

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

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13 **Abstract**

14 Recent research on the relationship between coral reef water temperature and fish
15 swimming activity stated that swimming speed is inversely correlated with temperature
16 (Johansen and Jones, 2011; Johansen *et al.* 2014). For tropical coral reefs, one anticipated
17 consequence of global warming is an increase of $\geq 3^{\circ}\text{C}$ in average water temperature in
18 addition to greater thermal fluctuations (IPCC 2007; Lough, 2007; Johansen and Jones,
19 2011). Evaluating the behaviour of coral reef associated fish species under different
20 temperatures can help to assess their sensitivity to climate change. In this paper, the speed
21 of freely swimming fish in a natural setting is investigated as a function of seasonal
22 changes in water temperature, as contrasted with systematic temperature increases in a fish
23 tank. Here we show that *Dascyllus reticulatus* swim faster as a function of increased water

24 temperature over the range from 20.9°C to 30.3°C. The experiments were carried out using
25 ~3.6 million fish trajectories observed at the Kenting National Park in Taiwan. Fish speed
26 was computed by detecting and tracking the fish through consecutive video frames, and
27 converting image speeds to scene speeds. Temperatures were grouped into 10 intervals.
28 The data shows ~2 mm/sec increase in average speed per additional degree of temperature
29 over the range from 20.9°C to 30.3°C. The Mann-Kendall test using mean and median of
30 speeds of each interval showed that there is a speed increase trend (not a random increase)
31 as temperature increases at the 0.05 significance level. Therefore, our results contradict
32 previous studies (Johansen and Jones, 2011) which also consider *Dascyllus reticulatus* and
33 which claim that fish speed decreases as water temperature increases (Myrick and Cech,
34 2000; Ojanguren and Braña, 2000; Lough, 2007; Johansen *et al.* 2014).

35

36 **Keywords**

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

39

40 **Introduction**

41 The relationship between coral reef water temperatures with fish metabolism and
42 activity has been studied previously in a fish-tank model, suggesting that, for many fish
43 species, swimming performance reduces at low temperatures (~10 °C), increases in
44 optimum temperatures (~15°C) and then decreases at higher temperatures (≥20 °C) such as
45 for California stream fish (Myrick and Cech, 2000), *Salmo trutta* (Ojanguren and Braña,
46 2000), *Oncorhynchus nerka* (Lee *et al.*, 2003) and *Oncorhynchus kisutch* (Lee *et al.*, 2003).

47 Similarly, more recent studies showed that increasing water temperature decreases the fish
48 swimming capacity (Johansen and Jones, 2011; Johansen *et al.* 2014). The effect of water
49 temperature increase on the swimming and metabolic performance of 10 different species
50 of damselfishes (including *Dascyllus reticulatus*) was studied (Johansen and Jones, 2011).
51 As fish tank's water temperature was increased to 3°C above the control temperature
52 (29°C), a significant decrease in swimming performance was observed even at 30°C for
53 five species including *Dascyllus reticulatus* (Johansen and Jones, 2011). The authors
54 suggested that such an increase in water temperature might even cause loss of species if
55 water warming increases more than 3°C degrees (Johansen and Jones, 2011). Similarly,
56 analysis of the swimming speed and the activity patterns of individual Coral trout
57 (*Plectropomus leopardus*) at four different temperatures (24, 27, 30 and 33°C) indicated
58 that their swimming speed decreased sharply when the temperature was 30°C and
59 decreased further at 33°C. Furthermore, Pörtner and Knust (2007) showed that water
60 temperature increase reduces fish growth and abundance and affects thermal tolerance of
61 marine fish through oxygen limitation. However, investigation of the impact of global
62 warming on coral reef fish in terms of the growth (Munday *et al.*, 2008; Nilsson *et al.*,
63 2010), survival behaviour (Munday *et al.*, 2008), reproduction (Munday *et al.*, 2008) and
64 feeding (Nilsson *et al.*, 2010) showed that small temperature changes are good for larval
65 development but have a negative effect on adult reproduction (Munday *et al.*, 2008).
66 Similarly, feeding, growth and reproduction capacity decreases (Nilsson *et al.*, 2010) when
67 water temperature is increased. These studies all point to ocean warming having an
68 important impact on underwater organisms and particularly fish.

69 In this paper, we investigated the relationship between water temperature and
70 swimming speed of *Dascyllus reticulatus* using data obtained from underwater videos in a
71 natural setting. We used almost a year of data which includes natural temperature changes,

72 contrasting with previous studies (Myrick and Cech, 2000; Ojanguren and Braña, 2000;
73 Lough, 2007; Johansen and Jones, 2011; Johansen *et al.*, 2014) where a smaller
74 temperature range acquired by changing fish tank water temperatures had the potential to
75 cause unrealistic fish trajectories or ignore possible adaptations in a natural environment.
76 We have discovered that the swimming speed of *Dascyllus reticulatus* at higher
77 temperatures is greater than at lower temperature, contradicting previous studies on
78 *Dascyllus reticulatus* (Johansen and Jones, 2011) and other reef fish species (Myrick and
79 Cech, 2000; Ojanguren and Braña, 2000; Lough, 2007; Johansen *et al.*, 2014).

80

81 **Data Set**

82 Underwater videos captured in open sea in Taiwan were used. The camera system was
83 set up at the intake bay of the third Nuclear Power Plant (NPP) inside Kenting National
84 Park. The park is located at the southern tip of Taiwan (latitude: 21.9553, longitude:
85 120.7544) where the water temperature can be 20-30°C and has Taiwan's largest coral reef
86 system. The NPP's water usage refreshes the bay's zooplankton and the abundant
87 Acropora coral provides shelter for fish. The fish assemblage inside the bay is dominated
88 by zooplankton feeders, forming large aggregations of *Dascyllus* and *Chromis*. One of the
89 most abundant damselfish species is *Dascyllus reticulatus*, which occurs in colonies,
90 commonly feeding on zooplankton above the coral and descending to the shelter of
91 branching coral for refuge.

92 The data analysis presented in this study is based on the Fish4Knowledge research tool
93 (Boom *et al.*, 2013) which aims to help marine ecologists by analyzing underwater videos,
94 including fish detection (Spampinato *et al.*, 2012), tracking (Spampinato *et al.*, 2012),
95 species recognition (Huang *et al.*, 2012) and visualization of the data. Videos from a single

96 camera (3.6 millimetre focal length, 2/3 inches CCD) were used as we assumed that fish
97 behaviour can vary at locations such as in the open sea, above or below a coral. The
98 camera used here was at 2 meters depth. The temperature data was obtained using a
99 temperature and pressure recorder (SeaBird SBE 39 Temperature and Pressure Recorder,
100 having initial accuracy ± 0.002 at -5 to 35°C , typical stability 0.0002°C per month) which
101 measured the temperature every 5 minutes. The measured data was stored in the
102 Fish4Knowledge database per video. The minimum recorded water temperature was 20.87
103 $^{\circ}\text{C}$ and the highest was 30.28°C .

104 In total 12247 videos (640x480 resolution, 10 minutes each, 24 frames per second)
105 were analyzed (see supplementary material for an example video); all were captured from
106 a single camera in daytime hours from the second half of December 2011 to December
107 2012 (except the dates from 4th of September 2012 to the middle of November 2012 and a
108 few days in the second half of December 2012 when the capture system was not working).
109 Examples of the camera fields of view are shown in Figure 1 (which varies slightly due to
110 repositioning after typhoons or camera lens cleaning). In total 3649007 trajectories of
111 *Dascyllus reticulatus* were identified and used in the analysis. The data analysis is based on
112 detected, tracked and recognized fish by the fish detection, tracking and species
113 recognition components of the Fish4Knowledge research tool (Boom *et al.*, 2013). To
114 assess the quality of this automatically detected and analyzed data, we manually examined
115 1000 of the 3.6 million fish trajectories where 100 trajectories from each temperature
116 intervals were chosen randomly (See results section for the description of 10 temperature
117 intervals). These correspond to 16504 detections in total of which 16210 are actually fish.
118 745 trajectories (11602 detections) out of the 1000 trajectories were correctly tracked from
119 one frame to the next which is used to estimate speeds. All 745 trajectories were correctly
120 recognized as *Dascyllus reticulatus*. Based on this manual examination, we estimate that

121 74.5% of the ~3.6 million trajectories are valid. Each trajectory contributes one speed
 122 estimate while the temperatures were measured per video, as described in the method
 123 section. Additionally, the median water temperature of each day is given in Figure 2,
 124 which shows some seasonal temperature changes.

125

126 **Method**

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

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

130

131 where (r,s) refers to the fish's position in an image and $f\hat{i}$ is the frame number. Calculating
 132 the fish speed in terms of pixels/frame using the fish positions given in Eq. 1 would be
 133 unrepresentative as fish nearer the camera would appear to move faster since fish swim in
 134 3-dimensions in the open sea. Therefore, we estimated the speed (mm/sec) using world
 135 coordinates. Estimating scene speed requires estimating scene position (in world
 136 coordinates). The unknown depth was estimated using camera and fish properties (such as
 137 fish height, since observed fish length can change from one frame to another as a fish is
 138 likely to change its orientation). The world coordinates of the i^{th} fish detection in
 139 temperature interval k (out of K total temperature intervals) are estimated using simple
 140 geometry to relate image position to scene position:

$$z_i = focal_length(mm) \times \frac{estimated_real_height_of_fish_k(mm)}{fish_height_in_the_image_i(pixels)} \times \frac{image_height(pixels)}{sensor_height(mm)} \quad (2)$$

$$\begin{aligned}
& \text{estimated_real_height_of_fish}_k(\text{mm}) \\
& = \text{fixed_real_height_of_fish}(\text{mm}) \\
& \quad \times \frac{\text{mode}(\text{fish_heights_in_the_image}_k(\text{pixels}))}{\sum_{j=1}^K \text{mode}(\text{fish_heights_in_the_image}_j(\text{pixels}))/K}
\end{aligned} \tag{3}$$

$$x_i = \left[\frac{\text{sensor_width}(\text{mm})}{\text{image_width}(\text{pixels})} \times r_i(\text{pixels}) \times z_i(\text{mm}) \right] / \text{focal_length}(\text{mm}) \tag{4}$$

$$y_i = \left[\frac{\text{sensor_height}(\text{mm})}{\text{image_height}(\text{pixels})} \times s_i(\text{pixels}) \times z_i(\text{mm}) \right] / \text{focal_length}(\text{mm}) \tag{5}$$

141

142 where z_i is the estimated distance to the fish in 3-dimension, x_i is the estimated horizontal
143 coordinate in 3-dimentional world coordinates and y_i is the estimated vertical coordinate
144 in 3-dimensional world coordinates using the image coordinates (r_i, s_i) from the i^{th}
145 detection. The image width and height are 640 and 480 pixels. The sensor width and height
146 are 8.8 and 6.6 mm. The focal length is 3.6 mm. The justification for Eqs. (2)-(5) is as
147 follows: based on the marine biology literature (Froese and Pauly, 2000; Shao 2014) the
148 maximum length of *Dascyllus reticulatus* is 90 mm. As the observed population might
149 contain juveniles, we assumed a typical average fish length of 60 mm (the fish detection
150 system did not detect small fish). The ratio of total body-length/body-height was calculated
151 using the specimen photos from (Froese and Pauly, 2000; Shao 2014) which is 1.8.
152 Therefore, for the typical fish length 60 mm, we used the typical height as 33.33 mm
153 (*fixed_real_height_of_fish*). Here, we use the fish height because the varying horizontal
154 orientation of the fish affects the length greatly but the height is only slightly affected by
155 its direction of facing. Because of the breeding cycle of the fish, the typical size of the fish
156 may vary by the time of the year. Fish image height distribution analysis shows that this is
157 true to a small extent, but does not have a significant effect. This is partly because the fish
158 detection system does not detect small fish, and so only more mature fish are observed.

159 We assume that, given the large numbers of fish observed, the 3-dimensional
160 spatial distribution of the detected fish is the same in each time interval and so any
161 differences in the observed image height distribution is proportional to differences in the
162 fish real heights in 3-dimensions. To account for seasonal effects and the typical fish real
163 height differences in each temperature interval, the nominal height and the distribution of
164 fish image heights for that temperature interval are used. The estimated real height of a fish
165 in the temperature interval k (*estimated_real_height_of_fish_k*) is found by rescaling the
166 nominal height of the fish (*fixed_real_height_of_fish*) by the ratio of the typical height
167 (*fish_height_in_the_image_k*) in that temperature interval to the typical height over all
168 observations (we used the mode of the data because of many outliers). By using the large
169 number of observations analyzed, the under and over estimates will roughly cancel each
170 other. Also, irrespective of the actual typical fish height (*fixed_real_height_of_fish*),
171 rescaling of the size implicitly rescales the speeds. So, the increasing speed trend with
172 temperature would remain, although the magnitude might be different. The ratios of
173 sensor_height, image_height or sensor_width, image_width convert image units (pixels) to
174 scene units (mm).

175 After the positions in the world coordinates are found, the speed of a fish is
176 estimated by dividing the sum of 3-dimensional position (P_i) differences between
177 consecutive fish detections (which is usually one frame) by the time of observations (total
178 frames observed-1 \times 1/24 sec/frame, Eq. 5).

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

179

180 where P_i is the estimated 3-dimensional position in frame i and F is the total number of
181 frames in the trajectory. A sample set of frames from a typical fish trajectory (originally
182 having 42 detections) is given in Figure 3 with a red fish detection bounding box showing
183 the tracked fish.

184

185 **Results**

186 *Dascyllus reticulatus* swimming speed increases as water temperature increases,
187 this is supported by the following results and associated significance tests. The
188 temperatures are divided into 10 bins where each bin has a similar number of trajectories.
189 An alternate way to represent the data would have been to divide them into bins where
190 each bin spans equal temperature intervals for example 1 °C. However, in our case, this is
191 not sensible since there are more data at some temperatures and much less data at other
192 temperatures. The temperature interval, number of trajectories, mean, median and standard
193 deviation of speeds with and without outliers, the number of outliers and the corresponding
194 calendar dates that the given data was observed are given in Table-1. The mode of the fish
195 image height distributions for each bin was 37, 37, 38, 37, 38, 37, 37, 37, 39, and 39 pixels
196 for bins 1 to 10 respectively and were used to calculate *estimated_real_height_of_fish*
197 using Eq. 3.

198 The highest mean, standard deviation and median speed is obtained when the
199 temperature interval is 28.146-30.281°C. The standard deviations are larger at higher
200 temperatures because the minimum speeds are roughly the same in each temperature
201 interval (minimum speed \approx 1 mm/sec) while slower fish are more frequent in lower
202 temperature intervals which makes the standard deviation smaller at those temperatures.
203 For each temperature interval the box plots are given in Figure 4. The central mark on the

204 box shows the median of the speeds, the edges of the box are the 25th and 75th percentiles,
205 the whiskers shows the most extreme speeds after the outliers are filtered. Outliers (with
206 highest speed of 651.25 mm/sec) are shown individually with plus signs and are the upper
207 ~7% of the data. Speed values smaller than 1 mm/sec were removed under the assumption
208 that this was a video capture or detection failure.

209 Histograms (see supplementary material) of individual speed estimates showed that
210 data in all temperature intervals are skewed to the left (more data having speeds less than
211 100 mm/sec) while at higher temperatures the distributions shift to higher speeds.
212 Additionally, the most frequent speed value for each bin increases as the temperature
213 increases. To assess whether the speeds in the different histograms are significantly
214 different, we applied the Kruskal-Wallis significance test. The results of this test showed
215 that the mean ranks of each temperature bins are significantly different (p-value=0) from
216 each other which means the speeds in each bin are significantly different ($\alpha<0.05$). The
217 Tukey-Kramer post hoc analysis was applied to analyze the speeds of each pair of
218 temperature intervals. Tukey-Kramer also showed that the speed distributions are
219 significantly different for each pair of bins. To test if the speed increase has a trend (such
220 as monotonically increasing or decreasing) or not (random), the Mann-Kendall test was
221 applied to the mean and median speeds of each temperature interval. The results showed
222 that mean and median of speeds have an increasing trend ($\alpha<0.05$) as a function of water
223 temperature with p-value 0.0056 and 0.0095 for mean and median speeds of each
224 temperature interval respectively.

225

226

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228 Discussion

229 To the best of our knowledge, this work is among the few that have investigated fish
230 swimming speed during natural changes of water temperature in an unconstrained natural
231 environment. Based on the large automatically acquired and analyzed dataset of
232 underwater natural scene videos, we have demonstrated that the natural swimming speed
233 of *Dascyllus reticulatus* increases as a function of water temperature over the range 20.87-
234 30.28°C. This result contradicts previous claims such as Johansen and Jones (2011) and
235 Johansen *et al.* (2014) which are based on evidence acquired using a fish tank and utilizing
236 a narrower temperature range.

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

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

251 for the viability of *Dascyllus reticulatus* and other fish species should ocean temperature
252 rise as a consequence of global warming.

253 One of the limitations of our work is utilizing the data coming from a single camera
254 location which might not represent species at a larger population level. As future work, the
255 proposed work can be repeated with data coming from multiple camera locations. The
256 developed approach may also have applicability in analyzing and interpreting the 3-
257 dimensional movements of individuals in natural populations in a changing environment
258 over time. As future work, stereo cameras could be used to measure directly the fish speed
259 in 3-dimensions which will improve certainty of the analysis of fish speed *versus* water
260 temperature.

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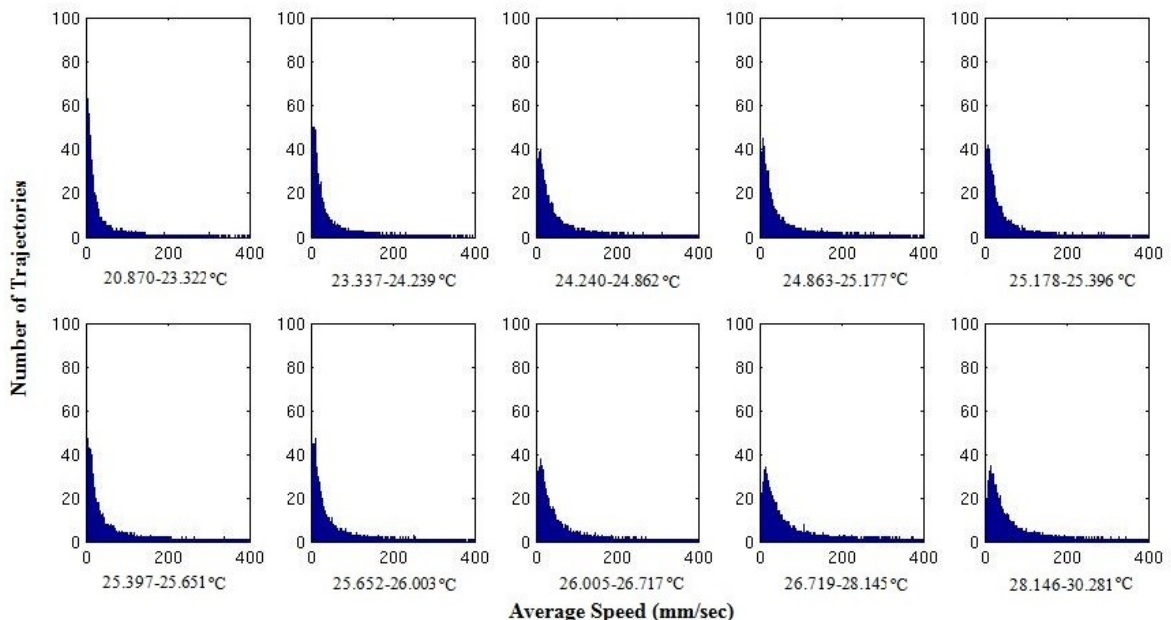
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330

331 Supplementary Material

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

335



339

Tables

340

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

Bin	Temperature Interval (°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).					

	25.652-26.003	365035	23.80/17.98	15.76/14.53	27.11/12.99	27141
7	Dates: February 2012 (5), March 2012 (4), April 2012 (6), August 2012 (1), November 2012 (2), December 2012 (6).					
	26.005-26.717	365975	29.35/22.76	20.07/18.62	31.83/15.91	26079
8	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).					
	26.719-28.145	363865	34.79/27.57	24.39/22.73	35.94/19.06	24479
9	Dates: March 2012 (9), April 2012 (1), May 2012 (15), June 2012 (9), July 2012 (10), August 2012 (10), September 2012 (2).					
	28.146-30.281	364645	36.93/29.89	26.52/24.89	35.29/19.13	24277
10	Dates: May 2012 (11), June 2012 (15), July 2012 (17), August 2012 (11).					

345

346

Figure Legends

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

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

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

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

357



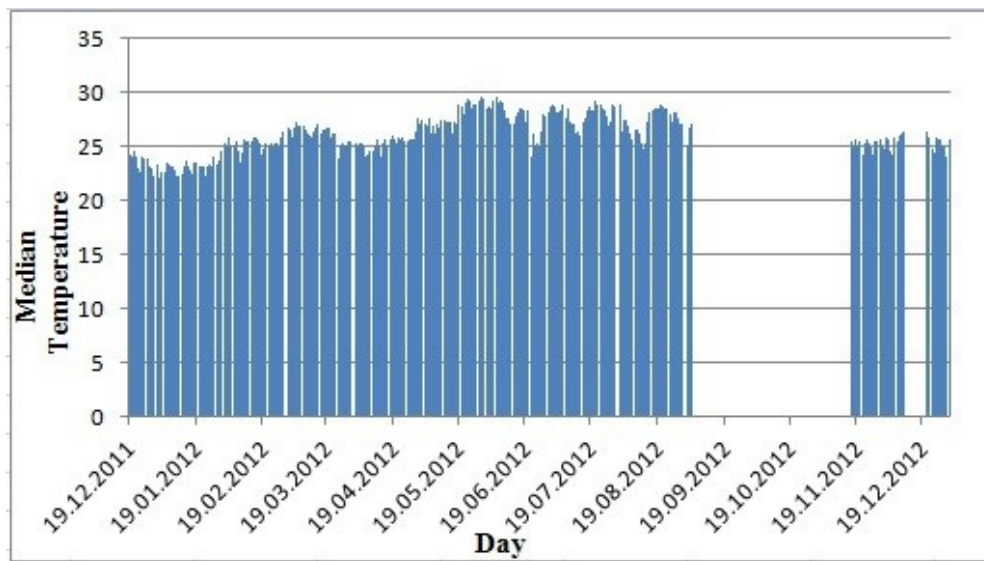
December 2011

May 2012

December 2012

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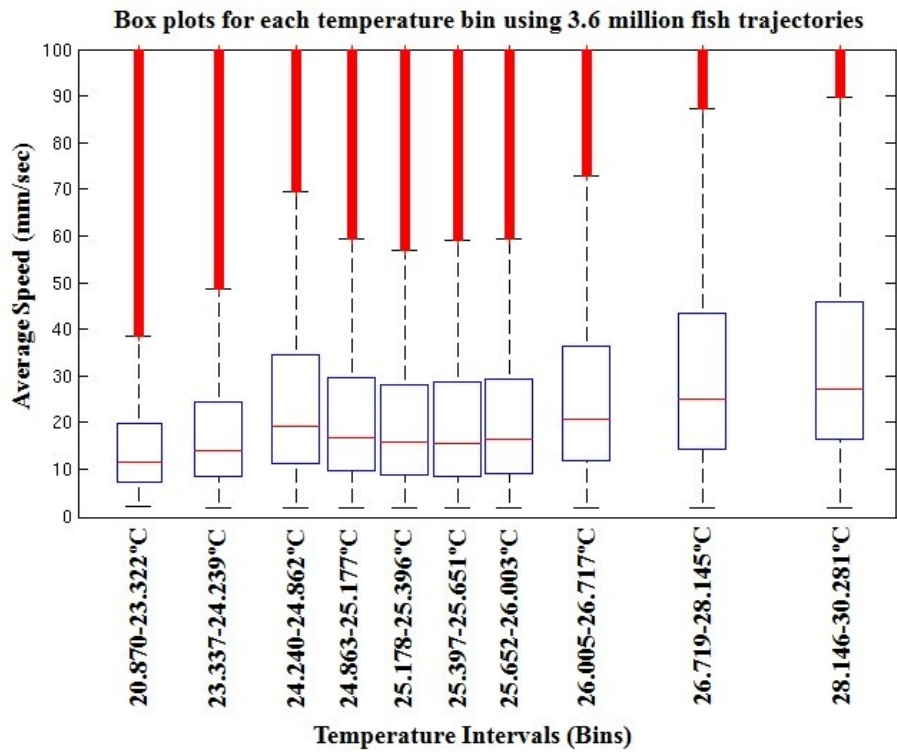
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