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Natural swimming speed of *Dascyllus reticulatus* increases with water temperature

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Recent research on the relationship between coral reef water temperature and fish swimming activity has stated that swimming speed is inversely correlated with temperature (Johansen, J. L., and Jones, G. P. 2011. Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. Global Change Biology, 17: 2971 – 2979; Johansen, J. L., Messmer, V., Coker, D. J., Hoey, A. S., and Pratchett, M. S. 2014. Increasing ocean temperatures reduce activity patterns of a large commercially important coral reef fish. Global Change Biology, 20: 1067 – 1074). For tropical coral reefs, one anticipated consequence of global warming is an increase of $\geq 3°C$ in average water temperature in addition to greater thermal fluctuations [IPCC (Intergovernmental Panel on Climate Change). 2007. Summary for policymakers. *In* Climate Change 2007: The Physical Science Basis. Contribution of Working, Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Ed. by S. Solomon, D. Qin, and M. Manning *et al.* Cambridge University Press, Cambridge, UK; Lough, J. 2007. Climate and climate change on the Great Barrier Reef. *In* Climate Change and the Great Barrier Reef. Ed. by J. Johnson and P. A. Marshall, pp. 15 – 50. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, Qld, Australia; Johansen and Jones, 2011]. Evaluating the behaviour of coral reef associated fish species at different temperatures can help to assess their sensitivity to climate change. In this study, the speed of freely swimming fish in a natural setting is investigated as a function of seasonal changes in water temperature, as contrasted with systematic temperature increases in a fish tank. We show that *Dascyllus reticulatus* swim faster as a function of increased water temperature over the range 20.9 – 30.3°C. The experiments were carried out using ~3.6 million fish trajectories observed at the Kenting National Park in Taiwan. Fish speed was computed by detecting and tracking the fish through consecutive video frames, then converting image speeds to scene speeds. Temperatures were grouped into 10 intervals. The data reveal an ~2 mm s^{-1} increase in average speed per additional temperature degree over the range of 20.9 – 30.3°C. The Mann – Kendall test using the mean and median speed for each interval revealed that there is a speed increase trend as temperature increases at the 0.05 significance level, rather than a random increase. Therefore, our results contradict previous studies (Johansen and Jones, 2011), which also consider *D. reticulatus* and which have reported that fish speed decreases as water temperature increases (Myrick, C. A. and Cech, J. J. 2000. Swimming performance of four California stream fishes: temperature effects. Environmental Biology of Fishes, 58: 289 – 295; Ojanguren, A. F. and Braña, F. 2000. Thermal dependence of swimming endurance in juvenile brown trout. Journal of Fish Biology, 56: 1342 – 1347; Lough 2007; Johansen *et al.*, 2014).

Keywords: *Dascyllus reticulatus*, fish swimming speed, fish trajectory, global warming, video analysis, water temperature.

Introduction

The relationship between coral reef water temperatures with fish metabolism and activity has been studied previously in a fish tank model, suggesting that, for many fish species, swimming performance reduced at low temperatures (~10°C), increased in optimum temperatures (~15°C), and then decreased at higher temperatures ($\geq 20°C$), such as for the California stream fish (Myrick and Cech, 2000), *Salmo trutta* (Ojanguren and Braña, 2000), *Oncorhynchus nerka* (Lee *et al.*, 2003), and *Oncorhynchus kisutch* (Lee *et al.*, 2003). More recent studies have shown that increasing the water temperature decreases the swimming capacity of fish (Johansen and Jones, 2011; Johansen *et al.*, 2014). The

effect of water temperature increase on the swimming and metabolic performance of 10 different species of damselfish (including *Dascyllus reticulatus*) was studied by Johansen and Jones (2011) using a fish tank model. As the water temperature of the tank was increased to 3°C above the control temperature (29°C), a significant decrease in swimming performance was observed even at 30°C for five species including *D. reticulatus* (Johansen and Jones, 2011). The authors suggested that such an increase in water temperature might even cause a loss of species if water warming increases >3°C (Johansen and Jones, 2011). Similarly, analysis of the swimming speed and activity patterns of individual Coral trout (*Plectropomus leopardus*) at four different temperatures (24, 27, 30, and 33°C) indicated that their swimming speed decreased sharply when the temperature was 30°C, and decreased further at 33°C. Furthermore, Pörtner and Knust (2007) showed that an increase in water temperature reduced fish growth and abundance, and affected the thermal tolerance of marine fish through oxygen limitation. However, an investigation of the impact of global warming on coral reef fish in terms of their growth (Munday *et al.*, 2008; Nilsson *et al.*, 2010), survival behaviour (Munday *et al.*, 2008), reproduction (Munday *et al.*, 2008), and feeding (Nilsson *et al.*, 2010) showed that small temperature changes were positive for larval development, but had a negative effect on adult reproduction (Munday *et al.*, 2008). Similarly, feeding, growth, and reproduction capacity decreased (Nilsson *et al.*, 2010) when water temperature was increased. These studies indicate that ocean warming has an important impact on underwater organisms, and in particular on fish.

In this study, we investigate the relationship between water temperature and swimming speed of *D. reticulatus* using data obtained from underwater videos in a natural setting. We have utilized almost a year's worth of data, which include natural temperature changes; this is in contrast with previous studies (Myrick and Cech, 2000; Ojanguren and Braña, 2000; Lough, 2007; Johansen and Jones, 2011; Johansen *et al.*, 2014) where a smaller temperature range acquired by changing fish tank water temperatures had the potential to cause unrealistic fish trajectories or ignore possible adaptations within a natural environment. We have discovered that the swimming speed of *D. reticulatus* at higher temperatures is greater than at lower temperatures, thereby contradicting previous studies on *D. reticulatus* (Johansen and Jones, 2011) and other reef fish species (Myrick and Cech, 2000; Ojanguren and Braña, 2000; Lough, 2007; Johansen *et al.*, 2014).

Dataset

Underwater videos captured in open sea in Taiwan were used. The camera system was established at the intake bay of the third Nuclear Power Plant (NPP) inside Kenting National Park. The park is located at the southern tip of Taiwan (latitude: 21.9553 and longitude: 120.7544), where the water temperature is between 20 and 30°C, and is the setting for Taiwan's largest coral reef system. Water usage by the NPP refreshes the zooplankton of the bay and the abundant Acropora coral provides shelter for fish. The fish population inside the bay is dominated by zooplankton feeders, which form large aggregations of *Dascyllus* and *Chromis.* One of the most abundant damselfish species is *D. reticulatus*, which occurs in colonies, commonly feeding on zooplankton above the coral and descending to the shelter of branching coral for refuge.

The data analysis presented in this study is based on the Fish4Knowledge research tool (Boom *et al.*, 2013), which aims to help marine ecologists by analysing underwater videos, and includes fish detection (Spampinato *et al.*, 2012), tracking (Spampinato *et al.*, 2012), species recognition (Huang *et al.*, 2012), and visualization of the data. Videos from a single camera (3.6 mm focal length, 2/3 inches CCD) were used as we assumed that fish behaviour can vary depending on location, such as in the open sea, and above or below coral. The camera used in this study was at a depth of 2 m. Temperature data were obtained using a temperature and pressure recorder (SeaBird SBE 39 Temperature and Pressure Recorder, initial accuracy ± 0.002 at −5 to 35°C, typical stability 0.0002°C per month), which measured the temperature every 5 min. The measured data were stored in the Fish4Knowledge database per video. The minimum recorded water temperature was 20.87°C and the highest was 30.28°C.

In total, 12 247 videos (640 × 480 resolution, 10 min each, 24 frames per second) were analysed (see Supplementary material for an example video); all the videos were captured from a single camera during daytime hours from the second half of December 2011 to December 2012, and cover the entire period except for the dates from 4 September 2012 to the middle of November 2012 and a few days in the second half of December 2012, when the capture system was not working. Examples of the camera fields of view are shown in Figure 1, where the slight variations are due to repositioning after typhoons or camera lens cleaning. In total, 3 649 007 trajectories of *D. reticulatus* were identified and used in the analysis. The data analysis is based on detected, tracked, and recognized fish by the fish detection, tracking, and species recognition components of the Fish4Knowledge research tool (Boom *et al.*, 2013). To assess the quality of the automatically detected and analysed data, we manually examined 1000 of the 3.6 million fish trajectories, with 100 trajectories from each temperature interval were chosen randomly (see the Results section for the description

December 2011   May 2012   December 2012

Figure 1. Examples of camera fields of view during different months. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

of 10 temperature intervals). These data correspond to 16 504 detections in total, of which 16 210 were actually fish. Seven hundred and forty-five trajectories (11 602 detections) out of the 1000 trajectories were correctly tracked from one frame to the next, which was used to estimate speeds. All 745 trajectories were correctly recognized as *D. reticulatus*. Based on this manual examination, we estimate that 74.5% of the ~3.6 million trajectories are valid. Each trajectory contributes one speed estimate while the temperatures were measured per video, as described in the Method section. The median water temperature of each day is presented in Figure 2, which shows some seasonal temperature changes.

Methods

Fish trajectories were defined by the centre of a rectangular bounding box, which tightly surrounds the detected fish in the image (Figure 3). A fish was tracked through n frames and the trajectory of the fish is represented as:

$$T = \{(r_{f1}, s_{f1}), (r_{f2}, s_{f2}), \ldots, (r_{fn-1}, s_{fn-1}), (r_{fn}, s_{fn})\} \quad (1)$$

where (r, s) refers to the fish's position in an image and fi is the frame number. Calculating the fish speed in terms of pixels/frame using the fish positions given in Equation (1) would be unrepresentative, as fish nearer the camera would appear to move faster since fish swim in three-dimensions in the open sea. Therefore, we estimated the speed (mm s^{-1}) using world coordinates. Estimating the scene speed requires estimating the scene position in world coordinates. The unknown depth was estimated using the properties of the camera and the fish, such as fish height, since the observed fish length can change from one frame to the next as a fish is likely to change its orientation. The world coordinates of the ith fish detection in temperature interval k (out of K total temperature intervals) were estimated using simple geometry to relate the image position to the scene position:

$$\begin{aligned} z_i = \ &focal\_length \, (\text{mm}) \\ &\times \frac{estimated\_real\_height\_of\_fish_k \, (\text{mm})}{fish\_height\_in\_the\_image_i \, (\text{pixels})} \\ &\times \frac{image\_height \, (\text{pixels})}{sensor\_height \, (\text{mm})} \end{aligned} \quad (2)$$

$$\begin{aligned} &estimated\_real\_height\_of\_fish_k \, (\text{mm}) \\ &= fixed\_real\_height\_of\_fish \, (\text{mm}) \\ &\times \frac{mode \, (fish\_heights\_in\_the\_image_k \, (\text{pixels}))}{\sum_{j=1}^{K} mode \, (fish\_heights\_in\_the\_image_j \, (\text{pixels}))/K} \end{aligned} \quad (3)$$

$$x_i = \left[\frac{sensor\_width \, (\text{mm})}{image\_width \, (\text{pixels})} \times r_i \, (\text{pixels}) \times z_i \, (\text{mm}) \right] / focal\_length \, (\text{mm}) \quad (4)$$

$$y_i = \left[\frac{sensor\_height \, (\text{mm})}{image\_height \, (\text{pixels})} \times s_i \, (\text{pixels}) \times z_i \, (\text{mm}) \right] / focal\_length \, (\text{mm}) \quad (5)$$

where z_i is the estimated distance to the fish in three-dimensions, x_i is the estimated horizontal coordinate in three-dimensional world coordinates, and y_i is the estimated vertical coordinate in three-dimensional world coordinates using the image coordinates (r_i, s_i) from the ith detection. The image width and height were 640 and 480 pixels. The sensor width and height were 8.8 and 6.6 mm. The focal length was 3.6 mm. The justification for Equations (2–5) is as follows: based on the marine biology literature (Froese and Pauly, 2000; Shao, 2014), the maximum length of *D. reticulatus* is 90 mm. However, as the observed population might contain juveniles, we assumed a typical average fish length of 60 mm (the fish detection system did not detect small fish). The ratio of the total body
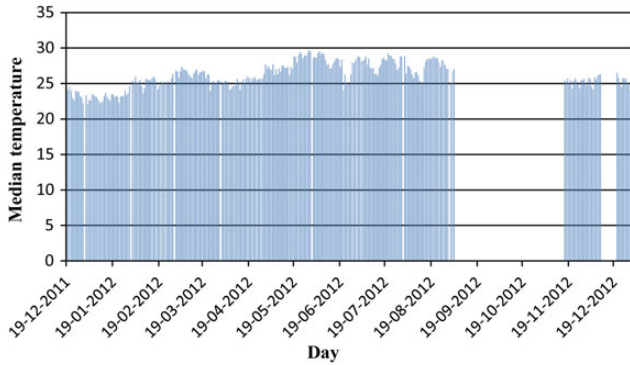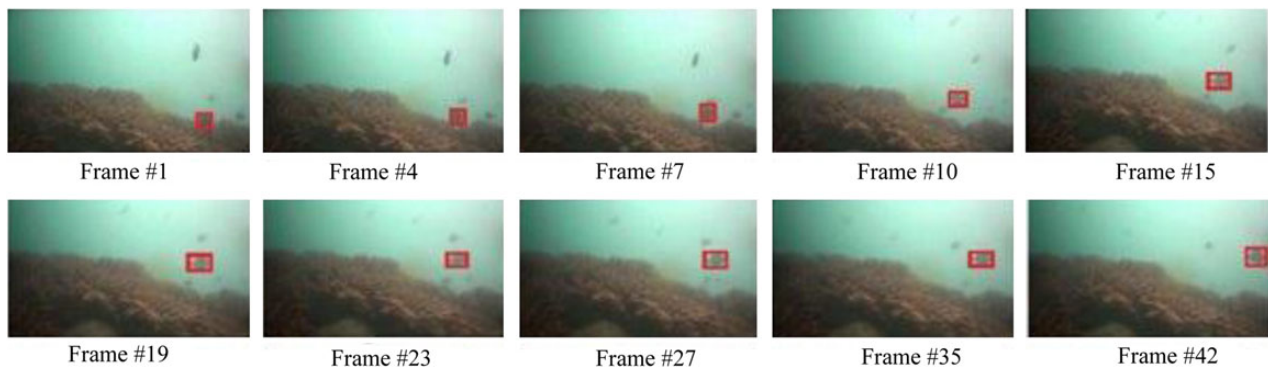

Figure 2. The median temperature per day. The highest temperature values were obtained between May 2012 and August 2012, whereas the lowest temperature values were recorded between December 2012 and January 2012. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Figure 3. An example *D. reticulatus* trajectory with some of the fish detection subsamples (red boxes).

length/body height was calculated using specimen photos (Froese and Pauly, 2000; Shao, 2014), which gave a value of 1.8. Therefore, for the typical fish length of 60 mm, we used a typical height of 33.33 mm (*fixed_real_height_of_fish*). The fish height was used because the varying horizontal orientation of a fish greatly affects the length, while height is only slightly affected by the direction in which a fish is facing. Because of the breeding cycle of the fish, their typical size may vary according to the time of year. Fish image height distribution analysis shows that this is true to a small extent, but that does not have a significant effect. This is partly because the fish detection system does not detect small fish and so only more mature fish were observed.

We assumed that given the large numbers of fish observed, the three-dimensional spatial distribution of the detected fish was the same during each time interval, and so any differences in the observed image height distribution were proportional to differences in the fish real heights in three-dimensions. To account for seasonal effects and the typical fish real height differences in each temperature interval, nominal height and distribution of fish image heights for a particular temperature interval were used. The estimated real height of a fish in the temperature interval k (*estimated_real_height_of_fish$_k$*) can be found by rescaling the nominal height of a fish (*fixed_real_height_of_fish*) by the ratio of the typical height (*fish_height_in_the_image$_k$*) for that temperature interval to the typical height over all the observations; the mode of the data was used due to the many outliers. By using the large number of observations analysed, the under- and overestimates roughly cancel each other out. In addition, irrespective of the actual typical fish height (*fixed_real_height_of_fish*), rescaling of the size implicitly rescales the speeds; therefore, the increasing speed trend with temperature remains, although the magnitude might be different. The ratios of the sensor_height, image_height or sensor_width, image_width convert the image units (pixels) to scene units (mm).

After the positions in the world coordinates had been determined, the speed of a fish can be estimated by dividing the sum of the three-dimensional position (P_i) differences between consecutive fish detections (which is usually one frame) by the time of observations [total frames observed—1 × 1/24 s frame^{-1}, Equation (5)].

$$V = \frac{24}{F-1} \sum_{i=1}^{F-1} ||P_{i+1} - P_i|| \tag{6}$$

where P_i is the estimated three-dimensional position in frame i and F is the total number of frames in the trajectory. A sample set of frames from a typical fish trajectory, originally with 42 detections, is shown in Figure 3, where a red fish detection-bounding box indicates the tracked fish.

Results

The overall finding was that the swimming speed of *D. reticulatus* was found to increases as the water temperature increased. The temperatures were divided into 10 intervals with each one containing a similar number of trajectories. An alternate way to represent the data would have been to divide them into intervals such that each spans equal temperature intervals, for example 1°C. However, in our case, this was not a sensible option since there were more data for some temperatures and much less data available for other temperatures. The temperature interval, number of trajectories, mean, median, and standard deviation of speeds with and without outliers, the number of outliers, and the corresponding calendar dates that the given data were observed are presented in Table 1. The mode of

the fish image height distributions for each temperature interval (bin) was 37, 37, 38, 37, 38, 37, 37, 37, 39, and 39 pixels for intervals 1–10, respectively, and these were used to calculate the *estimated_real_height_of_fish* using Equation (3).

The highest mean, standard deviation, and median speed were obtained when the temperature interval was 28.146–30.281°C. The standard deviations are larger at higher temperatures because the minimum speeds were roughly the same within each temperature interval (minimum speed ≈ 1 mm s^{-1}), with slower fish being more frequent within the lower temperature intervals which makes the standard deviation smaller for these temperatures. Box plots for each temperature interval are shown in Figure 4. The central mark on the box indicates the median speed, the edges of the box are the 25th and 75th percentiles, and the whiskers show the most extreme speeds after the outliers have been removed. Outliers are shown individually by plus symbols and are the upper ~7% of the data; the highest speed calculated was 651.25 mm s^{-1}. Speed values <1 mm s^{-1} were removed under the assumption that this was a video capture or detection failure.

Histograms (Supplementary material) of the individual speed estimates showed that data in all the temperature intervals were skewed to the left, i.e. more data having speeds <100 mm s^{-1}, while at higher temperatures the distributions shift to higher speeds. Additionally, the most frequent speed value for each temperature interval increases as the temperature increases. To assess whether the speeds in the different histograms were significantly different, we applied the Kruskal–Wallis significance test. The results of this test showed that the mean ranks for each temperature interval are significantly different (P-value = 0) from each other, which means that the speeds for each temperature interval are significantly different ($\alpha < 0.05$). Tukey–Kramer *post hoc* analysis was applied to analyse the speeds of each pairs of temperature intervals. The results again showed that the speed distributions are significantly different for each pair of temperature intervals. To test if the speed increase demonstrated a trend, such as monotonically increasing or decreasing, or was random, the Mann–Kendall test was applied to the mean and median speeds for each temperature interval. The results showed that the mean and median speeds show an increasing trend ($\alpha < 0.05$) as a function of water temperature, with a P-value of 0.0056 and 0.0095 for the mean and median speeds for each temperature interval, respectively.

Discussion

To the best of our knowledge, this work is one of only a few studies that have investigated fish swimming speed during natural changes of water temperature in an unconstrained natural environment. Based on the large automatically acquired and analysed dataset of underwater natural scene videos, we have demonstrated that the natural swimming speed of *D. reticulatus* increases as a function of water temperature over the range of 20.87–30.28°C. This result contradicts previous claims by Johansen and Jones (2011) and Johansen *et al.* (2014), which were based on evidence acquired using fish tanks and which utilized a narrower temperature range.

The main contributions of this work are (i) demonstrating the trend in fish speeds in different water temperatures using natural data and (ii) the use of a large number of videos which were required to generate a statistical power close to 1.0, thereby allowing us to demonstrate the trend in fish speed in different water temperatures. We have used >364 000 trajectories for each temperature interval, although 100 000 samples are sufficient to give a statistical power of 1.0.

Table 1. The results summarizing the observed relationship between the swimming speed of *D. reticulatus* and water temperature and the observed dates.

Interval	Temperature range (°C)	Number of trajectories	Mean with/without outliers (mm s^{-1})	Median with/without outliers (mm s^{-1})	Standard deviation with/without outliers	Number of outliers
1	20.870 – 23.322	364 946	16.26/12.00	10.73/9.91	19.21/8.01	28 912
	Dates: December 2011 (5), January 2012 (21).					
2	23.337 – 24.239	364 884	20.21/15.12	13.30/12.28	24.66/10.37	28 059
	Dates: December 2011 (5), January 2012 (8), February 2012 (2), March 2012 (1), April 2012 (2), June 2012 (1), December 2012 (2).					
3	24.240 – 24.862	365 258	27.84/21.45	18.74/17.30	30.12/15.11	26 740
	Dates: December 2011 (2), January 2012 (1), February 2012 (3), April 2012 (3), August 2012 (1), November 2012 (2), December 2012 (4).					
4	24.863 – 25.177	365 011	23.95/18.24	16.02/14.79	26.63/12.90	26 975
	Dates: February 2012 (5), March 2012 (3), April 2012 (3), June 2012 (2), September 2012 (1), November 2012 (3), December 2012 (2).					
5	25.178 – 25.396	364 543	22.71/17.32	15.18/14.02	25.72/12.45	26 284
	Dates: February 2012 (7), March 2012 (1), April 2012 (7), June 2012 (1), August 2012 (2), November 2012 (3).					
6	25.397 – 25.651	364 845	23.22/17.31	15.05/17.31	28.02/12.99	27 064
	Dates: February 2012 (5), March 2012 (2), April 2012 (6), November 2012 (5), December 2012 (3).					
7	25.652 – 26.003	365 035	23.80/17.98	15.76/14.53	27.11/12.99	27 141
	Dates: February 2012 (5), March 2012 (4), April 2012 (6), August 2012 (1), November 2012 (2), December 2012 (6).					
8	26.005 – 26.717	365 975	29.35/22.76	20.07/18.62	31.83/15.91	26 079
	Dates: February 2012 (1), March 2012 (10), April 2012 (2), May 2012 (4), June 2012 (2), July 2012 (3), August 2012 (5), December 2012 (4).					
9	26.719 – 28.145	363 865	34.79/27.57	24.39/22.73	35.94/19.06	24 479
	Dates: March 2012 (9), April 2012 (1), May 2012 (15), June 2012 (9), July 2012 (10), August 2012 (10), September 2012 (2).					
10	28.146 – 30.281	364 645	36.93/29.89	26.52/24.89	35.29/19.13	24 277
	Dates: May 2012 (11), June 2012 (15), July 2012 (17), August 2012 (11).					

The numbers inside the parentheses show the total number of days that the corresponding temperature values were observed for the corresponding month – year.
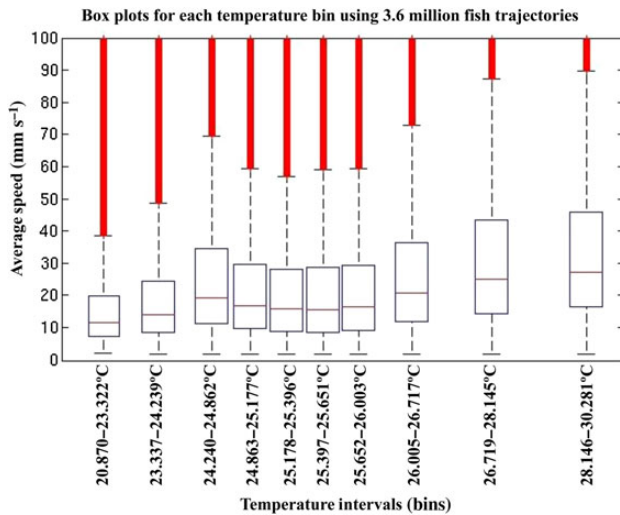
Figure 4. Box plots representing *D. reticulatus* speeds at each of the 10 selected temperature intervals. Speeds in the plot are limited to 100 mm s^{-1} to make the trend clearer, although the maximum speed was 651.25 mm s^{-1} (for 28.146–30.281°C). Outliers are shown individually with plus signs, although clustering makes them appears as thick bars. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

It is known that temperature can increase biological metabolism (biochemical reactions) and activities (such as in summer vs. winter). However, if the temperature is too warm or too cold and exceeds an acclimated upper limit or lower limit, then coral fish activities may slow down. The acclimated range of water temperatures for the tropical coral reef fish *D. reticulatus* is ~22–31°C, with the optimal range of 24–29°C. Our data suggest that fish speeds increase over this temperature range, even up to ~30°C, which contradicts earlier studies. However, we did not acquire any natural data at temperatures greater than 30.281°C; therefore, we cannot estimate at what temperature natural fish speeds decrease or even if they do. This swimming speed increase may have implications for the viability of *D. reticulatus* and other fish species should ocean temperatures rise as a consequence of global warming.

One of the limitations of our work is utilizing the data only from a single camera location, which may not represent fish species at the larger population level. As future work, the proposed work can be repeated with data coming from multiple camera locations. The developed approach may also have applicability in analysing and interpreting the three-dimensional movements of individuals within natural populations in a changing environment over time. In future work, stereo cameras could be used to directly measure the fish speeds in three-dimensions, which would improve the certainty of the analysis of fish speed vs. water temperature.

Supplementary material
Supplementary material is available at *ICESJMS* online.

Acknowledgement

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