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Research Article

Effect of Temperature Change on Maximum Swimming Speed of Whiting, *Merlangius merlangus* (Linnaeus, 1758)

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Abstract: Seasonal changes in sea temperature levels affect the swimming performance of fish. This study investigates if a change of 5°C from 7 to 12°C in water temperature has a significant effect on the maximum swimming performance of whiting, *Merlangius merlangus*, which is one of the most common species caught in the bottom trawl fisheries of the North Sea. The effect of this seasonal change on swimming performance was shown by two experiments. A temperature increase from 7°C to 12°C was shown to cause a decrease in the minimum twitch contraction time of the lateral muscle, when stimulated by an electric pulse, from 45.8ms to 33.9ms. This gives a maximum tail beat frequency of 10.9Hz at 7°C rising to 14.7Hz at 12°C.

In the second set of experiments, the escape response of fish to sound stimuli at these two temperatures was investigated. The Mauthner Escape Reflexes of the fish were found to be significantly slower at 7°C than at 12°C. Mean escape latency at 12°C (27.6) was significantly shorter than that at 7°C (34.8) (t test, $P< 0.001$). The mean value of the time taken to complete stage 1 at 12°C (45.6ms) was significantly faster than that at 7°C (57.7ms) (t test, $P< 0.001$). Similarly, the mean value of the time taken to complete stage 2 at 12°C (119.9ms) was significantly faster than that at 7°C (154.3ms) (t test, $P< 0.05$). The general underlying physiological effect of a temperature increase of 10°C was to almost double the speed of fish maximum swimming ability ($Q_{10°C}$ =1.81). The results of these experiments have shown that, due to low water temperature, the maximum swimming speed of whiting in late winter and spring is lower than that in late summer and autumn.

Key Words: *Merlangius merlangus*, temperature effect, muscle contraction, escape speed.

Sıcaklık Değişiminin Kuzey Denizi Mezgit Balığı (*Merlangius merlangus* (Linnaeus, 1758))'nın En Yüksek Yüzme Hızına Etkisi

Özet: Deniz suyu sıcaklığındaki mevsimsel değişiklikler, balıkların yüzme performanslarını etkilemektedir. Bu çalışmada su sıcaklığında 7°C ile 12°C arasındaki 5°C lik farkın, Kuzey Denizi dip trolü avcılığında en yaygın yakalanan türlerden biri olan, *Merlangius merlangus*'un maksimum yüzme performansına belirgin bir etkisi olup olmadığı araştırılmıştır. Bu mevsimsel değişimin yüzme performansına etkisi iki deneyle gösterilmistir. 7°C den 12°C ye kadar olan sıcaklık artışı, yanal kasların, bir elektirik palsıyla uyarıldığında, minimum kasılma sürelerinin 45.8ms den 33.9ms ye kadar düşmesine sebep olduğu görülmüştür. Bu değerler balığın maksimum kuyruk çırpma frekansının 7°C de 10.9Hz iken 12°C de 14.7Hz'e yükseldiği sonucunu vermektedir.

İkinci gurup deneylerde, balığın bu sıcaklıklarda sesle ürkütmelere verdiği kaçma tepkisi incelenmiş, ve 7°C deki Mauthner Kaçma Reflexlerinin 12°C dekinden önemli derecede daha yavaş olduğu bulunmustur. Sesin verilmesi ile kaçma başlangıcı arasındaki ortalama sürenin 12°C de (27.6) 7°C dekinden (34.8) önemli derecede daha kısa olduğu bulunmuştur (t test, $P< 0.001$). Balıkların ilk kuyruk çırpımının birinci aşamasını tamamlamak için geçen ortalama zamanın 12°C de (45.6ms) 7°C dekinden (57.7ms) önemli derecede daha hızlı olduğu bulunmuştur (t test, $P< 0.001$). Benzer şekilde ikinci aşama içinde yine 12°C deki ortalama zamanın (119.9ms) 7°C dekinden (154.3ms) önemli derecede daha hızlı olduğu bulunmuştur (t test, $P< 0.05$). 10°C lik bir sıcaklık artışının sebep olduğu genel fizyolojik etki balığın maximum yüzme hızını hemen hemen iki kat arttırmıştır ($Q_{10°C}$ =1.81). Bu deneylerin sonuçları Kuzey Denizi mezgit balığının düşük su sıcaklığı sebebiyle kış sonu ve ilkbahardaki en yüksek yüzme hızının yaz sonu ve sonbahara nispeten daha düşük olduğunu göstermiştir.

Anahtar Sözcükler: *Merlangius merlangus*, sıcaklık etkisi, kas kasılımı, kaçma hızı.

Introduction

It is generally recognised that the body temperatures of all fishes, except some large scombrids (1) and large sharks (2), follow the sea temperature in which they swim, even when working hard. Sea temperature varies according to time and location and has a profound impact on almost all aspects of fish physiology (3), including swimming performance (4-8).

The effect of temperature change on the maximum swimming speed of fish is closely related to their escape ability from a moving trawl codend. In order to escape from a fast-moving codend, most small fish have to swim at or very close to their fastest speed (6). Water temperature might limit a fish's maximum swimming ability and, therefore, its ability to escape. Özbilgin (9) and Özbilgin *et al.* (10) report a significant decrease in the selectivity of a trawl codend when towed in colder water temperatures. However, the results presented in these studies were for haddock, *Melanogrammus aeglefinus*. Whiting was the second-most abundant species encountered during these fishing trips. Data for this species was not strong enough to investigate the effect of seasonal change in selectivity. Laboratory experiments trying to explain the potential effect of water and fish muscle temperature on the escape speed of fish, however, were carried out for both species in a similar procedure.

The speed of a steadily swimming fish is the product of stride length and tail beat frequency (4). One fish stride is the distance moved forward after one complete left-right cycle of the tail at steady swimming speed. Each species seems to have a maximum stride length, and when swimming steadily, a fish simply modifies its speed by adjusting its tail beat frequency (7). To achieve the maximum swimming speed, therefore, fish have to use the best possible stride length with the highest tail beat frequency.

Wardle (4) suggested that the muscle contraction time of a fish was a limit for the maximum attainable tail beat frequency and thus the maximum swimming speed. Wardle (4, 5, 11) found that the contraction time of the white muscle of fish increased at higher temperatures. In these papers, he also reported that for fish of the same length, the minimum contraction time was similar when measured in the same environmental condition, irrespective of species: the larger the fish, the longer the muscle contraction time, thus the lower maximum tail beat frequency. These conclusions were later supported by Arimoto *et al.*, (12) who observed an increase of muscle contraction from 60-80ms for 20-30cm long fish (walleye pollock, *Theregra chalcogramma*) to 90-120ms for 40-50cm long fish, at a water temperature of 2°C.

Wardle (13) further showed that the contraction time of the myotomes near the head-end of mackerel, *Scomber scombrus*, was nearly half those near the tail. Wardle *et al.*, (14) found the same increase in bluefin tuna, *Thunnus thynnus*.

Escape reactions involving fast-start responses allow fish to avoid sudden, actual or potential danger in their environment (15). Fish that are unable to perform a fast-start escape response at their rested condition may possess other structural or behavioural anti-predator adaptations such as burrowing habits, colour adaptation to the background (16), spines and toxins (17).

Kinematics and the performance of fish during fast-start manoeuvres have received a lot of attention (18) since they may determine the outcome of predator-prey interactions in terms of feeding success or survival. The first detailed kinematic description of fast-start movement was made by Weihs (19) by separating the fast-start movements of trout, *Salmo trutta*, into three kinematic stages.

After Weihs (19) and Webb (20), most researchers used the synonymous term 'C-start' instead of 'L shape'. However, L- or, more recently, its synonymous C-starts are not the only modes of fast-start swimming. Harper and Blake (21) studied the fast-start performance of northern pike, *Esox lucius*, during prey capture. They reported that, kinematically, an S-shape was formed at the start of each strike. Webb (20) recorded both L- and S-starts as well as some ambiguous starts. He found that the percentage of L-starts decreased, while that of S-starts increased, with increasing length. Nevertheless, except for the largest group of fish (mean length 38.7cm), he found no significant difference in the duration of stage 1 and stage 2 between the L- and S-starts for any group of fish.

Domenici and Blake (18) stated that S-starts were used by predators when attacking prey, whereas C-starts are mainly employed by escaping prey. Although nothing is known about the mechanisms controlling S-starts (18, 22), C-starts are usually mediated by the Mauthner cells

and associated networks (16, 23-25). Eaton *et al.* (23) reported that the pathway and performance of the fish during the Mauthner-initiated component, stage 1, were found to be stereotypic from trial to trial, whereas components of stage 2, which is not mediated by the Mauthner cells (22), were quite variable.

Webb (26) investigated the effect of temperature (at 5, 10, 15, 20 and 25°C) on the acceleration performance of rainbow trout, *Oncorhynchus mykiss*, (of mean mass 23.5g.) during fast-starts initiated by an electric shock stimulus. He found that temperature had little effect on the details of the fast-start kinematics, but the time taken for each stage decreased with increasing temperature. Response latencies decreased from 23ms at 5°C to 6ms at 25°C, and the times to complete the first two stages decreased from 116ms at 5°C to 65ms at 25°C. Consequently, Webb (26) found significant differences in the distance covered by the end of fast-start stage 2, even for fish at 10°C compared with those at 20°C.

Though there has been a good number of studies investigating the effect of temperature on the swimming performance of fish, there is a gap in the research of estimating the effect of seasonal temperature variation on the escape ability of fish from commercial fishing gear. Experiments carried out in this study aimed to find out the changes in the maximum swimming speed of whiting in relation to changes in muscle and/or water temperature. Two different sets of experiments were performed. Firstly, the maximum tail beat frequency was theoretically calculated from the minimum contraction time of isolated muscle blocks. Secondly, fish were stimulated to escape in a 1.55m diameter tank and the time to perform their first two tail beats was measured. The results are discussed in a way to improve understanding of the effect of changes in seasonal water temperature on the avoidance and/or escape performance of fish during trawling operations.

Materials and Methods

Prediction of maximum tail beat frequency from muscle twitch experiments

Experiments were carried out with six fish of 27-30cm length in the Fish Behaviour Unit at the Marine Laboratory, Aberdeen in June 1997. The fish used in this experiment were kept in aquaria for a 9-month period.

To remove the muscle samples, the fish were killed by severing the spinal cord behind the head and then destroying the brain. Then, the total lengths of the fish were measured within an accuracy of 1cm. Two blocks representing the anterior dorsal white lateral muscles (3 x 1 x 1cm each) were removed from locations just behind the dorsal part of the gills from both sides. In order to follow the change in contraction time with temperature, the muscle samples were first placed in a refrigerator. Twenty minutes later, one of the samples (at about 8°C) was taken out of the refrigerator. To obtain a twitch, the sample was slightly stretched and placed on two needle electrodes 1.8cm apart, which were mounted in the PVC plate of a force transducer. The muscle tension was read as a line on the oscilloscope (Gould Data SYS 760, direct recording oscilloscope) and its level was adjusted to zero with an amplifier (Gould universal amplifier, model 13-4615-58). A single pulse 15V electric stimulus, generated by a Digitimer Stimulator DS9A, was applied to the muscle block for 2ms via the two needles. The stimulator pulse was also connected to the trigger and shown on the oscilloscope. The electric pulse stimulated a single muscle contraction known as a twitch. When the muscle was twitched, the force transducer converted the force to a voltage in a resistance bridge that was viewed as an oscilloscope trace showing voltage against time. Then, the temperature of the muscle block was measured using a needle thermometer (P.I. 8013 type K) inserted into its centre. The time from the start of the stimulus electric pulse to the peak (maximum force) of the contraction was measured by a moving cursor from the oscilloscope screen. This measurement represented the shortest contraction time (or twitch contraction time) of that block of muscle at the measured temperature. A series of measurements was made with the muscle until it reached 12-14°C. Then it was warmed above hot water in a bucket and the experiment continued up to 25°C. Immediately afterwards, the same procedure was repeated with the second sample, which had been left in the refrigerator 40-60min, and allowed to start from relatively lower temperatures.

Escape reactions of whiting in relation to temperature changes

For the investigation of fast-start escape responses of whiting at approximately 7 and 12°C water temperatures, first of all the fast-start escape responses were elicited by sound stimuli. The video recording

technique provided one fish image per 10ms. The analysis concentrated on the response time of the fish to the stimuli, and the times taken to complete the preparatory (stage 1) and propulsive (stage 2) strokes of the escape responses.

Experiments were carried out with five whiting in a 1.55m diameter flow-through circular tank with 0.6m water depth in October 1996 and March 1997. Total lengths of the fish were 25 ± 2 and 28 ± 2cm in October and March, respectively. Mean water temperatures in the experimental tank were 11.8°C (range 11.4 -12.1°C) in October 1996, and 7.0°C (range 6.8 - 7.2°C) in March 1997.

A video camera (Panasonic, WV CL 350) with an 8mm lens was mounted 0.9m above the tank. Recordings using this camera provided 50 TV frames per second (one frame for each 20ms). To improve the number of observations per second, illumination was generated by a strobe light (Dawe, Strobe torch, 1222 A) attached next to the camera lens. The strobe light was synchronised with the video camera so as to flash twice in each TV frame. When the video camera was used with this strobe light, any movement fast enough in the recorded field, showed up as two distinct images in each TV frame. In other words, for fast movements there was one observation every 10ms.

To eliminate distortion of the images by water splashes during recording, a PVC tank with a 45 x 85cm transparent bottom was floated on the water surface below the camera as in Wardle and Reid (27). Air bubbles accumulating between the water surface and the transparent raft were sucked out by a flexible plastic pipe prior to recording.

To maximise the image quality, the strobe lights were only switched on during the experiments. To obtain a high contrast view of fish movement with this dimly illuminating strobe light, the bottom of the tank was coated with reflex reflecting material (3M Scotchlite, 3270), as used by Wardle (4). The scotchlite was marked with crosses at the corners of 25cm squares that made it possible to measure the length of the fish without any disturbance once they were near the bottom of the tank. Scotchlite material almost fully reflects the light coming from the source back to the source, for this reason the strobe light was mounted next to the camera lens. With this arrangement, during the fast-starts, a dark silhouette appearance of 100 fish images per second with sharp outlines on the bright marked background was recorded on the video tape.

Fish were stimulated by a single gentle kick to the outer wall of the tank. The stimulus was applied while the view of the camera above the tank was being observed in a TV monitor in the tank room. In this way, the escape response of one to three fish were recorded at the same time. Each session was carried out until a minimum of ten responses were recorded. Each experiment was continued until one hundred responses were recorded with a minimum of 24h break between the sessions to allow the fish to recover from fatigue.

To identify the start of the sound stimulation, a hydrophone (Plessey MS83 wide-band device) was placed in the tank and connected to an oscilloscope (Telequipment, DM63). The oscilloscope was viewed by a camera (Panasonic, WV CL 350). This view was arranged to appear on the top part of the recordings of the experimental tank by using a view mixer (Primebridge, Micro-series Video Wiper PVW-1). This set-up made it possible to measure the time taken from the start of the stimulating sound to the start of the escape reaction which is the image prior to the first detectable head and/or tail displacement of the fish. This period was termed 'Response latency' by Webb (26). In this text, the same period is called 'Escape latency'.

Recorded video films of the escape responses were analysed frame by frame by using a standard VHS video recorder (Panasonic AG-7350-B) and a TV monitor (JVC BM-H2000PN). Three measurements were made; a) time taken from the start of stimulation to start of escape reaction, b) time taken for stage 1 and c) time taken for stage 2. During stage 2, fish showed two distinct behaviours. These were either to move the tail to the opposite side of the start of the stage as described by Weihs (19) or bring the tail blade near the swimming axis and glide away. Due to high variation in the time taken to complete the gliding finish to stage 2, data were rejected when the duration of stage 2 exceeded 100ms.

Results

Prediction of maximum tail beat frequency from muscle twitch experiments

Contraction times of muscles dissected from fish against temperature ranging from 1 to 25°C are shown in Figure 1.

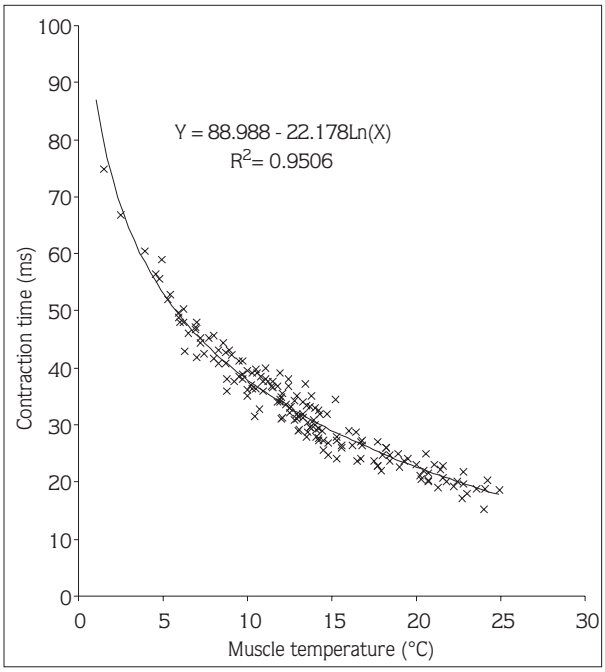

Figure 1. Muscle contraction time of 27-30cm whiting and logarithmic regression line fitted to the data points.

Figure 1 clearly indicates that muscle contraction time decreases logarithmically with increasing temperature. Equation of the logarithmic regression line fitted to the muscle twitch data was y = 88.988 - 22.178Ln(X), with a correlation coefficient (R^2) value of 0.9506. Muscle contraction times obtained from this equation at 7 and 12°C are 45.8 and 33.9ms, respectively. These are the mean values produced from the equation. Nevertheless, when considering the maximum speed, the relevant muscle twitch contraction time is the shortest recorded value, not the mean obtained from the curve. Therefore, the fastest muscle twitch for each temperature between 6 and 13°C and the tail beat frequencies calculated from these values are given in the Table. The maximum predicted tail beat frequencies are also presented in Figure 2. Note that the temperature measurements during the experiments were taken to one decimal point. However, to demonstrate the general trends in the Table and Figure 2, these values were rounded. Hence the maximum tail beat frequency of a fish, at 7°C for example, may have been calculated from a minimum muscle twitch time at any temperature between 6.5 and 7.4°C.

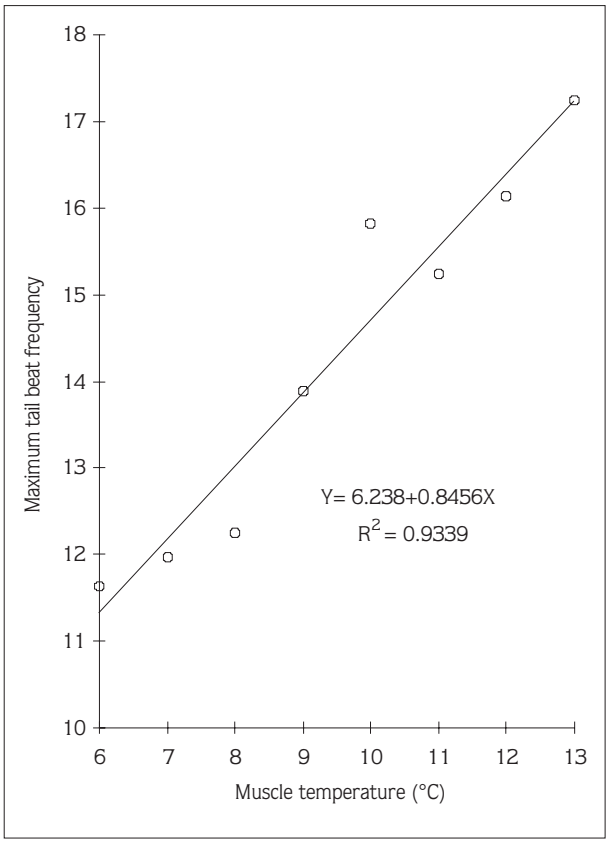

Figure 2. Predicted maximum tail beat frequencies of whiting between 6 and 13 °C muscle temperature.

Table. Observed Minimum Muscle Contraction Times (MMCT) (ms) at rounded temperatures and, from these values, calculated Maximum Tail Beat Frequencies (MTBF) of whiting.

Temperature to the nearest °C	MMCT.	MTBF.
6	43	11.6
7	41.8	12.0
8	40.8	12.3
9	36	13.9
10	31.6	15.8
11	32.8	15.2
12	31	16.1
13	29	17.2

Escape reactions of whiting in relation to temperature changes

Analysis of the video recordings was concentrated on the comparison of the time taken to complete the various stages of the fast-start escapes at two specific water temperatures. It was thought that the frequency (100Hz)

and the quality of the recorded video images were not sufficient to study the details of the kinematics. However, general patterns of the escapes are described below.

General observation on fast-start escape kinematics

Fast-start escape responses were usually divisible into three main stages, as described by Weihs (19). There was a stereotypical preparatory stroke (stage 1) in all the escapes where the fish were bent into a 'C' shape. Stage 1 was usually followed by a propulsive stroke (Stage 2) during which the tail was rapidly moved across to the opposite side to create the forward thrust. However, this was not a stereotypical movement. In some escapes, the propulsive stroke was a shortcut and fish preferred to glide away during stage 2, and used the tail to steer the body rather than propelling it. Gliding during stage 2 resulted in a relatively slow tail movement that lasted longer than 100ms. If the fish propelled during stage 2, stage 3 was either a rhythmic tail beat or gliding. As the diameter of the experimental tank (1.55m) was not large enough to provide sufficient space for continuous swimming, stage 3 was very often a glide.

On some occasions (less than 10% of the overall observations) ambiguous bendings that were in between an 'S' and 'C' shapes were observed at the end of stage 1 (as in Webb (20)). However, the duration of stage 1 and 2 of these starts were similar to the C-starts. Therefore, they were not excluded from the data.

Comparison of escape response at water temperatures of 7 and 12°C

An increase of water temperature from 7 to 12°C resulted in significantly faster escape responses (Figures 3-5). Minimum escape latency at 12°C (10ms) is shorter than that at 7°C (20ms). Mean escape latency at 12°C (27.6, se. 0.8) is significantly shorter than that at 7°C (34.8, se. 1.0) (t test, $P< 0.001$).

The fastest time to complete stage 1 is 30ms at 12°C whereas it is 40ms at 7°C. The mean value of the time taken to complete stage 1 at 12°C (45.6ms, se. 1.0) is significantly faster than that at 7°C (57.7ms, se. 1.2) (t test, $P< 0.001$).

When the fish were stimulated by sound, stage 2 very often resulted in a gliding movement which lasted, on some occasions, longer than 500ms. Therefore, variations in the duration of stage 2 are relatively higher than the variations in the results presented above. Time taken to complete stage 2 at 7 and 12°C are shown in Figure 5, although only if equal to or less than 100ms. The fish are significantly faster in completing stage 2 at 12°C than at 7°C. The minimum time to complete stage 2 are 40ms at both temperatures. However, the mean value of the time taken to complete stage 2 at 12°C (119.9ms, se. 10.0) is significantly faster than that at 7°C (154.3ms, se. 14.1) (t test, $P< 0.05$). All the responses involving gliding during stage 2 are included for calculations and the comparison of the means. However, only the responses that were equal to or faster than 100ms (n=67 at 12°C, 61 at 7°C) are displayed in Figure 5.

Discussion

Although the fastest burst swimmings are of very short endurance (5), they are of great survival value to the fish during their escape from a trawl codend (6). Results from both sets of experiments carried out in this study clearly indicate that the fastest swimming performances of these fish are temperature dependent. The maximum swimming speed is significantly lower at a water temperature of 7°C than it is at 12°C.

Wardle (4) demonstrated that when the minimum twitch contraction time of the white lateral muscle of a fish is known, maximum tail beat frequency can be calculated. At maximum swimming speed the duration of the tail beat period is the sum of the durations of the minimum contraction times of these muscles. It is demonstrated that muscle contraction time decreases logarithmically with increasing temperature. This also means that the maximum tail beat frequency increases at higher temperatures.

The physiological effects of temperature change are generally described as $Q_{10°C}$ effects, where $Q_{10°C}$ represents the increase in rate caused by an increase in temperature of 10°C (7). If a rate doubles over a temperature increase of 10°C, $Q_{10°C}$ is 2 or if it triples $Q_{10°C}$ is 3.

It is assumed that the shortest time to complete a tail beat is limited by muscle twitch contraction times, and the $Q_{10°C}$ for the group of 27-30cm whiting can be calculated in a temperature change from 7 to 12°C. Average tail beat frequencies of these fish, calculated from the logarithmic regression equations of muscle twitch time, are 10.9Hz at 7°C and 14.7Hz at 12°C. This gives a $Q_{10°C}$

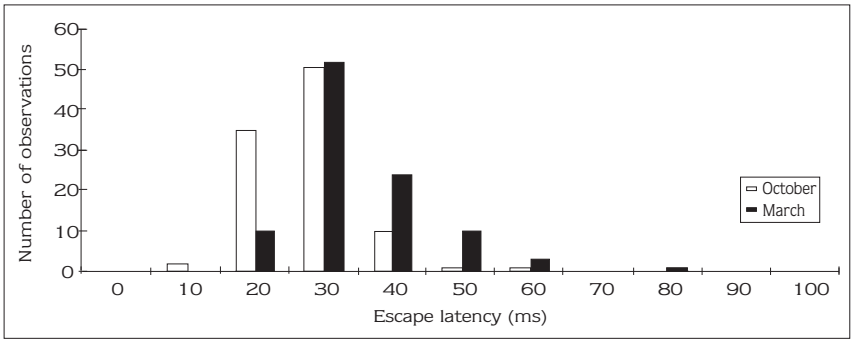

Figure 3. Comparison of the escape latencies of whiting at water temperatures of 12 and 7 °C to sound stimulus.

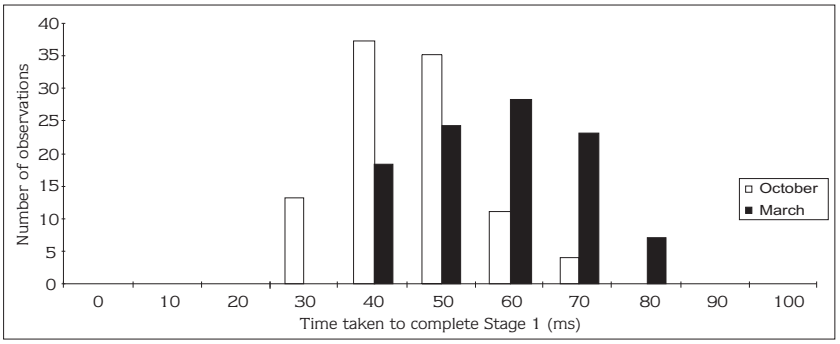

Figure 4. Comparison of time taken to complete stage 1 during the escape responses of whiting at water temperatures of 7 and 12 °C.

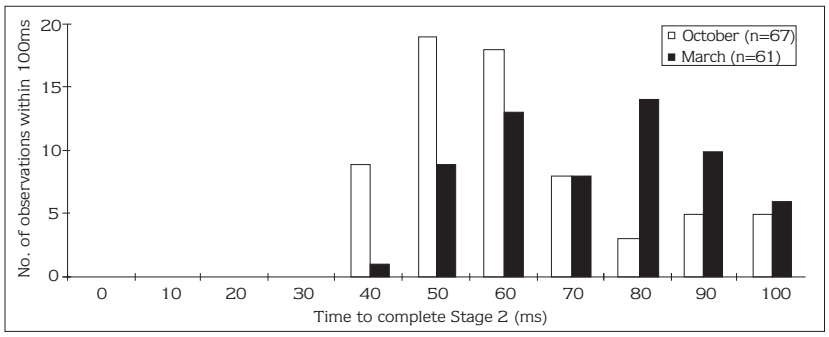

Figure 5. Comparison of time taken to complete stage 2 during the escape responses of whiting at water temperatures of 7 and 12 °C.

value of 1.82. Videler and Wardle (28) calculated $Q_{10°C}$ values of eight sizes of cod (from 20 to 84.5cm) at seven temperatures between 2 to 15°C. They found an average value of 2.06 (SD. 0.1). $Q_{10°C}$ values of about 2 are common for the rate of speeds of biological enzyme-catalysed chemical reactions (7, 28).

C-start escape responses of whiting to sound stimuli were also found to be significantly slower at 7°C than at 12°C water temperature (t tests, $P< 0.05$ for escape latency, $P< 0.001$ for stage 1 and 2). This is to be expected as the minimum muscle contraction time is significantly longer at 7°C than it is at 12°C. These results agree with the results of experiments carried out for haddock (29) under a very similar experimental protocol.

The results of these two sets of experiments clearly demonstrates that the maximum swimming capacity of whiting is rather limited in winter and early spring due to low water temperatures than it is in late summer and early autumn. However, the operation speed of most towed fishing gear remains constant throughout the year. For the same physiological condition and physical dimension of whiting, therefore, escaping from the codend of a trawl net is expected to be relatively easier in warm water than in cold water. This difference may lead to a better selectivity of trawl codends in late summer than it is in winter months as reported by Özbilgin *et al.* (10) for haddock.

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