Estimating field metabolic rates using 3D stereo-video reveals the pace of life of coral reef fishes in the wild

First author: Francesca Conte*, Nina M. D. Schiettekatte* Contributing authors (alphabetic order): Simon J. Brandl, Beverly French, Chris Fulton, Alexandre Merciere, Tommy Norin, Valeriano Parravicini, Sébastien Villéger

Introduction

Anthropogenic stressors such as intensive fishing and climate change are affecting fish communities at an unprecedented global scale. There is a growing concern that impoverished fish communities may not be able to sustain ecosystem functioning and provide the ecosystem services that are indispensable for human well-being (Cardinale et al., 2012). In order to take the pulse of the functioning of a community, it is essential to quantify key ecosystem processes on the individual level such as nutrient cycling, herbivory, predation, growth, etc (Brandl et al. 2019). Our ability to understand the role of fishes in a changing world hinges on our capacity to quantify the ecosystem processes of fishes in their natural environment.

The metabolic rate of living organisms is an essential determinant of the flow of energy and nutrients in any ecosystem (Brown et al. 2004; Allen et al. 2005). In aquatic systems, fishes contribute to a high proportion of the total consumer biomass and therefore are crucial actors in ecosystem functioning. Theory predicts that metabolic rate increases sub□linearly with body mass according to a power function with a scaling coefficient of approximately 0.75 (Gillooly et al 2001; Brown et al 2004). This theoretic value has been widely accepted and confirmed for fishes through meta-analysis (e.g. Barneche et al 2014). Thus, the metabolic rate per unit biomass diminishes with body mass: i.e. a community with many small individuals will consume more energy than a community of the same total biomass with few large individuals. Consequently, beyond the effect of fish biomass itself, community-level metabolic rates vary with the community size structure (Barneche et al. 2014; Allen et al. 2005).

Metabolic rates of fishes are generally evaluated through two metrics: I) standard metabolic rate (SMR; Fry, 1957; Winberg, 1956), which corresponds to the metabolic rate of an inactive and fasting individual (Clark et al., 2013), and II) maximum metabolic rate (MMR), which

corresponds to the aerobic metabolic rate of an animal that is exercising maximally (Norin and Clark, 2016). Knowledge of these two metrics allows for calculations of a fish's aerobic scope (FAS), which is the ratio between MMR and SMR and represents the capacity to elevate metabolic rate above maintenance to support energetically demanding tasks such as physical activity (Clark et al., 2013). FAS tends to increase with body mass, as the scaling coefficient of MMR is often observed to be higher than 0.75 (Killen et al. 2007: Glosier et al. 2005). Both SMR and MMR can be estimated quite accurately in the laboratory through measurements of oxygen uptake rates (Clark et al., 2013), however, animals in the wild rarely reside at SMR or exercise maximally, so without information on the activity rate of individuals, we cannot estimate the metabolic rate of wild animals going about their daily activities.

The field metabolic rate (FMR) represents the average metabolic rate of an individual in the wild (Chung et al., 2019, Nagy et al., 2011) and lies somewhere between SMR and MMR. As only a proportion of aerobic scope, on average, is actually used by free-living fishes in their natural habitats (e.g. Norin and Clark, 2016), the scope for activity (FSA) corresponds to the ratio between the FMR and the SMR of a fish and is a better reflection of energy expenditure in the wild (Chung et al., 2019), bearing in mind that energy is also used on processes such as digestion and reproduction. In terrestial vertebrates, the metabolic scaling coefficient of FMR tends to be higher than that of SMR (~0.8; Nagy et al. 2005). The metabolic scaling coefficient of MMR of active fishes is known to range around the same elevated value, but the FMR scaling coefficient remains highly unknown (but see Chung et al., 2019).

Although FMR is ecologically more relevant than SMR or MMR (Hudson et al., 2013; Treberg et al., 2016), it has only been estimated for a small number of fishes (Lucas et al., 1993; Murchie et al., 2011; Cruz-Font et al., 2016; Chung et al., 2019) because it is challenging to measure for water-breathing animals in the aquatic environment (Treberg et al., 2016). Different methods for estimating FMR of fishes have, however, been developed, including accelerometry and heart rate measurements calibrated with rates of oxygen uptake in the laboratory (see Treberg et al., 2016; Grans et al. 2008). A major limitation of biologgers is that their application is limited to large individuals as the tag should not exceeed 2% of the total biomass (Grans et al 2008). Alternatively, FMR has been estimated from the isotopic compo-

sition of carbon in fish otoliths (Chung et al., 2019), but the generality of these findings still needs to be assessed, and the approach may not always be possible given the destructive nature of otolith sampling. In order to scale up individual-level metabolic rates to the community level, it is nescessary to expore additional pathways to the quantification of the pace of life of fishes in the wild.

Here, we propose a new approach to estimate FMR and FSA in fishes, which relies on the reasonable assumption that FMR lies between SMR and MMR (Figure 1). More precisely, we measured SMR and MMR using classical respirometry techniques in the laboratory, and we quantified field swimming speeds of 7 reef fish species using underwater stereo-video systems to derive FMR and FSA on the basis of known relationships between metabolic rate and swimming speed. Further, we compared the metabolic scaling coefficients of SMR, MMR, and FMR for all 7 species. Finally, using underwater visual census data of fish sizes and abundances in 15 reef sites around Mo'orea, French Polynesia, we quantified the assemblage-level SMR and FMR to see how these vary depending on the species composition of the assemblage.

Methods

Model species and study system

All data was collected in Mo'orea, French Polynesia, between March 2018 and November 2018. We focused on seven fish species with varying body size, trophic strategy, and behaviour: **Cephalopholis argus** (family serranidae), a large sedentary piscivore; **Chaetodon ornatissimus** (family chaetodontidae), an obligate coral feeder; **Chromis iomelas** (family pomacentridae), a small planktivore; **Ctenochaetus striatus** (family acanthuridae), a medium sized detrivore; **Naso lituratus** (family acanthuridae), a large herbivore feeding on macroalgae; **Odonus niger** (family ballistidae), a large schooling planktivore; and **Zebrasoma scopas** (family acanthuridae), a herbivore feeding on filamentous algae.

Standard and maximum metabolic rate estimations through respirometry

To quantify SMR and MMR, we conducted intermittent-closed respirometry experiments at 28°C (cf. Steffensen, 1989; Clark et al., 2013) on a total of 68 individuals of the seven

study species, which were collected in the lagoon (depth range 1-6m) around Mo'orea with hand nets and clove oil. After an acclimatisation and fasting period of 48 h in aquaria in the laboratory, the fish were transferred individually to a water-filled tub at 28°C and manually chased by the experimenter until exhausted (Norin and Malte, 2011; Clark et al., 2012), after which they were placed in respirometry chambers submersed in an ambient and temperature-controlled tank, where they were left for ~24 h. The intermittent respirometry cycles started immediately after a fish was placed in its respirometry chamber and consisted of a measurement (sealed) period followed by a flush period during which the respirometry chambers were flushed with fully aerated water from the ambient tank. Because fish were exhausted right before entering the respirometry chambers, it is possible to measure the approximate MMR. Depending on fish size, 8 respirometry chambers ranging in volume (including tubes and pumps) from 0.4 to 1.2 L were run in parallel, and measurement and flush periods lasted between X to X min and X to X min, respectively. SMR was calculated as the average of the 10 % lowest $\dot{M}O_2$ values measured during the entire period, after the removal of outliers (Chabot et al., 2016). MMR was calculated from the slope of the first measurement period (see Supporting Information Table 1) while SMR was calculated as the average of the 10% lowest $\dot{M}O_2$values measured during the entire ~24 h respirometry trial, after removal of any outliers (Chabot et al., 2016).

Swimming speed estimations through stereo-video analysis

We used two underwater stereo-video systems that were placed on the seafloor during to record fish movements. Each video system had 2 cameras (GoPro Hero6 Black), spaced at 90 cm from each other at an angle of approximately 6°. This method allows three-dimensional (3D) measurements (Butail and Paley, 2012; Hughes and Kelly, 1996). To analyse the recorded videos, we used VidSync, an open-source Mac application providing accurate 3D measurements thanks to its mathematical methods [described by Neuswanger et al. (2016)], which allow the synchronisation, calibration, and navigation of videos. We recorded calibration videos to correct for the nonlinear optical distortion of the images due to camera lenses and underwater housings, and to define the 3D coordinate system (x, y, z) used throughout the analyses, to calculate the fishes' 3D positions. Errors in length measurements through

video analysis increase with distance from the cameras (Neuswanger et al., 2016). Thus, for each underwater stereo-video system, we fitted a linear regression model describing the error in measurements in function of their distance from the nearest camera, which we used to adjust all measurements of distances and fish lengths (see Supporting Information Figure 1). We recorded twenty stationary stereovideos between the 19th of November 2018 and the 12th of December 2018. Videos were recorded at 12 to 14 m depth on the reef slope at the Tiahura site in Mo'orea (17 ° 29 '00.6 " S, 149 ° 54' 20.9 " W) and at five different time-periods: 5:00–7:00, 8:00–10:00, 11:00–13:00, 14:00–16:00, and 17:00–18:00. Each recording lasted for as long the battery lasted (~1 h). We then took measurements during three 10 min sequences with intervals of 10 min starting at the end of an acclimatisation period of 2 min to account for the presence of divers, which could affect fish behaviour (Hill and Wilkinson, 2004). We took measurements for all fishes visible by both cameras for 3 to 5 s during the three 10 min sequences. For each individual, fork length was measured three times from the videos as the straight-line distance between the fish's head and its tail fork, and three to five consecutive swimming speeds were measured as the distance the fish moved over the 3 to 5 s. Final fish lengths and swimming speeds were then calculated as the mean of the repeated measurements (see Supporting Information Table 2). In total, we recorded lengths and speeds for 634 fish.

Maximum swimming speed

We extracted maximum swimming speeds (U_{crit}) from Fulton et al. (2007). U_{crit} was defined by Brett (1964) as the swimming speed at which a fish becomes exhausted and stops swimming when it is exposed to regular incremental changes in speed in an experimental flume. In these experimental conditions, $\dot{M}O_2$measured at U_{crit} corresponds to the MMR (Norin and Clark, 2016). In Fulton et al. (2007), U_{crit} of 192 individuals of five families and their corresponding lengths were measured, and these measurements were then used in the present study (see Supporting Information Table 3) to related maximum swimming speed with body size at the family-level.

Data analysis

We quantified FMR and factorial scope for activity (FSA) by combining multiple regression models, describing the relationships between SMR and MMR with body mass, swimming speed (U), and maximum swimming speed [U_{crit}; from Fulton et al. (2007)] with body size. First, we used the respirometry data to fit a relationship between either SMR or MMR and body mass using a Bayesian hierarchical model, while taking into account the covariation between MMR and SMR measurements. We define the log_{10} transformation of SMR and MMR to be normally distributed with a mean (μ) and a standard deviation (σ) as follows:

$$log_{10}(MR)_i \sim Normal(\mu_i, \sigma)$$

,

$$\mu_i = (a + a_{j,k}) + (b + b_{j,k}) log_{10}(weight)_i$$

where i is the individual, j is the species, k is the type of metabolic rate (SMR or MMR), a is the global intercept of the regression; $a_{j,k}$ is the effect on the intercept for each species and type of metabolic rate, b is the global slope of $log_{10}(weight)$, $b_{j,k}$ is the effect on the slope of for each species and type of metabolic rate. We obtained the mean intercept and slope per species by summing global- and species-level parameters. We used an informative normal prior for the global slope coeficient (i.e. scaling coefficient) with average 0.75 and 0.1 as the standard deviation (West et. al, 1997). For all other parameters, we used uninformative priors as defined by Bürkner (2017).

Second, using the data retrieved from the video analyses, we fitted a hierarchical Bayesian regression model for estimating fish swimming speed in function of body length. We define the log_{10} transformation of speed to be student-t distributed with degrees of freedom (ν), mean (μ), and a standard deviation (σ).The student's t-distribution was applied to build a robust regression, as the nature of our data includes outliers (Motulsky and Brown, 2006).

$$log_{10}(speed)_i \sim Student(\nu, \mu_i, \sigma)$$

,

$$\mu_i = (a + a_j) + (b + b_j) log_{10}(length)_i$$

where i is the individual, j is the species, a is the global intercept of the regression, a_j is the effect on the intercept for each species, b is the global slope , b_j is the effect on the slope of for each species. For each species, their corresponding regression coefficients were estimated by summing two effects of the model: the global parameter and the species-specific effect on the global parameter.

Thirdly, we fitted a model, similar to the previous one to predict maximum swimming speed in function of body length on the family level using data extracted from Fulton et al. (2007):

$$log_{10}(speed)_i \sim Student(\nu, \mu_i, \sigma)$$

,

$$\mu_i = (a + a_j) + (b + b_j) log_{10}(length)_i$$

where i ,j is the family, a is the global intercept of the regression, a_j is the effect on the intercept for each family, b is the global slope of , b_j is the effect on the slope of for each family. Here, we also applied the student's t-distribution and used general uninformative priors. We note that this regression is based on family-level data, by grouping multiple species that are different from our stiuidy species (Fulton et al., 2006).

Factorial aerobic scope, field metabolic rate and factorial scope for activity calculations

We predicted the factorial aerobic scope (FAS), field metabolic rate (FMR), and factorial scope for activity (FSA) for the full size range of all model species (per cm). To estimate the fish's FAS at each possible length, we first predicted their SMR and MMR by calculating their weight by using published length-weight relationship accessed through FishBase (Froese et al., 2014; Table S4), and making predictions based on our model parameters. For each iteration of the prediction, FAS was calculated as $FAS = \frac{MMR}{SMR}$ (Fry, 1947; Killen et al., 2016). Finally we summarised the FAS per size per species by taking means, standard deviations, and

95% credible intervals.

Factorial scope for activity (FSA) is the factor obtained by dividing the fish's FMR ($\dot{M}O_2$ at average speed U) by their SMR. To describe the relationship between $\dot{M}O_2$ and swimming speed (U), Brett (1964) used the traditional power function: $\dot{M}O_2 = a10^{bU}$. Here, we applied the log_{10}-transformed form (Korsmeyer et al., 2002). Consequently, the following equation was used in this study to determine individual FMR:

$$log(FMR) = log(SMR) + \frac{log(MMR) - log(SMR)}{U_{crit}}$$

where we consider the slope $b = \frac{log(MMR) - log(SMR)}{U_{crit}}$. Here, U is predicted through our model relating length and swimmminh speed, $Ucrit$ is predicted for each length and species using our model for family-level maximum swimming speeds, and SMR and MMR is predicted as stated above. To include an estimate of uncertainty, we included 1000 iterations of estimates of the swimming speed U. For U_{crit}, SMR and MMR we used the median of the predicted values in this step.

Once FMR was determined, we calculated FSA with the following equation:

$$FSA = \frac{12FMR + 12SMR}{24SMR}$$

. We repeated this for each iteration and then summarised FSA per species per size. We assumed that fish rested for 12 h, representing the typical behavioural feature of sleep, common in many fish species (Shapiro and Hepburn, 1976). As such, for all studied species we assumed that they are active during the day and inactive during the night. This assumption is a generalization, and may introduce bias if fish are active at night as well.

Scaling up to assemblage-level

In 2016, reef fish communities were monitored in 13 sites on the outer reef around Mo'orea using underwater visual census. During each census a diver swam along a transect of 25m and counted all fishes within a width of 2m. All fishes were identified to the species level and their length was estimated to a preciscion of 1cm. Each transect covered an area of 50 m²,