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Effect of temperature on the swimming endurance and post-exercise recovery of jack mackerel *Trachurus japonicus* as determined by ECG monitoring

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Abstract The effect of temperature on the swimming performance of jack mackerel *Trachurus japonicus* was examined in a flume tank by measuring the swimming endurance time and heart rate. The lower swimming performance was observed at 10°C (the lowest temperature tested), manifesting as the shortest endurance time and the slowest maximum sustained speed. ECG measurements of the heart rate under free-swimming conditions at zero flow velocity revealed a temperature effect, with 25.3 beats/min observed at 10°C, 38.9 at 15°C, and 67.2 at 22°C. The heart rate also increased with swimming speed to maximum levels of 60, 125, and 208 beats/min, respectively, at these three temperatures. Heart rate recovery times measured after the fish had been swimming at prolonged speed tended to increase with temperature, while a negative correlation resulting in relatively short recovery times was observed after swimming at close to the burst swimming speed at each water temperature.

Keywords ECG · Heart rate · Jack mackerel · Prolonged speed · Recovery time · Sustained swimming speed · Swimming endurance

Introduction

The swimming performances of target and non-target fish play important roles in determining the selectivity and efficiency of mobile fishing gear [1–3]. This is because many of these fish are only capable of swimming at or below their maximum sustained swimming speed for long periods [4, 5]. Fish swimming endurance is influenced by respiratory and metabolic processes that are reflected in the heart rate, since the heart is the pumping mechanism for the blood circulation system in the body, and the heart rate represents the gas exchange and chemical processes needed to metabolize the energy used when a fish is swimming. The heart rate can also be used to accurately predict oxygen consumption at different levels of exercise and recovery [6].

Changes in temperature affect the rates of all physiological processes in fish, such as respiratory, metabolic and cardiac output [7], as well as muscle contraction [8, 9]. Temperature changes can therefore have a significant impact on swimming endurance, which is also negatively affected by increased swimming speed [10]. The objective of this work was to examine the effect of temperature on the swimming endurance of jack mackerel *Trachurus japonicus*, and to assess its physiological impact on the fish during exercise. The heart rate was used as an indicator of the level of fatigue in relation to swimming endurance and post-exhaustion recovery in order to examine the stress experienced by the fish during the capture process and during post-exhaustion conditions after escaping from the gear.

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Materials and methods

Experimental fish

Jack mackerel of fork length 18.5 ± 0.8 cm (average ± SD, $n = 249$) were obtained from a fish farmer in Suruga Bay, Japan. All of the fish were transported by a tank-lorry for live fish transportation to a holding tank 2.0 m long by 0.9 m wide by 1.0 m deep at the Fish Behavior Laboratory of the Tokyo University of Marine Science and Technology. The fish were fed on fish meal pellets every day during both the acclimation and experimental periods.

Flume tank and observation system

The flume tank (West Japan Fluid Engineering Laboratory, PT-70) used in this study was specially designed to provide most of the test section (70 cm long by 30 cm wide by 20 cm deep) with a steady water flow (Fig. 1). One side of the wall of the test section was covered by a panel upon which square grids were drawn as visual cues for maintaining position in the flow through the optomotor response [3, 11, 12]. When a test fish was maintaining its position relative to the oncoming flow, the swimming speed of the fish was considered to be equivalent to the flow speed. The water temperature of the flume tank was maintained at either 10, 15, or 22°C. The water temperature was changed to the target temperature at a rate of 1°C per day.

As shown in Fig. 1, a video camera (Sony, CCD-TRV 96) was set 1.0 m above of the test section in order to observe the swimming activity of the fish. The video camera was connected to a video recorder (Sony, EVO-9720) via a video timer (FOR-A, VTG-55D) to superimpose the time elapsed in 0.01 s.

Measurement of swimming endurance

The endurance time trials were carried out during the period from November 2007 to May 2008. After two days of temperature acclimation in the holding tank, swimming endurance was examined. The endurance trials for individual fish were carried out within one week of acclimation to the artificial conditions in the holding tank, during which the temperatures of both the holding and the experimental tanks were maintained at the desired temperature using a digital thermocontroller (REI-SEA, TC-100, Japan).

Individual fish were randomly selected and introduced to the test section of the flume tank. After 10 min and a subsequent 30 min of adaptation under still-water and low-flow (12.4 cm/s) conditions, respectively, the flow speed of the flume tank was set at the required speed (20.4, 39.3, 55.4, 74.3, 93.1, 112.0, 128.1, 147.0 or 160.4 cm/s). The swimming endurance at each flow speed was determined as the time taken for the fish to discontinue swimming. If the fish was still swimming after a predetermined maximum time of 200 min, the endurance trial was terminated anyway [2, 11].

The swimming speed was categorized into three levels—sustained, prolonged, and burst speeds—as done in previous studies [13]. The "sustained swimming speed" is defined as the swimming speed that can be maintained for the full 200 min of the swimming endurance trial. Once the swimming speed exceeds the upper limit of this level, the "maximum sustained speed," anaerobic white muscle activity is incorporated into red aerobic muscle activity, and so swimming endurance is dramatically decreased and is terminated by fatigue [11]. This second level of swimming speed is termed the "prolonged swimming speed." The highest level of swimming speed is the "burst speed," which the fish can sustain for less than 15 s [13].

The endurance time data (E, in seconds) were plotted against the swimming speed using semi-log coordinates, and the endurance time was regressed against the swimming speed by the least squares method in order to establish the relationship between swimming speed and endurance as a swimming endurance model equation [14]. The maximum sustained swimming speed and the threshold of the burst speed were determined by substituting swimming endurances of 200 min (12,000 s) and 15 s into the equation, respectively.

Measurement of heart rate by the ECG technique

A pair of electrodes for electrocardiographic (ECG) measurements were implanted in the pericardial cavity of each jack mackerel (Fig. 2) under anesthesia due to FA100 (0.008%) for 15–20 min. The electrodes were made of enamel-insulated tungsten pins (MT Giken), and were 15 mm long and 0.2 or 0.3 mm in diameter. The outer insulation of the electrode was removed from both tips for a length of 1 mm, and the electrodes were inserted into the pericardial cavities of the fish from the ventral side. Electrodes were fixed to the left and right sides of the ventricle of the heart to monitor the heartbeat [15–18]. The electrodes were connected to copper wire cable (Tsurumi Seiki, T-GA XBT cable) and covered with superglue (Aron Alpha, Toagosei). The other end of the wire cable was connected to a digital oscilloscope (Iwatsu, DS-5102) via a bio-amplifier (Nihon Kohden, Bioelectric Amplifier AB-632J), as shown in Fig. 1.

After recovering for 180 min from the anesthesia, the heart rate (beat/min) of each fish was measured in still water for 10 min. The average heart rate was taken to be the control heart rate, and this was then compared with the average heart rates observed during exercise at a given flow

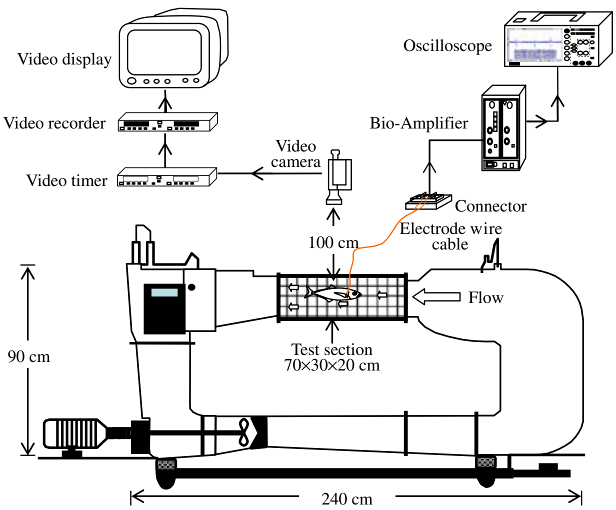

Fig. 1 Experimental apparatus for swimming endurance and electrocardiogram monitoring

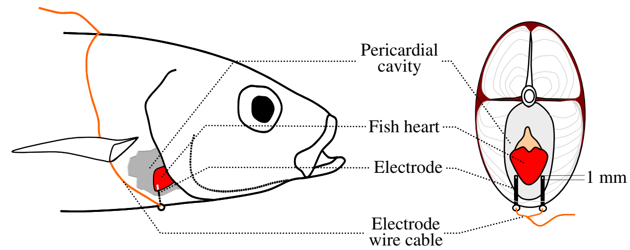

Fig. 2 Position of the pair of electrodes used to monitor the heart beat

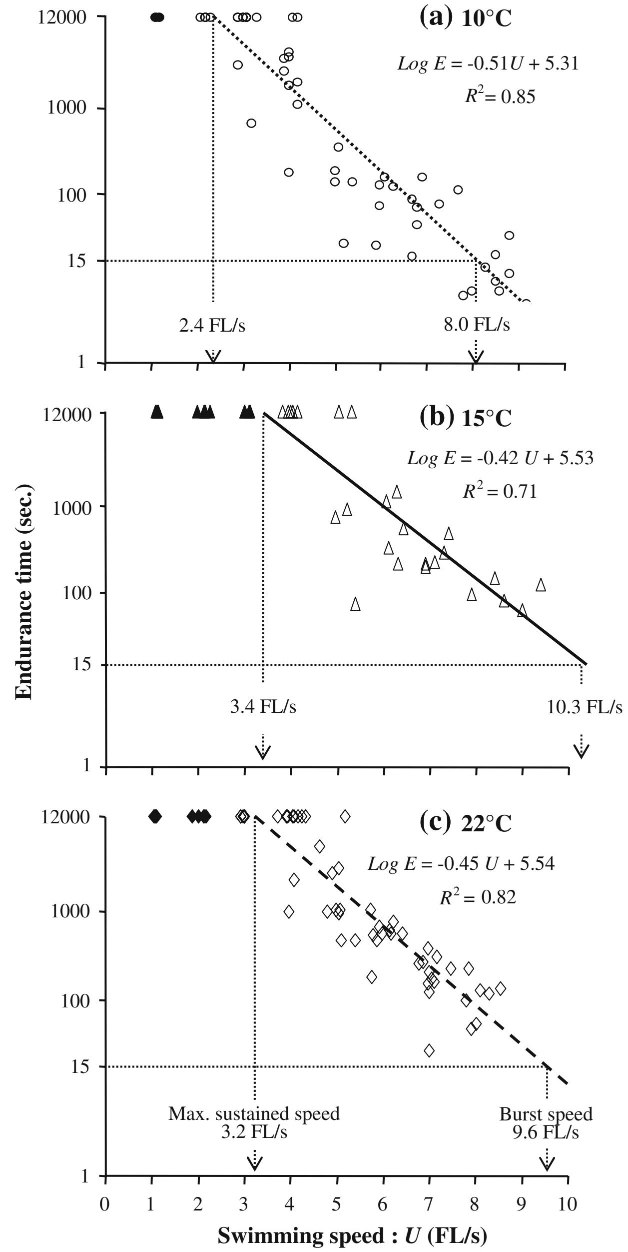

Fig. 3 Relationship between swimming endurance and speed (FL/s) at **a** 10°C; **b** 15°C; **c** 22°C. *Filled symbols* indicate excluded data, and *unfilled symbols* were regressed in semi-log linear regression analyses to estimate the maximum sustained speed and the burst speed

speed and during post-exercise recovery in still water. For the measurements taken during exercise, the flow speed was elevated as per the protocol for the endurance trial. Data collection was continued during the post-exercise recovery period until the heart rate had stabilized to the control heart rate level. The recovery time was defined as the time taken for the 10 min moving average to reach the same level as the maximum value recorded for each minute during the control measurements [17].

Results

Swimming speed and endurance

Figure 3 shows the results of the endurance time trials performed at temperatures of 10, 15, and 22°C. The data for the swimming endurance trials that were terminated after the maximum observation time of 200 min were excluded from analysis. This is because the inclusion of those data, shown as filled symbols in Fig. 3, could lead to bias and underestimation during analysis.

The swimming endurance was independent of the body length of the fish at the same flow speed ($P > 0.05$; regression analysis). In addition, there was no significant difference in the average body lengths of the fish that were used for the swimming endurance trials at the same flow speed but different temperatures (ANOVA, $P > 0.05$). These results allowed the average swimming endurance to be compared at each swimming speed in terms of the average body length (>5.0 FL/s) using one-way ANOVA. The data were then subjected to semi-log linear regression analysis in order to derive the equation for the swimming curve, as shown in Fig. 4. Experimental analysis indicated that the average endurance time at 10°C was significantly lower than those at higher temperatures (15 and 22°C; ANOVA, $P < 0.01$). The swimming curve for 15°C indicated that the fish performed better at this temperature than at 22°C, which may imply that the optimal or near-optimal water temperature for the jack mackerel in terms of its swimming performance is 15°C. However, there was no significant difference between 15 and 22°C in the average endurance time at the same swimming speed (ANOVA, $P > 0.05$).

The maximum sustained speeds were estimated from the semi-log linear regression lines in Fig. 3 to be 2.4 FL/s at 10°C, 3.4 at 15°C, and 3.2 FL/s at 22°C. At sustained swimming speeds, the fish could continue their steady tail oscillations and maintain their positions relative to the flow at each temperature. At low prolonged swimming speeds, the fish were occasionally carried backward against the flow, but they could propel themselves forward using kick-and-glide maneuvers. This behavior became more common at each temperature as the flow speed increased.

At 10°C, several individuals were not able to swim for more than 15 s when the swimming speed was around 8 FL/s or faster. At the higher temperatures of 15 and 22°C, all of the fish were able to swim for more than 15 s in the range of the swimming speeds observed. The thresholds for the burst speed were estimated to be 8.0 FL/s at 10°C, 10.3 FL/s at 15°C, and 9.6 FL/s at 22°C, based on the semi-log line regression analysis, as shown in Fig. 3.

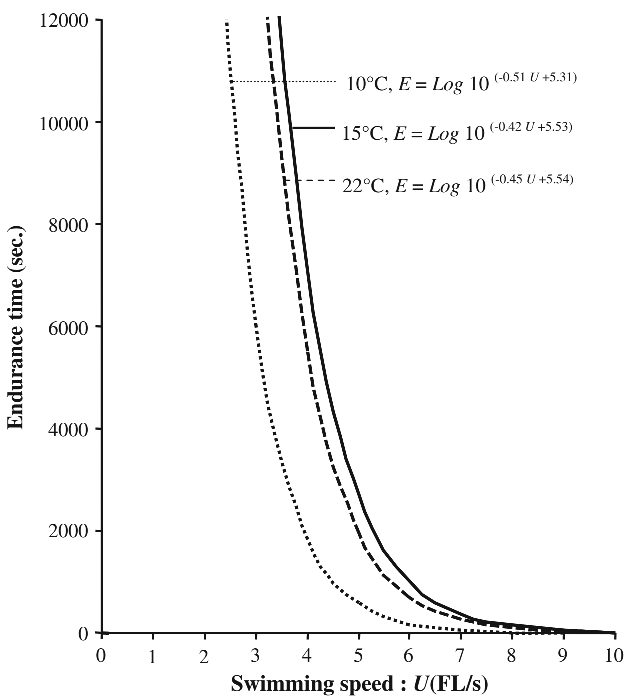

Fig. 4 Swimming curves that can be used to compare the endurance times of jack mackerel at 10, 15, and 22°C

Heart rate during exercise

Figure 5 shows an example of the ECG pattern of jack mackerel, which is quite similar to those of mammals, including humans. The heart rate during the control phase varied at each temperature but was affected by the water temperature. The heart rates were 13–37 beats/min (25.3 ± 5.7, $n = 16$) for 10°C, 27–71 beats/min (38.9 ± 11.1, $n = 29$) for 15°C, and 42–95 beats/min (67.2 ± 13.2, $n = 45$) for 22°C, as shown in Fig. 6. During the swimming exercise, the heart rate increased according to

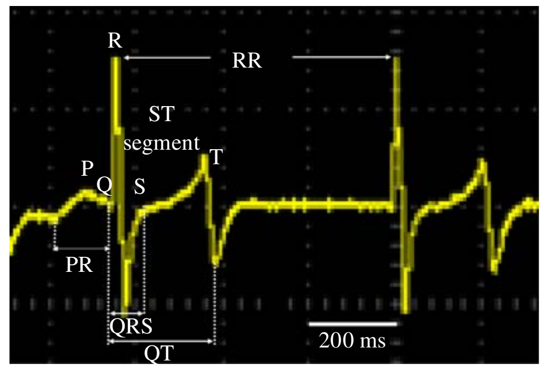

Fig. 5 ECG pattern for jack mackerel, *Trachurus japonicus*. *P-wave* represents the depolarization of the atrium, which is the process used to pump the blood into the ventricle. *QRS* represents the depolarization of the ventricle, which is the process used to pump the blood into all body parts through the arteries and capillaries. *ST segment* represents the ventricular redepolarization process and *PR* represents the time interval from the onset of atrial depolarization (P-wave) to the onset of ventricular depolarization (QRS complex). *QRS* represents the duration of ventricular muscle depolarization. *QT* represents the duration of ventricular depolarization and repolarization, and *RR* represents the duration of the ventricular cardiac cycle (an indicator of the ventricular rate), while *PP* represents the duration of the atrial cycle (an indicator of the atrial rate) [24]

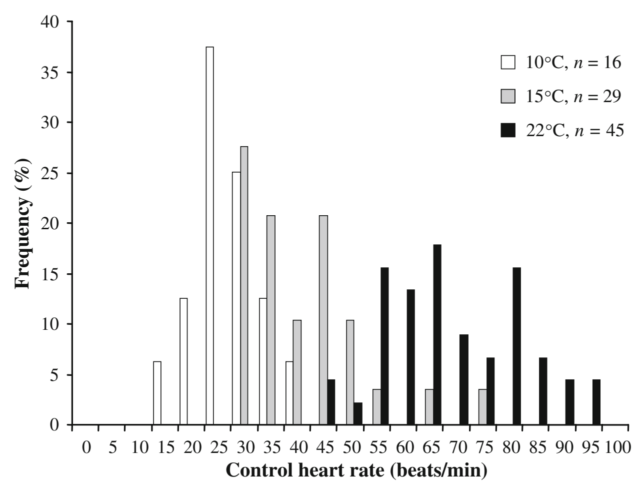

Fig. 6 Frequency histogram for the heart rate at each temperature during the control phase

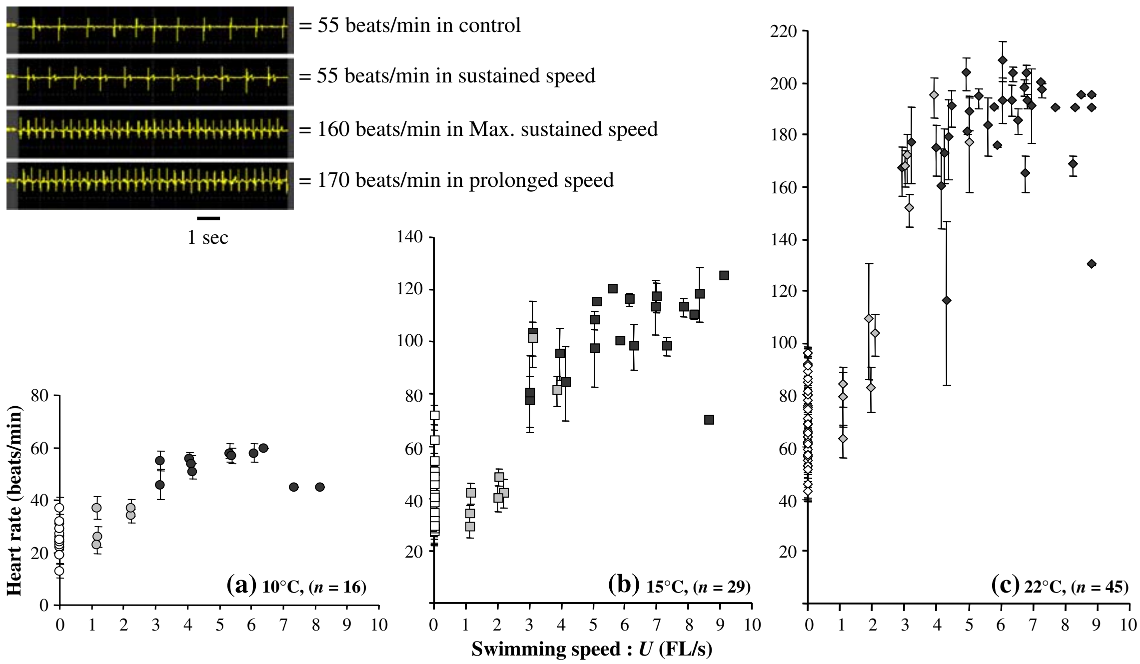

Fig. 7 Average heart rates during swimming exercise at **a** 10°C, **b** 15°C, and **c** 22°C. The heart rates at each temperature are compared for different swimming speeds: during the control phase (*unfilled symbols*); at sustained speed (*gray symbols*); and at prolonged speed (*dark symbols*). The *vertical line* accompanying each mark indicates the standard deviation. Examples of the ECG patterns for different swimming speed levels at 22°C are also shown

the swimming speed level. Figure 7 shows the increasing trend with swimming speed and the maximum heart rate at high speed for each temperature, together with examples of the recorded ECG patterns for 22°C.

From Fig. 7a, at the temperature of 10°C, the heart rate at sustained speed tended to be approximately the same level as it was during the control period. It started to increase when the speed moved above the maximum sustained speed, until it reached its maximum level of up to 60 beats/min at prolonged speed. Similar patterns in heart rate at sustained swimming speed (i.e., it was the same level as during the control phase) were observed at 15 and 22°C, while the heart rate tended to start to increase at around 2 FL/s at these temperatures. At prolonged speeds and higher temperatures, large increases in the heart rate were observed (70–125 beats/min for 15°C, and 115–208 beats/min for 22°C), and asymptotic trends to the maximum rates were seen at the highest swimming speeds.

Post-exercise recovery

Data on recovery times after exercise are shown in Fig. 8, which compare the recovery times observed at sustained and prolonged speeds at the three temperatures. At low swimming speeds of 1–2 FL/s, the heart rate was observed to be the same as it was during the control period, both during and after swimming, so no fatigue occurred during

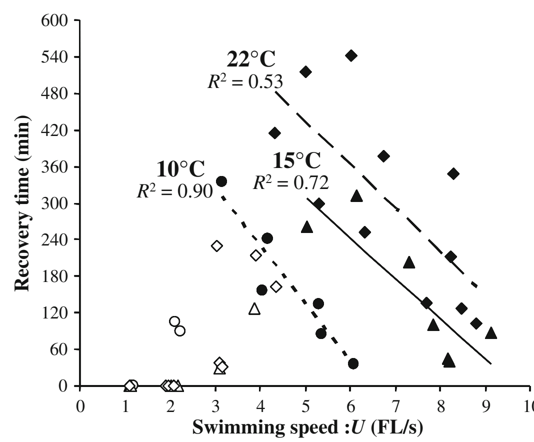

Fig. 8 Recovery time in relation to swimming speed at different water temperatures. The recovery times at sustained speed (*open marks*) at 10°C (*unfilled circles*), 15°C (*unfilled triangles*), and 22°C (*unfilled diamonds*) and at prolonged speed (*solid marks*) at 10°C (*filled circles*), 15°C (*filled triangles*), and 22°C (*filled diamond*) are shown, as are linear regression lines for the data obtained at prolonged swimming speeds

exercise and no recovery time was recorded. At higher sustained speeds of 3–4 FL/s, the recovery time increased with the swimming speed.

At prolonged swimming speeds, higher temperatures generally resulted in longer recovery times. For swimming speeds of 5–7 FL/s at 22°C, the heart rate took 103–543 min to recover to the control level. However, the

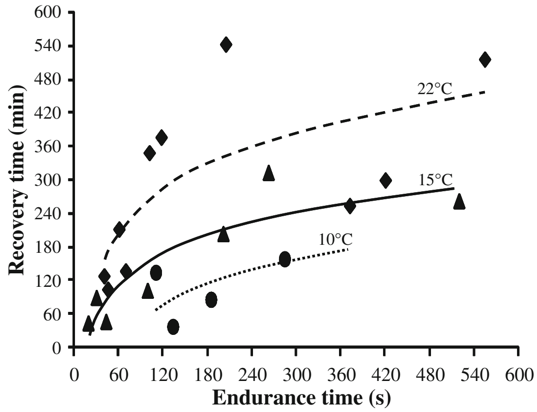

Fig. 9 Recovery time versus endurance time at prolonged swimming speeds at each temperature: 10°C (*filled circles*), 15°C (*filled triangles*) and 22°C (*filled diamonds*)

recovery times decreased at higher swimming speeds of 8–10 FL/s, as shown in Fig. 8. This was due to the shorter endurance times observed at higher speeds, since recovery time was correlated with endurance time. Figure 9 shows trend curves for recovery time versus endurance time at prolonged speeds. Here, the longest recovery times were seen at the highest water temperature of 22°C, with high levels of variation observed among the trials. This can be used to evaluate the level of fatigue caused by the swimming, and will be discussed later.

Discussion

Swimming performance, such as the maximum sustained and burst swimming speeds as well as the endurance time at prolonged swimming speeds, was severely reduced at the lowest water temperature tested, 10°C. This type of temperature effect has already been well described for several fish species, and has implications for trawl towing strategies [8, 19, 20]. For example, Woodhead [21] demonstrated the inability of sea sole *Solea vulgaris* to avoid capture by a trawl at low temperatures during the cold winter season. Underwater video observations of walleye pollack *Theragra chalcogramma* in the mouth of a trawl at a temperature of around 2°C showed that the fish were inactive and unable to keep swimming when the trawl was towed at 4–5 knots (2.0–2.5 m s^{-1}) [19].

The heart rates of the jack mackerel studied in this work did not increase at low sustained swimming speeds. This illustrates that the energy cost of swimming was effectively metabolized to sustain the same level of swimming speed for an extended period. As Priede [22] stated, it is probable that the rate of respiratory function and blood flow for a fish swimming at moderate speeds agrees with the rate of metabolism, which closely reflects the rate of the change in cardiac output. A previous study monitoring the heart rates of jack mackerel, where the effect of strobe light stimuli on the heart rate was analyzed [15, 16], showed similar variations in the control heart rate to those seen in the present study. In that study, the heart rate was affected by the individual conditions of the fish, which were related to the sympathetic (excitatory) and parasympathetic (inhibitory) divisions of the autonomic nervous system for example [23]. Other factors that can affect the heart rate during exercise are environmental factors such as ambient temperature and dissolved oxygen level. Namba [24] noted that these environmental factors can affect the pacemaker cells responsible for decreasing or increasing the heart rate. Observing the heart rate during exercise and post-exercise recovery can therefore provide a good method of evaluating the fatigue level.

At speeds above the maximum sustained swimming speed, the heart rates of the jack mackerel reached maximum levels of 60 beats/min at 10°C, 125 beats/min at 15°C, and 208 beats/min at 22°C. These increases in heart rate can accelerate blood circulation, enabling extra energy to be directed to reducing the effects of anaerobic muscle activity at prolonged speeds. Ito et al. reported that in carp *Cyprinus carpio*, heart rate was related to the possible contraction time of the heart muscle with temperature, and that there was no chance of exceeding the limit on the maximum heart rate [25]. Severe exercise resulting in the maximum possible heart rate caused high stress and high fatigue levels, shortening the endurance time, as shown by the swimming curve analysis.

The recovery time analysis for the post-exercise phase (see Fig. 8) revealed that recovery times were minimal at low swimming speeds, but increased sharply in the vicinity of the maximum sustained swimming speed. The fact that recovery times were required at high sustained speeds results in a discrepancy in the definition of the sustained swimming speed, as "sustainable" implies that the activity can be performed continuously without fatigue [11]. This can be explained by noting that the fish swimming in the narrow volume of the test section were forced to swim against the flow while maintaining their swimming positions, which is a difficult task and is a close analogy to swimming in the cod-end when captured by a trawl net.

The fluctuations in recovery time observed after the fish had been swimming at speeds close to the maximum sustained swimming speed can be explained by noting that it is difficult for the fish to swim with electrode wire cables attached to them. In this paper, the speed range categories were derived from endurance time trials of free-swimming fish (i.e., fish without electrode wire cables attached). When ECG monitoring was performed during exercise with the electrode wire cables attached to the fish, lower endurance times at maximum sustained speed were obtained compared with the free-swimming data, as shown in Fig. 4, due to the difficulty involved in performing kick-and-glide maneuvers at high speeds.

The recovery time after prolonged swimming exercise increased with the water temperature. Longer endurance times at warmer temperatures made the fish completely exhausted, and so they recovered from this fatigue less quickly. The ambient water temperature may thus directly affect the recovery time. However, specific evidence of this was not obtained from the heart rate monitoring performed in the present study, and we will focus on this aspect in the future.

Chopin and Arimoto [26] stated that the fish swimming in the cod-end of the trawl during the capture process will be forced to perform severe exercise. This can result in mortality, which has been attributed to various capture stressors, even when the fish could escape from the net. This study demonstrated that the magnitude of the stress imposed on the fish during exercise at prolonged swimming speeds was reflected in their heart rates for up to 543 min (9.05 h) under laboratory conditions. This result suggests that, due to fatigue, fish that have escaped the mobile fishing gear cannot then show their optimal swimming performance when they are again chased by the gear.

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