvable angle of fish vision. Bull. Kor. Soc. Fish. Tech., 33, 43-51.
- Kim, Y.H. and C.S. Wardle. 1997. Modelling of swimming ability limits for marine fish. J. Kor. Fish. Soc., 30, 929-935.
- Kim, Y-H. and C.S. Wardle. 1998. Modelling the visual stimulus of towed fishing gear. Fish. Res., 34, 165-177.
- Kim, Y-H. and C.S. Wardle. 2003. Optomotor response and erratic response: quantitative analysis of fish reaction to towed fishing gears. Fish. Res., 60, 455-470
- Kim, Y.H. and C.S. Wardle. 2005. Basic modelling of fish behaviour in a towed trawl based on chaos in decision-making. Fish. Res., 73, 217-229.
- Lemke, J.L. and C.H. Ryer. 2006. Risk sensitivity in three juvenile (age-0) flatfish species: does estuarine dependence promote risk prone behavior? J. Exp. Mar. Biol. Ecol., (in press).
- Main, J. and G.I. Sangster. 1981. A study of the fish capture process in a bottom trawl by direct observation from a towed underwater vehicle. Scot. Fish. Res. Rep., 23, 1-23.

- Main, J. and G.I. Sangster. 1982a. A study of separating fish from *Nephrops norvegicus* L in a bottom trawl. Scot. Fish. Res. Rep., 24, 1-8.
- Main, J. and G.I. Sangster. 1982b. A study of a multi-level bottom trawl for species separation using direct observation techniques. Scot. Fish. Res. Rep., 26, 1-17.
- Ramm and Y. Xiao. 1995. Herding in groundfish and effective pathwidth of trawls. Fish. Res., 24, 243-259.
- Somerton, D.A. and P. Munro. 2001. Bridle efficiency of a survey trawl for flatfish. Fish. Bull., 99, 61-65.
- Tanaka, E., K. Matuda and N. Hirayama. 1991. A simulation model of gear efficiencies of trawlers for flatfish. Nippon Suisan Gakkaishi, 57, 1019-1028.
- Walsh, S.J. and W.M. Hickey. 1993. Behavioural reactions of demersal fish to bottom trawls at various light conditions. In: Fish behaviour in relation to fishing operations. Wardle, C.S. and C.E. Hollingworth, Eds. Proc. ICES Marine Science Symposia, 11-13 June 1993, Bergen, Norway, Vol. 196, 68-76.
- Wardle, C.S. 1983. Fish reaction to towed fishing gears. In: Experimental Biology at Sea. Macdonald A.G. and I.G. Priede, Eds. Academic Press. London, 167-196.
- Wardle, C.S. 1993. Fish behaviour and fishing gear. In: Behaviour of Teleost Fishes (2nd Edition). Pitcher, T.J., Ed. Chapman & Hall., London, 609-644.
- Webb, P.W. 1981. The effect of the bottom on the fast start of flatfish (*Citharichthys stigmaeus*). Fish. Bull., 79, 271-276.
- Weinberg, K.L., D.A. Somerton and P.T. Munro. 2002. The effect of trawl speed on the footrope capture efficiency of a survey trawl. Fish. Res., 58, 303-313.
- Winger, P.D., P. He and S.J. Walsh. 1999. Swimming endurance of American plaice (*Hippolossoides platessoides*) and its role in fish capture. ICES J. Mar. Sci., 56, 252-265.
- Winger, P.D., S.J. Stephen, P. He and J.A. Brown. 2004. Simulating trawl herding in flatfish: the role of fish length in behaviour and swimming characteristics. ICES J. Mar. Sci., 61, 1179-1185.
- Videler, J.J. and C.S. Wardle. 1991. Fish swimming stride by stride: speed limits and endurance. Rev. Fish Biol. Fish., 1, 23-40.

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