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Natural Swimming Speed of *Dascyllus reticulatus* Increases with Water Temperature

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Abstract

Recent research on the relationship between coral reef water temperature and fish swimming activity stated that swimming speed is inversely correlated with temperature (Johansen and Jones, 2011; Johansen *et al.* 2014). For tropical coral reefs, one anticipated consequence of global warming is an increase of ≥3ºC in average water temperature in addition to greater thermal fluctuations (IPCC 2007; Lough, 2007; Johansen and Jones, 2011). Evaluating the behaviour of coral reef associated fish species under different temperatures can help to assess their sensitivity to climate change. In this paper, 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. Here we show that *Dascyllus reticulatus* swim faster as a function of increased water temperature over the range from 20.9ºC to 30.3ºC. 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, and converting image speeds to scene speeds. Temperatures were grouped into 10 intervals. The data shows ~2 mm/sec increase in average speed per additional degree of temperature over the range from 20.9ºC to 30.3ºC. The Mann-Kendall test using mean and median of speeds of each interval showed that there is a speed increase trend (not a random increase) as temperature increases at the 0.05 significance level. Therefore, our results contradict previous studies (Johansen and Jones, 2011) which also consider *Dascyllus reticulatus* and which claim that fish speed decreases as water temperature increases (Myrick and Cech, 2000; Ojanguren and Braña, 2000; Lough, 2007; Johansen *et al.* 2014).

Keywords

Fish trajectory, fish swimming speed, water temperature, video analysis, Dascyllus reticulatus, global warming

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 reduces at low temperatures (~10 ºC), increases in optimum temperatures (~15ºC) and then decreases at higher temperatures (≥20 ºC) such as for 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).

Similarly, more recent studies showed that increasing water temperature decreases the fish swimming capacity (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 damselfishes (including *Dascyllus reticulatus)* was studied (Johansen and Jones, 2011). As fish tank's water temperature was increased to 3ºC above the control temperature (29ºC), a significant decrease in swimming performance was observed even at 30ºC for five species including *Dascyllus reticulatus* (Johansen and Jones, 2011*)*. The authors suggested that such an increase in water temperature might even cause loss of species if water warming increases more than 3ºC degrees (Johansen and Jones, 2011). Similarly, analysis of the swimming speed and the activity patterns of individual Coral trout (*Plectropomus leopardus*) at four different temperatures (24, 27, 30 and 33ºC) indicated that their swimming speed decreased sharply when the temperature was 30ºC and decreased further at 33ºC. Furthermore, Pörtner and Knust (2007) showed that water temperature increase reduces fish growth and abundance and affects thermal tolerance of marine fish through oxygen limitation. However, investigation of the impact of global warming on coral reef fish in terms of the 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 are good for larval development but have a negative effect on adult reproduction (Munday *et al.*, 2008). Similarly, feeding, growth and reproduction capacity decreases (Nilsson *et al.*, 2010) when water temperature is increased. These studies all point to ocean warming having an important impact on underwater organisms and particularly fish.

In this paper, we investigated the relationship between water temperature and swimming speed of *Dascyllus reticulatus* using data obtained from underwater videos in a natural setting. We used almost a year of data which includes natural temperature changes, contrasting 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 in a natural environment. We have discovered that the swimming speed of *Dascyllus reticulatus* at higher temperatures is greater than at lower temperature, contradicting previous studies on *Dascyllus reticulatus* (Johansen and Jones, 2011) and other reef fish species (Myrick and Cech, 2000; Ojanguren and Braña, 2000; Lough, 2007; Johansen *et al.*, 2014).

Data Set

Underwater videos captured in open sea in Taiwan were used. The camera system was set up 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, longitude: 120.7544) where the water temperature can be 20-30ºC and has Taiwan's largest coral reef system. The NPP's water usage refreshes the bay's zooplankton and the abundant Acropora coral provides shelter for fish. The fish assemblage inside the bay is dominated by zooplankton feeders, forming large aggregations of *Dascyllus* and *Chromis.* One of the most abundant damselfish species is *Dascyllus 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 analyzing underwater videos, including 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 millimetre focal length, 2/3 inches CCD) were used as we assumed that fish behaviour can vary at locations such as in the open sea, above or below a coral. The camera used here was at 2 meters depth. The temperature data was obtained using a temperature and pressure recorder (SeaBird SBE 39 Temperature and Pressure Recorder, having initial accuracy ± 0.002 at -5 to 35ºC, typical stability 0.0002ºC per month) which measured the temperature every 5 minutes. The measured data was stored in the Fish4Knowledge database per video. The minimum recorded water temperature was 20.87 ºC and the highest was 30.28 ºC.

In total 12247 videos (640x480 resolution, 10 minutes each, 24 frames per second) were analyzed (see supplementary material for an example video); all were captured from a single camera in daytime hours from the second half of December 2011 to December 2012 (except the dates from 4th of 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 (which varies slightly due to repositioning after typhoons or camera lens cleaning). In total 3649007 trajectories of *Dascyllus 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 this automatically detected and analyzed data, we manually examined 1000 of the 3.6 million fish trajectories where 100 trajectories from each temperature intervals were chosen randomly (See results section for the description of 10 temperature intervals). These correspond to 16504 detections in total of which 16210 are actually fish. 745 trajectories (11602 detections) out of the 1000 trajectories were correctly tracked from one frame to the next which is used to estimate speeds. All 745 trajectories were correctly recognized as *Dascyllus 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. Additionally, the median water temperature of each day is given in Figure 2, which shows some seasonal temperature changes.

Method

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

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

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 Eq. 1 would be unrepresentative as fish nearer the camera would appear to move faster since fish swim in 3-dimensions in the open sea. Therefore, we estimated the speed (mm/sec) using world coordinates. Estimating scene speed requires estimating scene position (in world coordinates). The unknown depth was estimated using camera and fish properties (such as fish height, since observed fish length can change from one frame to another as a fish is likely to change its orientation). The world coordinates of the i^{th} fish detection in temperature interval k (out of K total temperature intervals) are estimated using simple geometry to relate image position to scene position:

$$z_i = focal\_length(mm) \times \frac{estimated\_real\_height\_of\_fish_{\,k}(mm)}{fish\_height\_in\_the\_image_i(pixels)} \times \frac{image\_height\ (pixels)}{sensor\_height\ (mm)} \tag{2}$$

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

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

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

where z_i is the estimated distance to the fish in 3-dimension, x_i is the estimated horizontal coordinate in 3-dimenisonal world coordinates and y_i is the estimated vertical coordinate in 3-dimensional world coordinates using the image coordinates (r_i, s_i) from the i^{th} detection. The image width and height are 640 and 480 pixels. The sensor width and height are 8.8 and 6.6 mm. The focal length is 3.6 mm. The justification for Eqs. (2)-(5) is as follows: based on the marine biology literature (Froese and Pauly, 2000; Shao 2014) the maximum length of *Dascyllus reticulatus* is 90 mm. 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 total body-length/body-height was calculated using the specimen photos from (Froese and Pauly, 2000; Shao 2014) which is 1.8. Therefore, for the typical fish length 60 mm, we used the typical height as 33.33 mm (*fixed_real_height_of_fish*). Here, we use the fish height because the varying horizontal orientation of the fish affects the length greatly but the height is only slightly affected by its direction of facing. Because of the breeding cycle of the fish, the typical size of the fish may vary by the time of the year. Fish image height distribution analysis shows that this is true to a small extent, but 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 are observed.

We assume that, given the large numbers of fish observed, the 3-dimensional spatial distribution of the detected fish is the same in each time interval and so any differences in the observed image height distribution is proportional to differences in the fish real heights in 3-dimensions. To account for seasonal effects and the typical fish real height differences in each temperature interval, the nominal height and the distribution of fish image heights for that temperature interval are used. The estimated real height of a fish in the temperature interval *k* ($estimated\_real\_height\_of\_fish_k$) is found by rescaling the nominal height of the fish (*fixed_real_height_of_fish*) by the ratio of the typical height ($fish\_height\_in\_the\_image_k$) in that temperature interval to the typical height over all observations (we used the mode of the data because of many outliers). By using the large number of observations analyzed, the under and over estimates will roughly cancel each other. Also, irrespective of the actual typical fish height (*fixed_real_height_of_fish*), rescaling of the size implicitly rescales the speeds. So, the increasing speed trend with temperature would remain, although the magnitude might be different. The ratios of sensor_height, image_height or sensor_width, image_width convert image units (pixels) to scene units (mm).

After the positions in the world coordinates are found, the speed of a fish is estimated by dividing the sum of 3-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 sec/frame, Eq. 5).

$$V = \frac{24}{F-1}\sum_{i=1}^{F-1} ||P_{i+1} - P_i|| \tag{5}$$

where P_i is the estimated 3-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 having 42 detections) is given in Figure 3 with a red fish detection bounding box showing the tracked fish.

Results

Dascyllus reticulatus swimming speed increases as water temperature increases, this is supported by the following results and associated significance tests. The temperatures are divided into 10 bins where each bin has a similar number of trajectories. An alternate way to represent the data would have been to divide them into bins where each bin spans equal temperature intervals for example 1 ºC. However, in our case, this is not sensible since there are more data at some temperatures and much less data at 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 was observed are given in Table-1. The mode of the fish image height distributions for each bin was 37, 37, 38, 37, 38, 37, 37, 37, 39, and 39 pixels for bins 1 to 10 respectively and were used to calculate *estimated_real_height_of_fish* using Eq. 3.

The highest mean, standard deviation and median speed is obtained when the temperature interval is 28.146-30.281ºC. The standard deviations are larger at higher temperatures because the minimum speeds are roughly the same in each temperature interval (minimum speed≈1 mm/sec) while slower fish are more frequent in lower temperature intervals which makes the standard deviation smaller at those temperatures. For each temperature interval the box plots are given in Figure 4. The central mark on the box shows the median of the speeds, the edges of the box are the 25th and 75th percentiles, the whiskers shows the most extreme speeds after the outliers are filtered. Outliers (with highest speed of 651.25 mm/sec) are shown individually with plus signs and are the upper ~7% of the data. Speed values smaller than 1 mm/sec were removed under the assumption that this was a video capture or detection failure.

Histograms (see supplementary material) of individual speed estimates showed that data in all temperature intervals are skewed to the left (more data having speeds less than 100 mm/sec) while at higher temperatures the distributions shift to higher speeds. Additionally, the most frequent speed value for each bin increases as the temperature increases. To assess whether the speeds in the different histograms are significantly different, we applied the Kruskal-Wallis significance test. The results of this test showed that the mean ranks of each temperature bins are significantly different (p-value=0) from each other which means the speeds in each bin are significantly different ($\alpha<0.05$). The Tukey-Kramer post hoc analysis was applied to analyze the speeds of each pair of temperature intervals. Tukey-Kramer also showed that the speed distributions are significantly different for each pair of bins. To test if the speed increase has a trend (such as monotonically increasing or decreasing) or not (random), the Mann-Kendall test was applied to the mean and median speeds of each temperature interval. The results showed that mean and median of speeds have an increasing trend ($\alpha<0.05$) as a function of water temperature with p-value 0.0056 and 0.0095 for mean and median speeds of each temperature interval respectively.

Discussion

To the best of our knowledge, this work is among the few that have investigated fish swimming speed during natural changes of water temperature in an unconstrained natural environment. Based on the large automatically acquired and analyzed dataset of underwater natural scene videos, we have demonstrated that the natural swimming speed of *Dascyllus reticulatus* increases as a function of water temperature over the range 20.87-30.28ºC. This result contradicts previous claims such as Johansen and Jones (2011) and Johansen *et al.* (2014) which are based on evidence acquired using a fish tank and utilizing a narrower temperature range.

The main contributions of this work are *i)* showing the trend in fish speeds in different water temperatures using **natural data** and *ii)* using **a large amount of video** which is required for generating a statistical power near to 1.0 (we have more than 364000 trajectories for each temperature bin while 100000 samples are enough for power=1.0) as allowing to show a trend in fish speed in different water temperatures.

It is known that temperature can increase biological metabolism (biochemical reactions) and activities (such as in summer *versus* winter). However, if the temperature is too warm or too cold and exceeds an acclimated upper limit or lower limit, then coral fish activities might slow down. The acclimated range of water temperatures for *Dascyllus reticulatus*, as a tropical coral reef fish, is about 22-31ºC with 24-29ºC as optimal. Our data suggests that fish speeds increase over the temperature range even up to ~30ºC which still contradicts the studies given above. However, we did not acquire any natural data from temperatures more than 30.281ºC, so we cannot estimate at what temperature level natural fish speeds decrease (if it does). On the other hand, this increase might have implications for the viability of *Dascyllus reticulatus* and other fish species should ocean temperature rise as a consequence of global warming.

One of the limitations of our work is utilizing the data coming from a single camera location which might not represent species at a 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 analyzing and interpreting the 3-dimensional movements of individuals in natural populations in a changing environment over time. As future work, stereo cameras could be used to measure directly the fish speed in 3-dimensions which will improve certainty of the analysis of fish speed *versus* water temperature.

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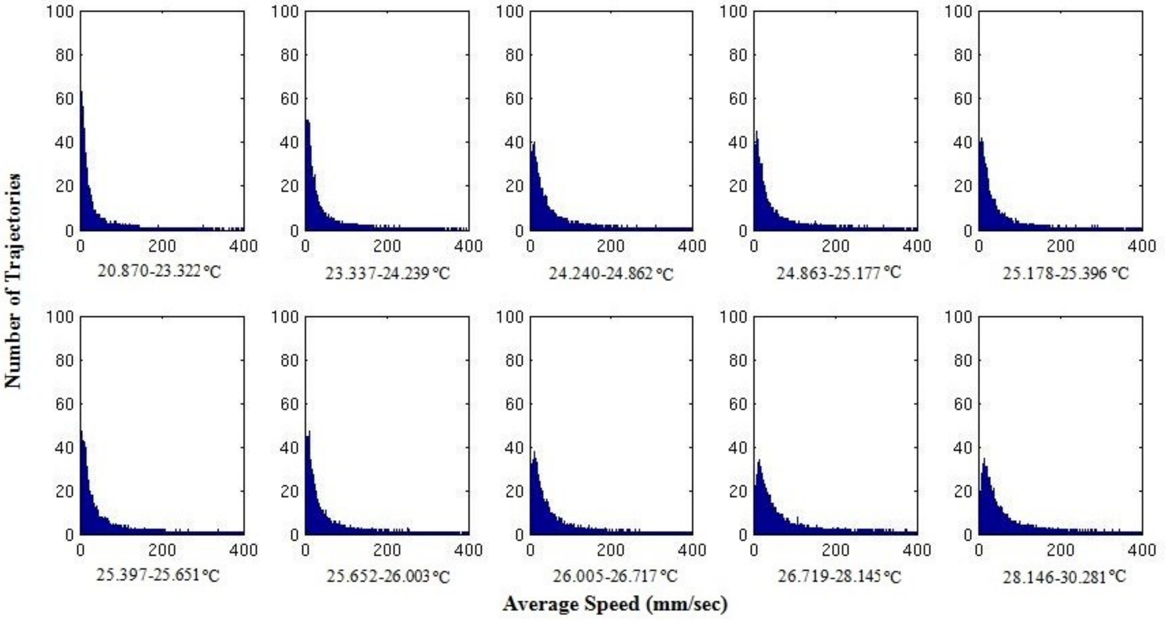
Supplementary Material

An example of underwater videos which are used in this paper and the histograms of individual speed estimate (0- 400 mm/sec) for each bin are available at ICESJMS online as supplementary material.



Tables

Table-1: The results summarising the observed relationship between *Dascyllus reticulatus* swimming speed and water temperature with the observed dates. The numbers inside of the parentheses show the total number of day that corresponding temperature values were observed for the corresponding month-year.

Bin	Temperature Interval (^{o}C)	Number of Trajectories	Mean with/without Outliers (mm/sec)	Median with/without Outliers (mm/sec)	Standard Deviation with/without Outliers	Number of Outliers
1	20.870-23.322	364946	16.26/12.00	10.73/9.91	19.21/8.01	28912
	Dates: December 2011 (5), January 2012 (21).					
2	23.337-24.239	364884	20.21/15.12	13.30/12.28	24.66/10.37	28059
	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	365258	27.84/21.45	18.74/17.30	30.12/15.11	26740
	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	365011	23.95/18.24	16.02/14.79	26.63/12.90	26975
	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	364543	22.71/17.32	15.18/14.02	25.72/12.45	26284
	Dates: February 2012 (7), March 2012 (1), April 2012 (7), June 2012 (1), August 2012 (2), November 2012 (3).					
6	25.397-25.651	364845	23.22/17.31	15.05/17.31	28.02/12.99	27064
	Dates: February 2012 (5), March 2012 (2), April 2012 (6), November 2012 (5), December 2012 (3).					

7	25.652-26.003	365035	23.80/17.98	15.76/14.53	27.11/12.99	27141
	Dates: February 2012 (5), March 2012 (4), April 2012 (6), August 2012 (1), November 2012 (2), December 2012 (6).					
8	26.005-26.717	365975	29.35/22.76	20.07/18.62	31.83/15.91	26079
	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	363865	34.79/27.57	24.39/22.73	35.94/19.06	24479
	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	364645	36.93/29.89	26.52/24.89	35.29/19.13	24277
	Dates: May 2012 (11), June 2012 (15), July 2012 (17), August 2012 (11).					

Figure Legends

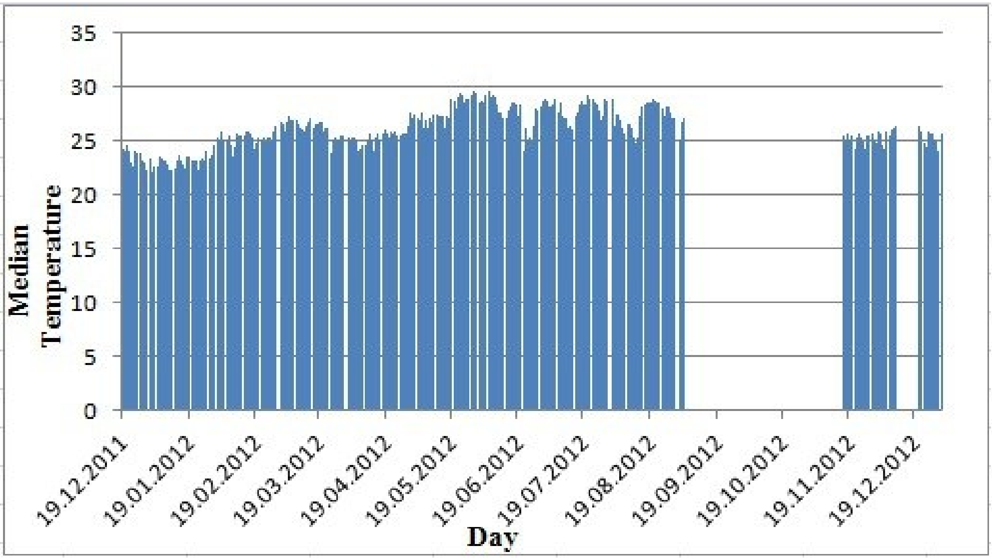
Figure 1: Examples of camera fields of view in different months.

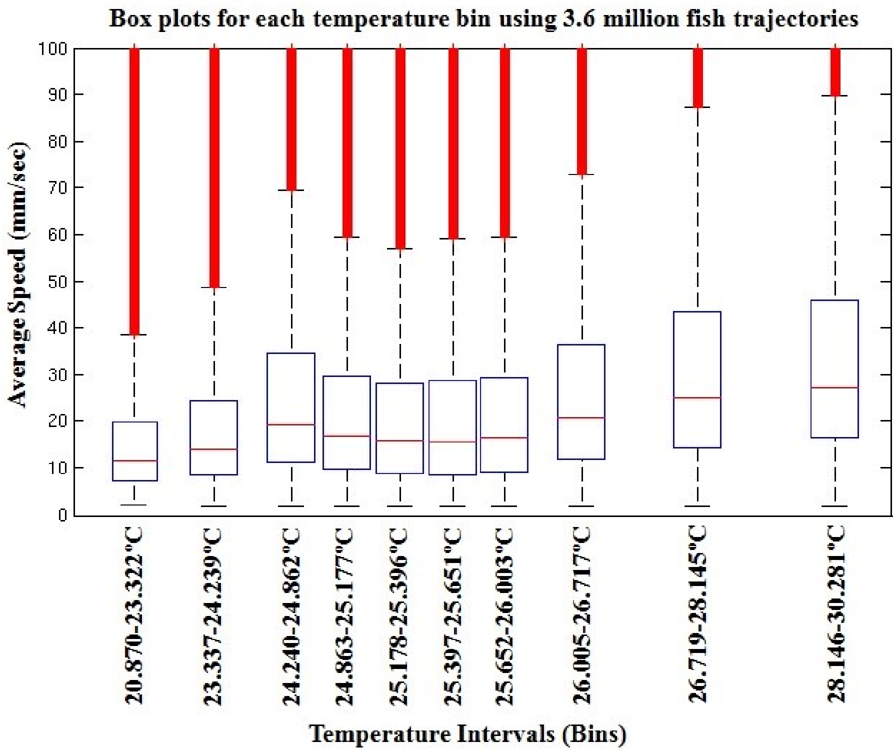
Figure 2: The data set used in terms of median temperature per day (the highest temperature values were obtained between May 2012 and August 2012 while the lowest temperature values belong to December 2012 to January 2012).

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

Figure 4: Box plots representing *Dascyllus reticulatus* speeds at each of the 10 selected temperature bins. Speeds in the plot are limited at 100 mm/sec to make the trend clearer although the maximum speed is 651.25 mm/sec (belongs to bin 10). Outliers are shown individually with plus signs (the clustering of these makes them appears as thick bars).

December 2011 May 2012 December 2012




Box plots for each temperature bin using 3.6 million fish trajectories
Average Speed (mm/sec)
0
10
20
30
40
50
60
70
80
90
100
20.870-23.322°C
23.337-24.239°C
24.240-24.862°C
24.863-25.177°C
25.178-25.396°C
25.397-25.651°C
25.652-26.003°C
26.005-26.717°C
26.719-28.145°C
28.146-30.281°C
Temperature Intervals (Bins)