**A Appendix**

(in italics = model parameter name, DW = dry weight, WW = wet weight, BL = body length)

Our model was designed to be adaptable to a wide range of reef fish species of different functional groups, which the user can specify based on key life history features such as activity patterns or feeding guilds via the pre-defined species definition parameters (see A.3 initialization for details). Combined with the possibility to use local habitat maps we hope our generic application will be useful to analyze and evaluate various local scenarios and habitat settings. The simulations tested and analyzed in the present study are exemplified for parrotfishes as diurnal herbivores (set as default values), a functional group of great ecological and economic importance in coastal ecosystems like coral reefs (Hughes et al., 2007; Lokrantz et al., 2008; Welsh and Bellwood, 2014) and seagrass beds (Unsworth et al., 2007). Specific parameter values were derived from empirical studies mainly with the Daisy parrotfish (*Chlorurus sordidus*), a ubiquitous and well-studied member of this functional group.

**A.1 Details for entity “fish”**

**A.1.1 Fish state variables**

* Spatial coordinates (*position)* and velocity (composed of two vectors, *velocity.x* and *velocity.y*, in m s -1) to depict individual movement behavior
* Body compartments (*gut*, *shorttermStorage*, *excessStorage*, *bodyProtein*, *bodyFat*, and a *reproductionStorage*) to model the fish’s bioenergetics
* Biomass (*biomass*, g wet weight) calculation based on energy values of body compartments to determine energy demand and to analyze biomass development on the population level
* Body length (*length*, standard length in cm) calculation based on *biomass* to allow for length-based sex change and analysis of size-frequency distributions on the population level
* Age (*age*, years) to follow age distributions of fish population
* Hunger state (Boolean, *hungry* or *not hungry*)depending on the fish’s current energy level and gut fullness
* Movement strategy (*moveMode*: *RANDOM* or *PERCEPTION*)
* Behavior mode (*behaviourMode:* *FORAGING*, *RESTING*, or *MIGRATING*) depending on diel cycle
* Maturity state (*sex*: *JUVENILE, FEMALE or MALE*) depending on life phase and *sexChangeMode* and to regulate reproduction processes
* Life phase (*phase*: *initialPhase or terminalPhase*)changes based on length-phase parameter for hermaphrodite fish species (note: individuals of gonochoristic species keep their initial sexes and only change from JUVENILE to an adult phase (i.e. (reproductive) *INITIAL phase* in our model)
* Sex change (*sexChangeMode*: *PROTOGYNOUS, PROTANDROUS* or *GONOCHROISTIC*) to allow for different reproductive strategies typical of reef fishes
* Feeding guild (*feedingGuild*: *HERBIVORE*, *PISCIVORE* (incl. invertebrate-feeders), *OMNIVORE, PLANKTIVORE, DETRIVORE*) defined as a functional group based on feeding behavior

**A.1.2 Activity repertoire (sorted by execution order)**

* Moving
* Feeding (food intake)
* Growing (digestion, energy budget including activity costs, somatic growth)
* Reproducing (reproduction costs and creation of offspring)

All processes in a fish’s life loop described below were updated every time step unless stated otherwise.

**A.1.2.1 Moving**

Determined by the abiotic factor *daytime* (see A.2.3 for details) as the major constraint of a fish’s diel activity and its movement behavior, the diurnal model fish was either foraging (day), resting (night), or migrating from resting to feeding areas (sunrise) or vice versa (sunset). These three different behavior modes (*FORAGING*, *RESTING*, and *MIGRATING*) were each associated with a different speed factor (*speed*, in body length per second to change dynamically with a fish’s body size) and thus varying energy costs (net cost of swimming in kJ, see A.1.2.3 for details on calculation): *foragingSpeedFactor* was set to 2.1 [BL s-1] (following (Korsmeyer et al., 2002)), while *restingSpeedFactor* was defined as 0 [BL s-1] (parrotfishes sleep in caves or under boulders (Ogden and Buckman, 1973) and are thus stationary when resting) and *migratingSpeedFactor* as 2.7 [BL s-1] (following (Wainwright et al., 2002)). To mimic natural variation among individuals a random component (*SPEED\_DEVIATION* of 10 % (following (Korsmeyer et al., 2002)) was added to the selected speed value using a uniform distribution over the interval *speedFactor* ± SPEED\_DEVIATION. We implemented a uniform distribution instead of a normal distribution to delimit both the extent of the speed variation and computational costs. The actual movement step was modelled discretely using vector-based walking algorithms based on the step length defined by the current speed value and the turning angle determined by one of two possible move modes (*moveMode*, either *RANDOM* or *PERCEPTION*). The move mode was selected prior to the start of a particular simulation run, which was always tested consecutively with each of the two move modes (movement strategy I-II, see table A1 for scenario overview) in three contrasting habitat setups (scenario A-C, see A.2 for details on the environment). To be able to compare differences in population dynamics depending on different movement strategies and habitat configurations, each parameter setting was replicated at least 3 times, for each scenario (scenario A.I to C.II).

*RANDOM* (complete random walk)

To simulate movement behavior as a stochastic process, in which the fish travels at random with no knowledge of its surroundings and thus no capabilities to respond to any environmental stimuli like predation risk or food availability, a simple random walk algorithm (RW) was implemented. A RW is one of the most basic and minimalistic ways to depict individual movements (Lima and Zollner, 1996) and a common method to model animal movement in the fields of biology (Codling et al., 2008). Thus, RW scenarios will serve as comparison to illustrate differences between different algorithms when modelling movement behavior. When applying RW in our model, the direction for the next movement step of an individual fish was chosen randomly within the fish’s maximum turn speed (*maxTurnSpeed* in ° s-1) using a uniform distribution (see above). The *maxTurnSpeed* parameter delimited the maximum angle a fish could turn at high temporal resolutions to ensure the emergence of complete random walk patterns at a minutely resolution (Jopp and Reuter, 2005). Since individuals could not interact with their environment, the behavior mode *MIGRATION* and *RESTING* were set to be equivalent to the *FORAGING* mode but with a different speed factor (*migratingSpeedFactor* and *restingSpeedFactor*, respectively) and without the fish feeding.

*PERCEPTION* (movement algorithm based on artificial potential fields representing the main environmental stimuli of the benthic seascape)

To compute the movement direction of an “intelligent” fish that can perceive and navigate through its surroundings we used vector field path planning based on artificial potential fields (Arkin et al., 1987; Arkin, 1989; Connell, 1990; Dudek and Jenkin, 2010; Khatib, 1986). The attractive and repulsive forces in our model were the level of food availability and the level of predation risk, respectively. By treating the pathfinding of “intelligent” model fishes as a flow field problem the calculation of the direction for the next movement step was composed of three basic steps following (Hagelbäck, 2012): First, depending on the fish’s behavioral mode different potential subfields of relevant landscape features were generated and normalized. Second, these subfields were individually weighted and then added to integrate the motivational basis of a fish to move (e.g. a fish in the behavior mode FORAGING moves to “to feed effectively, yet safe”). Third, based on the gradients of the summed potentials, a vector-based flow field was computed indicating the direction to the most attracting position (given the current motivation) in the fish’s near surroundings. In case the calculated direction vector was neutral (zero vector), i.e. the fish was located at the currently most favorable position, the direction for the next movement step was chosen randomly using a uniform distribution on all directions (360°). Thereby a fish was restrained from getting stuck in local minima, a known drawback of artificial potential field methods (Raja and Pugazhenthi, 2012).

More specifically, if a fish’s behavior mode was set to *FORAGING*, two potential subfields were generated based on food availability (*foodPotentialMap*. see A.2.2.1 for details on food availability) and predation risk (*riskPotentialMap*, see A.2.2.2 for details on predation risk), respectively, as the two main drivers considered for diel fish movements. For the generation of the (dynamic) *foodGrid* each grid cell was assigned a normalized positive (attractive) value between 0 and 1 mirroring the actual food density value of the food grid, while the (static) riskGrid consisted of normalized negative (repulsive) values between -1 and 0 displaying the habitat-dependent level of predation risk. Due the static nature of the latter calculating the *riskPotentialMap* was a relatively simple process, which was executed once per simulation run when the first individual of a fish species to which the *riskPotentialMap* was assigned, entered the simulation. In contrast, the *foodPotentialMap* was updated globally at every time step based on changing food densities due to foraging activities of the fish and/or re-growth of food resources. To further incorporate the perception range of an individual fish as an informational window to its environment (“look-a-head”), we used a blurring filter (Gaussian blur kernel) on the *riskPotentialMap*, in which each grid cell in the resulting risk map had a value equal to the average value of its neighboring cells weighted by their distance in the input map. The number of neighboring cells considered was defined by the *perceptionRadius*, which was set to 3 m as a typical reactive distance (Gotanda et al., 2009). For computational reasons the inclusion of the dynamic habitat feature food availability in the decision-making process was limited to the next eight directly adjacent cells representing a perception range with a reactive distance of 1 m (as part of step 3, see below) and no additional perception range parameter was applied.

In the second step, the two subfields (*foodPotentialMap* and *riskPotentialMap*) were weighted by a field-specific weighing factor (*PathfindingWeights.FOOD and PathfindingWeights.RISK*) and added to form the aggregated potential field (1).

1. , where *n* is the number of subfields affecting position (*x, y*) and *wi* is the weight for subfield *i* *(**H**a**g**e**l**bäck, 2012)*

By the implementation of a field-specific weighing factor our model framework explicitly allows for adaptive decision-making, which is an important characteristic of (realistic) fish movement behavior: Given that the hunger level is known to change the compromise between feeding and antipredator behavior (Bélisle, 2005; Hart, 1993; Lima and Dill, 1990; Milinski, 1993) and a starving fish, for example, might take greater risks, simulation results can reflect these trade-offs by dynamically adjusting the weighing factor depending on the fish’s energetic state. In our present study, however, we did not focus on adaptive decision-making but on how general habitat settings may influence fish movement behavior. We, therefore, set the parameters *weightFood* to a fixed value of 1 and *weightRisk* to twice the weight of food availability as predation directly impacts survival and is known to strongly influence feeding behavior (Catano et al., 2016).

Lastly, the vector-based flow field designating the direction of movement for each grid cell as a two-dimensional normalized vector was generated based on the gradients of the summed potentials. As a fish was set to evaluate the aggregated potential in all positions within a 1 m2 range of its own position, unit vectors for all directions (east, south, west, north) including diagonale der

s (southeast, southwest, northwest, northeast), pointing to the respective neighboring cell (2), were multiplied with the potential of the indicated cell. All eight vectors were then added resulting in the final unit direction vector for the next movement step (, (3)).

Similarly, the direction vector for a fish in the behavior mode *MIGRATING*, which was applied during twilight periods, was computed. However, instead of considering food density levels, the second subfield was generated based on the habitat type of the benthic seascape (*toForagePotentialMap,* *toRestPotentialMap*) as the fish’s motivation to move changed during these time periods from safely finding food to safely finding the appropriate habitat type for either resting or vice versa (depending on a fish’s activity pattern and daytime). The potential of the target habitat(s), defined by the parameters *foragingHabitat* and *restingHabitat*, respectively, was set to 1 as the most attractive locations. As soon as a fish reached its target or the twilight period had passed, the fish switched to the next behavior mode (*FORAGING* or *RESTING*), again depending on its activity pattern and time of day. If a fish was set to *RESTING*, it solely considered predation risk as a relevant landscape feature according to its only motivation to survive while resting.

Based on the direction given as a unit vector () calculated by either one of the two movement algorithms and the behavior-mode-dependent step length (i.e. the speed value as the vector length) the new velocity of a fish was calculated by multiplying the two (4). For fishes in the move mode *PERCEPTION* the speed (vector length) was further adjusted depending on the habitat type of the fish’s current position as fishes are known to be able to sense changes in food availability or predation risk in different habitats and adapt their velocity (Milinski, 1993). In unfavorable habitat patches, for instance, steps will be longer and we therefore increased the speed value for low complexity habitats like sand by 50% and rock by 25% (*SANDYBOTTOM\_SPEED\_FACTOR* and *ROCK\_SPEED\_FACTOR*). Fish in the move mode *RANDOM*, on the other hand, were not able to perceive their surroundings and were therefore not able to adapt their speed to landscape features.

The (individual) movement decision-making-process was, to summarize in short, thus either arbitrary and unaffected by any environmental stimuli when moving at *RANDOM* or influenced by how the fish perceived (via its perception range) and evaluated (via the motivation-specific weighing factors) the risk and benefits of the surrounding landscape features and adapted its speed accordingly taking into account its internal state (energy budget).

Once the fish had moved to its new position on the simulation grid, the habitat-dependent predation risk (indicated by the complexity of the habitat types (McCormick and Lönnstedt, 2013) was applied (see A.2.2.2 for details on predation risk). Additionally, a fish could die due to natural mortality (*naturalMortalityRisk* of 0.519 year-1 without fishing (McIlwain and Taylor, 2009)). In most cases the fish would survive and start executing the next activity scheduled for the respective behavior mode (i.e. *FORAGING*: start feeding module, *RESTING* or *MIGRATING*: skip feeding and start growing module).

**Table A1. Overview of scenarios tested with two different movement strategies (I-II) and three alternative habitat settings (scenario A-C).**

|  |  |
| --- | --- |
| **Movement strategy (*moveMode*)** | |
| **I. *RANDOM*** (complete random walk) | **II. *PERCEPTION*** (walk algorithm based on potential fields) |
| Basic assumptions:   * Behavioral minimalism (Lima and Zollner, 1996), i.e. individuals travel at random, no drift in any particular direction * Individuals have no knowledge of the surrounding environment and thus no organismal movement response to (changing) habitat features occurs | Basic assumptions:   * Behavioral explicit with adaptive (movement) decision-making, i.e. individuals are able to navigate in space and time and can adapt their behavior to changing environmental conditions * Individuals can sense and respond to (changing) habitat features via their perception range, which serves as an informational window to the surrounding seascape |
| **Scenario A** (adjacent habitat types) | |
| **A.I** | **A.II** |
| **Scenario B** (habitats separated by (land) barrier) | |
| **B.I** | **B.II** |
| **Scenario C** (mixed habitat types) | |
| **C.I** | **C.II** |

**A.1.2.2 Feeding (food intake)**

A model fish in the behavior mode *FORAGING* was set to feed until it was satisfied (i.e. *not hungry*) and consumed food (*foodIntake*, (5)) according to its mass-specific ingestion rate (*maxIngestionRate*, 0.03 g DW food (g WW fish)-1 h-1 following (Polunin et al., 1995)) or if not enough food was found on the current food cell (see A.2.2.1 for details on food availability) the available amount. The maximum ingestion rate was used instead of the mean rate to allow for compensation of short time periods of food scarcity. *Not hungry* was defined as the state, in which a model fish had either reached the maximum capacity of its gut or acquired enough energy to fill all its body compartments (to their respective limits, following (Dill, 1983)) and had additionally stored the energy equivalent needed for 5 hours resting in its excess storage (see A.1.2.3 for details on the fish’s bioenergetics). Thereby it was ensured that a well-fed fish had an energy surplus for a certain amount of time to execute non-feeding activities (resting and/or migrating) without necessarily loosing biomass. The food intake was converted to an energy value *(ingestedEnergy* in kJ) as the model’s “currency” (6) based on the energy content of epilithic algal turf (*energyContentFood*, 17.5 kJ per g dry weight food following (Bruggemann et al., 1994), the main food source of *C. sordidus* (Froese and Pauly, 2015).

1. Maximum food intake in [g DW food] = *maxIngestionRate* [g DW food (g WW fish)-1 h-1] \* biomass [g WW fish]
2. Energy intakein[kJ] *= foodIntake* [g DW food] \* *energyContentFood* [kJ (g DW food)-1]

**A.1.2.3 Growing** (**digestion, energy metabolism, somatic growth)**

To model the fish’s bioenergetics, different body compartments with specific functions were implemented following (Hölker and Breckling, 2005): the gut, a short-term storage representing carbohydrates, an excess storage to regulate the fish’s hunger state, body fat as a medium-term energy storage, and body protein as a long-term storage. Female individuals also possessed a reproduction compartment to account for the dynamics of the reproduction process (Hölker and Breckling, 2005) and the high energy demand for ovarian growth. Energy costs associated with the maturation of testes can often be considered as negligible compared with the costs of ovarian maturation (Wootton, 1979) and even though this may vary from species to species, male individuals in our model were assumed to have neglectable reproduction costs (see A.1.2.4 for details on the reproduction process). All body compartments were limited by a maximum and minimum capacity, which in most cases were calculated from the fish’s biomass or from the size-dependent resting metabolic rate (table A2). To ensure a realistic growth pattern, the protein compartment was limited not based on the state variable *biomass* but on the theoretical biomass (*expectedBiomass*) a fish would have reached at the current age under ideal conditions based on the species-specific von-Bertalanffy-growth function (7), one of the most widely used growth curve in fisheries science, and the weight-length relationship (to convert length to biomass) (8).

1. von-Bertalanffy-growth function for *C. sordidus* to calculate the expected length of a fish at a given age: Lt [SL in cm] = 39.1 [SL in cm]\*(1-e(-0.15\*(t+1.25))) (El-Sayed Ali et al., 2011)
2. Weight-length relationship for *C. sordidus* to calculate the expected biomass (g WW) of a fish at a given length (SL in cm): Biomass (g WW) = 0.0309\*(L[SL in cm])2.935 (El-Sayed Ali et al., 2011)

The fish was set to starve if its biomass was less than 60 % of the expected biomass (Letcher et al., 2011), e.g. due to scarce food resources, and it would stop growing when reaching a weight close to the expected biomass (maximum 120 % of *expectedBiomass*). All other compartment limits were derived from the approximate composition of a fish’s biomass following (Al-Jedah et al., 1999; Wootton, 1985).

**Table A.2 Details on the different body compartments (gut, short-term storage, excess storage, protein storage, fat storage, and reproduction compartment,) of a model fish including upper and lower limits (if applied) as well as the respective factors for the conversions between biomass and energy.**

|  |  |  |  |
| --- | --- | --- | --- |
| **Constant** | ***Constant name* (model)** | **Value [unit]** | **Comment & reference** |
| ***Gut storage*** | | | |
| Upper limit | *UPPER\_LIMIT\_FOOD\_PER\_BIOMASS* | 17 [mg DW \*food g WW fish-1] | (Polunin et al., 1995) |
| ***Short-term storage*** | | | |
| Upper limit | *UPPER\_LIMIT\_RMR* | 9 [h] | Maximum capacity of short-term storage based on resting metabolic rate (REF?) |
| ***Excess storage*** | | | |
| Desired energy value | *DESIRED\_EXCESS\_RMR* | 5 [h] | Energy a fish needs to sustain its resting metabolism (based on resting metabolic rate) over the given period of time. If a fish has reached this desired value, its hunger state is set to *not hungry*. (REF?) |
| ***Fat storage*** | | | |
| Upper limit | *UPPER\_LIMIT\_BIOMASS\_FRACTION* | 0.1 [% of *biomass*] | Following the approximate composition of a fish’s biomass (Al-Jedah et al., 1999) |
| Lower limit | *LOWER\_LIMIT\_BIOMASS\_FRACTION* | 0.05 [% of *biomass*] | Following the approximate composition of a fish’s biomass (Al-Jedah et al., 1999) |
| Growth fraction | *GROWTH\_FRACTION\_FAT* | 0.05  (0.035)\*  [% of *biomass*] | Fraction of surplus energy that flows to the fat compartment (magnitude following (Al-Jedah et al., 1999)) \*for reproductive, female individuals |
| Loss factor  (re-metabolizing energy) | *LOSS\_FACTOR* | 0.87 [%] | Loss factor for exchanging energy with the fat storage (following (Brett and Grooves, 1979)) |
| Conversion factor  (mass to energy) | *KJ\_PER\_GRAM\_FAT* | 36.3 [kJ g-1] | Metabolizable energy (kJ) from 1 g fat ( following (Brett and Grooves, 1979; Videler, 1993) |
| ***Protein storage*** | | | |
| Upper limit | *UPPER\_LIMIT\_EXP\_BIOMASS\_FRACTION* | 1.2 [% of *expectedBiomass*] | 1.2 \* expected biomass1 |
| Lower limit | *LOWER\_LIMIT\_EXP\_BIOMASS\_FRACTION* | 0.6 [% of *expectedBiomass*] | 0.6 \* expected biomass1, i.e. starvation following (Letcher et al., 2011) |
| Growth fraction | *GROWTH\_FRACTION\_PROTEIN* | 0.95 [% of *biomass*] | Fraction of surplus energy that flows to the protein compartment (magnitude following (Al-Jedah et al., 1999) |
| Loss factor  (re-metabolizing energy) | *LOSS\_FACTOR* | 0.90 [%] | Loss factor for exchanging energy with the protein storage (Brett and Grooves, 1979) |
| Conversion factor  (mass to energy) | *KJ\_PER\_GRAM\_PROTEIN* | 6.5 [kJ g-1] | Metabolizable energy (kJ) from 1 g protein following (Al-Jedah et al., 1999; Willmer et al., 2005) |
| ***Reproduction storage*** | | | |
| Upper limit | *UPPER\_LIMIT\_BIOMASS\_FRACTION* | 0.25 [% of *biomass*] | Following (Wootton, 1985) |
| Lower limit | *LOWER\_LIMIT\_BIOMASS\_FRACTION* | 0.1 [% of *biomass*] | Following(Wootton, 1985) |
| Growth fraction | *GROWTH\_FRACTION\_REPRO\_*  *REPRODUCTIVE* | 0.015 [%] | Fraction of reproduction energy growth from total for reproductive fish (magnitude following (Wootton, 1985) |

1 *expected biomass* refers to the biomass a fish would have reached under ideal growth conditions following the species-specific von-Bertalanffy-Growth function Lt [SL in cm] = 39.1 [SL in cm]\*(1-e(-0.15\*(t+1.25))) and length-weight relationship: (g WW) = 0.0309\*(L[SL in cm])2.935 (El-Sayed Ali et al., 2011).

*Digestion.* The energy ingested in the current time step was transferred as one energy portion to the gut compartment, which was modelled as a queue to mimic digestion. This portion was only available for the model fish’s metabolism after a certain amount of time (*gutTransitDuration*, 54 min for herbivore fish (Polunin et al., 1995)). After digestion energy losses due to egestion, excretion, and specific dynamic actions (*lossFactorDigestion*, 0.43 following (Brett and Grooves, 1979) were subtracted from the digested energy portion (9) and the resulting net energy (*netEnergy*) was available to meet the fish’s energy requirements.

1. Net energy in [kJ] = *lossFactorDigestion*\**energyIntake* [kJ]

*Energy consumption.* The fish’s overall energy costs (*consumedEnergy*) for the current time step were composed of the resting metabolism, which was calculated based on the size-dependent resting metabolic rate (*restingMetabolicRate*, metabolic rate of a resting but non-fasting individual at zero speed) following (Winberg, 1960) (10) plus the net swimming costs, i.e. the energy amount the fish used for its activities defined by its behavior mode (see above) calculated following (Korsmeyer et al., 2002) (11). We used an oxicaloric value of 14.2 J mg O2-1 to convert oxygen consumption rates into energy units (Ohlberger et al., 2006).

1. Resting metabolic rate (RMR) [ml O2 h-1] = 0.307 \* (biomass[g wet weight])0.81 (Winberg, 1960)

Conversion to [kJ h-1] = RMR [ml O2 h-1] \* 1.429 [mg ml O2-1]\*0.0142 [kJ mg-1]

1. Net cost of swimming [ml O2 h-1] = 1.193 + 1.660 \* log(speed [cm s-1]) (Korsmeyer et al., 2002)

Conversion to [kJ h-1]: Net cost of swimming [ml O2 h-1] \* 0.0142 [kJ mgO2-1]

1. Consumed energy [kJ] = RMR per time step [kJ]+ net cost of swimming per time step [kJ]

Subsequently, the consumed energy (12) was subtracted from the available net energy of the gut and the excess storage and any remaining energy was added to the short-term storage. If, however, the available energy was not sufficient to cover all energetic demands, the lacking amount was taken from the short-term storage. In case the consumed energy could still not be covered, e.g. due to food scarcity, the energy deficit was compensated by successively re-metabolizing energy from body resources, first from the fat, then from the protein storage, each associated with a compartment-specific loss factor (see table A2). If both compartments were depleted (i.e. reaching their lower limits), the fish would die from starvation.

*Somatic growth.* In case the energy accumulating in the short-term storage exceeded its maximum capacity, the surplus energy was allocated in different proportions to the medium- and long-term storage fat (*GROWTH\_FRACTION\_FAT*, 5 % of the surplus energy) and protein (*GROWTH\_FRACTION\_PROTEIN,* 95 %), respectively. For (reproductive) females another compartment is added and the allocation proportions are *growthFractionProtein* 95 % , *growthFractionFat*, 3.5 % and GROWTH\_FRACTION\_REPRO*,*1.5 %.. The energy sum of the short-term, fat, and protein compartment represented the fish’s *biomass*, which was updated in each time step. A fish would grow, i.e. increase its *length* when the updated *biomass* value exceeded any previously calculated value for this fish. If all of compartments were filled to their upper limits, any remaining energy was added to the excess storage. If the latter reached the desired amount (*DESIRED\_EXCESS\_RMR,* see A.1.2.2 feeding module for details), the fish was set to *not hungry* and stopped feeding until the energy level in the excess storage fell below the desired value again.

A fish would not grow during a time step, i.e. keep its *biomass* and *length*, if the energy level in short-term storage remained below its upper limit and no energy was added to the fish’s body compartments. In case, however, the energy amount in the short-term storage had dropped below its lower limit and the fish had to use energy from its fat and/or protein compartment to satisfy its energy demands, the fish would lose the amount of its biomass equivalent to the lacking energy while its length remained unchanged (growth in body length is generally considered to be unidirectional for vertebrates). The state variable *biomass* (and in the following also the *biomass*-dependent *length*) was updated based on the sum of energy in all body compartments (13) (except gut and reproduction storage, which are not considered for somatic growth) using the respective energy-to-mass conversion factors (i.e. inverse of mass-to-energy conversion factor, see table A2), and the species-specific weight-length relationship, respectively (4).

1. Conversion energy to biomass: *biomass* [g wet weight] =  (body compartment [kJ] \* compartment-specific conversion factor)

Subsequently, all biomass- and length-dependent variables like *restingMetabolicRate* and e*xpectedBiomass* as well as the capacities of the protein, fat and reproduction compartment were updated.

**A.1.2.4 Reproduction**

Depending on the updated *length* variable and the fish’s current maturity state (*sex*; *JUVENILE*, *FEMALE* or *MALE*) a fish might become mature (i.e. reproductive) and/or change its sex if hermaphrodite (*sexChangeMode.PROTOGYNOUS* or *sexChangeMode.PROTANDROUS*): As most parrotfishes are protogynous hermaphrodites a model fish changed its sex from juvenile to female as the initial phase (IP) and later to male as the terminal phase (TP) when exceeding a certain body length (note: due to their relatively low abundance, primary males were not considered in the model (see (McIlwain and Taylor, 2009)). In our simulations a juvenile fish became female (IP) when exceeding a standard length of 12.0 cm (*initialPhaseLength*, following (McIlwain and Taylor, 2009)) and an IP female became male (TP) when reaching a standard length of 17.0 cm (*terminalPhaseLength,* following (McIlwain and Taylor, 2009)). Both transitions were modelled using with a length-dependent likelihood, i.e. the larger the fish, the higher the probability to change sex. In contrast to female model fishes, male individuals had no functional role in the reproduction process, but contributed to processes related to population densities and food depletion.

As soon as the fish became an initial phase FEMALE, it started filling its reproduction compartment (see rules above in A.1.2.3 *Somatic growth*). Once the reproduction compartment reached 25 ± 2.5 % (using a uniform distribution) of the fish’s total current biomass, the fish had gathered enough energy supplies to reproduce (following (Wootton, 1979)). When reproducing, the reproduction compartment was set back to an energy level of 10 ± 1 % (using a uniform distribution) of the fish’s biomass following (Wootton, 1979) to compensate for the energetic costs of spawning. Spawning could occur during each time step as parrotfishes like *C. sordidus* are known to spawn on a daily basis and throughout the year with no clear seasonal patterns (McIlwain and Taylor, 2009). The number of off-spring (*numOffspring*) that was assumed to survive the larval stage (note: only post-settlement fish were considered in the population dynamics) and be able to settle within the population was set to two individuals per female and spawning event (REF?). The offspring was initialized with a biomass (*initialBiomass*) calculated from the von-Bertalanffy-growth function at the post-settlement age of three months (*postSettlementAge*, (McIlwain and Taylor, 2009)) and which was allocated to the different body compartments following the approximate composition of a fish’ body tissue ((Al-Jedah et al., 1999), see above). These new individuals entered the simulation when the timespan of *postsettlementAge* (here: 120 days) had passed and were placed randomly on the simulation grid.

**A.2 Details for the entity “environment”**

The virtual environment simulated in our model was represented by four main components we assumed essential to represent the fish-seascape link and its potential key drivers (food availability, predation risk) at the spatio-temporal scale of diel movement patterns: two spatial grids of identical sizes (500 x 750 pixel) and resolutions (1 pixel corresponds to 1 m2) depicting (i) the seascape with different habitat types and (ii) the habitat-dependent food resources, respectively, (iii) information on the habitat-dependent predation risk for the model species as well as (iv) the abiotic factor daytime (*TimeOfDay*). The simulated area thus equaled a total area of 0.375 km2 encompassing a typical home range (defined as “the area in which an individual spends the majority of its time and engages in most of its routine activities including foraging and resting” following (Green et al., 2015) ) of diurnal herbivores like parrotfishes (Green et al., 2015). We further assumed conditions to be uniform within one grid cell regarding habitat type, food resources, and predation risk. We kept track of each individual’s location and fate in the population and noted its velocity and energetic state. On population level total abundance and biomass, the abundances and biomass grouped by sexes (juveniles, females, males), and age-frequency distributions (grouped in five evenly distributed age classes) were noted at regular intervals (see table A.3). On the environmental level the duration of habitat use of all fishes per habitat type were recorded to allow for an analysis of habitat use patterns.

**A.2.1 Seascape (habitat grid)**

The habitat grid was based on an artificial seascape map, which was composed of different habitat types. In total, six distinct habitat types typically found in tropical coastal regions (coral reef, seagrass bed, mangroves, sandy bottom, and rock) were implemented as well as a type called “mainland” to simulate coastlines. For computational reasons a model fish in the move mode *RANDOM* was simply set back to its former position when attempting to move towards/onto mainland, while a fish in the moveMode *PERCEPTION* would automatically avoid mainland borders due to the forces of the potential fields (see A.1.2.1 for details on potential fields). Independent of the move mode all individuals were reflected at the margins of the simulation grid by inverting the respective velocity component (i.e. on vertical borders *velocity.x* and on horizontal ones *velocity.y*). Furthermore, the benthic map was made exchangeable to allow for tests of effects due to changing habitat structures and to enable the adaptation of the model to different study locations.

**A.2.2 Biotic factors (food availability and predation risk)**

**A.2.2.1 Food availability**

Food availability, as one of the two main seascape features driving fish movement behavior considered in our model, was estimated following (Clifton, 1995) and implemented as a grid-based, habitat-dependent amount of epilithic algae per unit surface area (i.e. grid cell), the main food source of parrotfishes like *C. sordidus* (Froese and Pauly, 2015). Depending on the underlying habitat type each food grid cell was initialized with a food value (*foodDensity*, algal mass density in g algal DW m-2), which was set randomly between habitat-dependent minimum and maximum values (coral reef = 5.0 – 14.0, seagrass bed= 5.0 – 10.0, mangrove = 3.0 – 5.0, rock = 2.0 – 5.0, sandy bottom = 0.1 – 3.0 g algal DW m-2) for every grid cell. The minimum value for algal mass density was implemented to avoid total (unnatural) depletion of food resources and ensure a realistic regrowth of algal cover. Based on a fish’s current position on the food grid and the pre-defined accessible foraging radius (*accessibleForagingRadius* in m, see table A.3), the ingestible amount of food (*availableFood* in g algal DW m-2) was calculated at each time step a fish was feeding using a radial neighbourhood (14) and made available for the fish, if in the behavior mode *FORAGING*. The amount of food on each accessible food grid cell was divided by a distance-factor to decrease the available amount with increasing distance to the fish.

1. Available food in [g algal DW]: *availableFood* [g algal DW] = ∑ (available food on accessible grid cells [g algal DW m-2]) / (1+(distance to fish’s position [m])2)

The algal mass density of the current and neighboring food cells was then depleted accordingly by the actually ingested amount, which was dependent on the fish’s maximum ingestion rate and energy budget (if *hungry* or *not hungry*). To incorporate feedback processes between individual fishes and the food resources a habitat-dependent algal re-growth function (15) (following (Bruggemann et al., 1994)) was applied daily (i.e. every first time step of a 24-h cycle) and added to the current food value.

1. Algal regrowth [mg algal DW m-2 d-1] per grid cell = 0.01 [d-1] \* (*foodDensity* of grid cell [g algal DW]) \* (1 - (*foodDensity* of grid cell [g algal DW]) / maximum *foodDensity* [g algal DW])

**A.2.2.2 Predation risk**

For reasons of simplicity the habitat-dependent risk of predation, as the second of the two modelled (external) driving forces for small-scale fish movement patterns, was implemented as an additional mortality rate, which changed in dependence of the topographic complexity of each habitat type (McCormick and Lönnstedt, 2013). However, due to the lack of empirical values for habitat-related mortality rates we assumed the predation-based mortality rate to be in the same order of magnitude as the rate for natural mortality (see above A.1.2.1) and set the predation risk of low complexity habitats such as sandy bottoms to 50 % of the natural mortality and for rock as habitats of intermediate complexity to 25 %. For high complexity habitats like coral reefs, seagrass beds, and mangroves, which may provide better protection for prey organisms, no additional predation-based mortality was implemented.

**A.2.3 Abiotic factors (daytime)**

Currently, abiotic factors implemented in the model are restricted to the factor daytime (T*imeOfDay*). As the main controlling force of a fish’s activity (i.e. *behaviourMode*: *FORAGING, RESTING; MIGRATING*) (Bellwood, 1995; Helfman, 1993)), T*imeOfDay* consisted of four distinct phases representing a 24-h cycle: sunrise, day, sunset, and night. Each phase was associated with a start- and end-time and durations were approximated for tropical regions following (Helfman, 1993): sunrise (6:01-7:00 h), day (7:01-18:00 h), sunset (18:01-19:00 h), and night (19:01-6:00 h).

**A.3 Initialization/Start values**

**Table A.3 Start parameters for simulation runs**

|  |  |  |
| --- | --- | --- |
| **Parameter** | **Default value [Unit]** | **Comment & reference** |
| ***General parameter settings*** | | |
| *seed* | 23 (long) | With identical seeds the same sequence of pseudorandom numbers is generated |
| *mapImageFilename* | "CoralEyeHabitatMapGUI.png" | File name of habitat map image. Any appropriate habitat map file (i.e. habitat types are represented by pre-defined color values) can be loaded with the map size (in pixel) determining the extension of the simulation world |
| *mapScale* | 1 | Used for conversions between the continuously modelled simulation world and the discretely modelled map space (value of 1 means: 1 pixel corresponds to 1 m) |
| *outputPopulationInterval* | 1 [day] | Time interval for writing population data to file |
| *outputAgeInterval* | 1 [day] | Time interval for writing age data to file |
| *outputStayDurationsInterval* | 1[month] | Time interval for writing stay durations data to file. Larger interval chosen due to large amount of data. |
| *algalGrowthRate* | 0.01 [day-1] | Proportional increase of algae per time unit. |
| ***Definition of the functional group DIURNAL HERBIVORE*** *(as a default setting)* ***derived from empirical data from the literature*** | | |
| **General parameters** | | |
| *name* | Diurnal herbivore (parrotfishes) | Name of functional group of modelled fish |
| *activityPattern* | Diurnal | Tick box to choose activity pattern of model species (diurnal or nocturnal with DIURNAL: sets resting time to night, foraging time to “day”, migrating to feeding areas to “sunrise”, and migrating to sleeping area to sunset; and NOCTURNAL: set resting time = day, foraging time = night, migrating to feeding areas: sunset, migrating to sleeping area = sunrise |
| *PreferredHabitats.FORAGING* | CORALREEF & SEAGRASS | Tick box to choose main foraging habitat of model species (options: all habitat types). This parameter is used during twilight (i.e. sunrise for diurnal fishes), when fish moves from resting to feeding habitats (*behaviourMode* *MIGRATION*) |
| *PreferredHabitats.RESTING* | CORALREEF | Tick box to choose main resting habitat of model species (options: all habitat types). This parameter is used analogue to *foragingHabitat* during twilight (i.e. sunset for diurnal fishes), when fish moves from feeding to resting habitats (*behaviourMode MIGRATION*) |
| *initalNum* | 500 [individuals] | Due to computational limitation we chose a relatively small initial number, that was still within the range reported for typical densities of parrotfish populations (Choat et al., 2012). The initial age- and gender-distribution was set to represent a typical parrotfish population (probability for: juvenile phase = 0.6, initial phase=0.35, terminal phase = 0.05). |
| *naturalMortalityRisk* | 0.519 [year-1] | Natural mortality rate (McIlwain and Taylor, 2009) |
| *postsettlementAge* | 120 [days] | Post-settlement age (REF) |
| *maxAgeAverage* | 10 [years] | (McIlwain and Taylor, 2009) |
| *MAX\_AGE\_DEVIATION* | 0.1 [%] (constant) | Deviation range of maximum ager |
| *PredationRisks.CORALREEF* | 0 [year-1] | Predation risk in CORALREEF habitat |
| *PredationRisks.SEAGRASS* | 0 [year-1] | Predation risk in SEAGRASS habitat |
| *PredationRisks.MANGROVE* | 0 [year-1] | Predation risk in MANGROVE habitat |
| *PredationRisks.ROCK* | 0.12975 [year-1] | Predation risk in ROCK habitat |
| *PredationRisks.SANDYBOTTOM* | 0.2595 [year-1] | Predation risk in SANDYBOTTOM habitat |
| **Movement related parameters** | | | |
| *maxTurnSpeed* | 5.0 [° s-1] | Maximum turning angle of a fish depending on time step duration (see (Jopp and Reuter, 2005)) | |
| *moveMode* | RANDOM | Drop-down list to choose movement strategy for current simulation run (options: *RANDOM* or *PERCEPTION*) | |
| *perceptionRadius* | 3 [m] | Radius in which a fish can perceive its surroundings, if in move mode *PERCEPTION* | |
| *SPEED\_DEVIATION* | 0.1 [%] (constant) | Following (Korsmeyer et al., 2002). | |
| *SpeedFactors.FORAGING* | 2.1 [BL s-1] | Following (Korsmeyer et al., 2002) | |
| *SpeedFactors.MIGRATING* | 2.7 [BL s-1] | Following (Wainwright et al., 2002) | |
| *SpeedFactors.RESTING* | 0 [BL s-1] | Parrotfish sleep in holes, caves or under boulders and are thus stationary when resting (Ogden and Buckman, 1973) | |
| *PathfindingWeights.FOOD* | 1 | Weighing factor for the potential subfield *foodPotentialMap*, if in move mode *PERCEPTION* and behavior mode *FORAGING* | |
| *PathfindingWeights.RISK,* | 2 | Weighing factor for the potential subfield *riskPotentialMap*, if in move mode *PERCEPTION* | |
| *PathfindingWeights.BOUNDARY* | 1 | Weighing factor for the potential subfield *boundaryPotentialMap*, if in move mode *PERCEPTION* | |
| *PathfindingWeights.BOUNDARY* | 1 | Weighing factor for the potential subfield *boundaryPotentialMap*, if in move mode *PERCEPTION* | |
| *PathfindingWeights.TO\_FORAGE* | 1 | Weighing factor for the potential subfield *toForagePotentialMap*, if in move mode *PERCEPTION* | |
| *PathfindingWeights.TO\_REST* | 1 | Weighing factor for the potential subfield *toRestPotentialMap*, if in move mode *PERCEPTION* | |
| ***Foraging related parameters*** | | | |
| *accessibleForagingRadius* | 1 [m] | Radius accessible for model fish around its current position on food grid; used to calculate amount of available food | |
| *energyContentFood* | 17.5 [kJ (g DW food)-1] | Following (Bruggemann et al., 1994) | |
| *feedingGuild* | HERBIVORE | Tick box to classify the modelled fish as a functional group according to its feeding habits (options: HERBIVORE, PISCIVORE (including invertebrate feeders), OMNIVORE, PLANKTIVORE, DETRIVORE). The *feedingGuild* also sets the values of the constants *gutTransitDuration* (3240 [s] for HERBIVORE (Polunin et al., 1995) and XX for all other functional groups) and *lossFactorDigestion* (0.43 for HERBIVORE and 0.59 for all others (Brett and Grooves, 1979)). Based on the l*ossFactorDigestion* the useable percentage of digested energy (net energy) after subtraction of loss due to assimilation, digestion, excretion, specific dynamic actions (SDA) is calculated. | |
| *maxIngestionRate* | [0.03 g DW food (g WW fish)-1 h-1] | Following (Polunin et al., 1995)  Maximum amount of food a model fish can consume per g biomass within a time span of 1 hour | |
| **Growth related parameters** | | | |
| *asymptoticLength* | 39.10 [SL in cm] | Parameter *L∞* of the von-Bertalanffy-growth function (El-Sayed Ali et al., 2011) | |
| *growthCoeff* | 0.15 | Growth coefficient *K* of the von-Bertalanffy-growth function (El-Sayed Ali et al., 2011) | |
| *zeroSizeAge* | -1.25 [years] | Parameter t0 of the von-Bertalanffy-growth function (El-Sayed Ali et al., 2011) | |
| *lengthMassCoeff* | 0.0309 | Coefficient (intercept) *a* of the weight-length relationship: W (in g WW) = a\*L (SL in cm)b  (El-Sayed Ali et al., 2011) | |
| *lengthMassExponent* | 2.935 | Parameter (exponent) *b* of the weight-length relationship: W (in g WW) = a\*L (SL in cm)b  (El-Sayed Ali et al., 2011) | |
| **Reproduction related params** | | | |
| *sexChangeMode* | Protogynous | Tick box to choose sex change mode of model species (options: protogynous (female to male), protandrous (male to female), gonochroistic (fixed sexes)) | |
| *FEMALE\_PROBABILITY* | 0.5 [%] (constant) | Applies only to gonochoristic (sexChangeMode.GONOCHORISTIC) species only: probability that a fish becomes female, when initialized | |
| *initalPhaseLength* | 12.0 [cm] | Following (McIlwain and Taylor, 2009)  Standard length at which fish may change its sex from JUVENILE to its (reproductive) initial phase (IP) | |
| *terminalPhaseLength* | 17 [cm] | Following(McIlwain and Taylor, 2009)  Standard length at which fish may change its sex from its initial phase (IP) to its terminal phase (TP) | |
| *numOffspring* | 2 | Ref? | |

**References**

Al-Jedah, J.H., Ali, M.Z., Robinson, R.K., 1999. The nutritional importance to local communities of fish caught off the coast of Qatar. Nutr. Food Sci. 99, 288–294. doi:10.1108/00346659910290349

Arkin, C., Riseman, E., Hanson, A., 1987. AURA: An architecture for vision-based robot navigation. Proc. DARPA Image Underst. Work. 417–431.

Arkin, R.C., 1989. Motor Schema-Based Mobile Robot Navigation. Int. J. Rob. Res. 8, 92–112.

Bélisle, M., 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology. Ecology 86, 1988–1995. doi:10.1890/04-0923

Bellwood, D., 1995. Direct estimate of bioerosion by two parrotfish species on the Great Barrier Reef, Australia. Mar. Biol. 121, 419–429. doi:Doi 10.1007/Bf00349451

Brett, J.R., Grooves, T.D.D., 1979. Physiology Energetics, in: Hoar, W., Randall, D., Brett, J. (Eds.), Fish Physiology. Academic Press, New York, pp. 279–352.

Bruggemann, J., Begeman, J., Bosma, E., Verburg, P., Breeman, A., 1994. Foraging by the stoplight parrotfish Sparisoma viride II. Intake and assimilation of food, protein and energy. Mar. Ecol. Prog. Ser. 106, 57–71. doi:10.3354/meps106057

Catano, L.B., Rojas, M.C., Malossi, R.J., Peters, J.R., Heithaus, M.R., Fourqurean, J.W., Burkepile, D.E., 2016. Reefscapes of fear: Predation risk and reef hetero-geneity interact to shape herbivore foraging behaviour. J. Anim. Ecol. 85, 146–156. doi:10.1111/1365-2656.12440

Choat, J.H., Carpenter, K.E. Clements, K.D., Rocha, L.A., Russell, B., Myers, R., Lazuardi, M.E., Muljadi, A., Pardede, S., Rahardjo, P., 2012. Chlorurus sordidus. The IUCN Red List of Threatened Species 2012 [WWW Document]. World Wide Web Electron. Publ. version.

Clifton, K.E., 1995. Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish Scarus iserti. Mar. Ecol. Prog. Ser. 116, 39–46. doi:10.3354/meps116039

Codling, E.A., Plank, M.J., Benhamou, S., 2008. Random walk models in biology. J. R. Soc. Interface 5, 813–834. doi:10.1098/rsif.2008.0014

Connell, J.H., 1990. Minimalist Mobile Robotics. Academic Press, San Diego.

Dill, L., 1983. Adaptive flexibility in the foraging behaviour of fishes’. Can. J. Fish Aquat. Sci. 40, 398–408. doi:10.1139/f83-058

Dudek, G., Jenkin, M., 2010. Computational Principles of Mobile Robotics, 2nd editio. ed. Cam, Cambridge. doi:10.1016/S0005-1098(02)00083-3

El-Sayed Ali, T., Osman, A.M., Abdel-Aziz, S.H., Bawazeer, F.A., 2011. Growth and longevity of the protogynous parrotfish, Hipposcarus harid, Scarus ferrugineus and Chlorurus sordidus (Teleostei, Scaridae), off the eastern coast of the Red Sea. J. Appl. Ichthyol. 27, 840–846. doi:10.1111/j.1439-0426.2010.01566.x

Froese, R., Pauly, D.E., 2015. FishBase [WWW Document]. World Wide Web Electron. Publ. version.

Gotanda, K.M., Turgeon, K., Kramer, D.L., 2009. Body size and reserve protection affect flight initiation distance in parrotfishes. Behav. Ecol. Sociobiol. 63, 1563–1572. doi:10.1007/s00265-009-0750-5

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J., White, A.T., 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol. Rev. 90, 1215–1247. doi:10.1111/brv.12155

Hagelbäck, J., 2012. Potential-field based navigation in StarCraft. 2012 IEEE Conf. Comput. Intell. Games, CIG 2012 388–393. doi:10.1109/CIG.2012.6374181

Hart, P., 1993. Teleost foraging: facts and theories, in: Pitcher, T.J. (Ed.), The Behaviour of Teleost Fishes. Chapman & Hall, London, pp. 253–284.

Helfman, G., 1993. Fish behaviour by day, night and twilight, in: Pitcher, T. (Ed.), The Behaviour of Teleost Fishes. Chapman & Hall, London, pp. 479–512.

Hölker, F., Breckling, B., 2005. A spatiotemporal individual-based fish model to investigate emergent properties at the organismal and the population level. Ecol. Modell. 186, 406–426. doi:10.1016/j.ecolmodel.2005.02.010

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. Curr. Biol. 17, 360–365. doi:10.1016/j.cub.2006.12.049

Jopp, F., Reuter, H., 2005. Dispersal of carabid beetles—emergence of distribution patterns. Ecol. Modell. 186, 389–405. doi:10.1016/j.ecolmodel.2005.02.009

Khatib, O., 1986. Real-Time Obstacle Avoidance for Manipulators and Mobile Robots. Int. J. Rob. Res. 5, 90–98.

Korsmeyer, K.E., Steffensen, J.F., Herskin, J., 2002. Energetics of median and paired fin swimming, body and caudal fin swimming, and gait transition in parrotfish (Scarus schlegeli) and triggerfish (Rhinecanthus aculeatus). J. Exp. Biol. 205, 1253–1263.

Letcher, B.H., Rice, J.A., Crowder, L.B., Binkowski, F.P., 2011. Size-Dependent Effects of Continuous and Intermittent Feeding on Starvation Time and Mass Loss in Starving Yellow Perch Larvae and Juveniles. Trans. Am. Fish. Soc. 8659, 1–5. doi:10.1577/1548-8659(1996)125<0014:SDEOCA>2.3.CO;2

Lima, S.L., Dill, L.M., 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Lima, S.L., Zollner, P.A., 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. 11, 131–135. doi:10.1016/0169-5347(96)81094-9

Lokrantz, J., Nyström, M., Thyresson, M., Johansson, C., 2008. The non-linear relationship between body size and function in parrotfishes. Coral Reefs 27, 967–974. doi:10.1007/s00338-008-0394-3

McCormick, M.I., Lönnstedt, O.M., 2013. Degrading habitats and the effect of topographic complexity on risk assessment. Ecol. Evol. 3, 4221–4229. doi:10.1002/ece3.793

McIlwain, J.L., Taylor, B.M., 2009. Parrotfish population dynamics from the Marianas Islands, with a description of the demographic and reproductive characteristics of Chlorurus sordidus 61pp.

Milinski, M., 1993. Predation risk and feeding behaviour, in: Pitcher, T.J. (Ed.), The Behaviour of Teleost Fishes. Chapman & Hall, London, pp. 285–306.

Ogden, J.C., Buckman, N.S., 1973. Movements, Foraging Groups, and Diurnal Migratons of the Striped Parrotfish Scarus Croicensis Bloch (Scaridae). Ecology 54, 589–596. doi:10.2307/1935344

Ohlberger, J., Staaks, G., Hölker, F., 2006. Swimming efficiency and the influence of morphology on swimming costs in fishes. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 176, 17–25. doi:10.1007/s00360-005-0024-0

Polunin, N.V.C., Harmelin‐Vivien, M., Galzin, R., 1995. Contrasts in algal food processing among five herbivorous coral‐reef fishes. J. Fish Biol. 47, 455–465. doi:10.1111/j.1095-8649.1995.tb01914.x

Raja, P., Pugazhenthi, S., 2012. Optimal path planning of mobile robots: A review. Int. J. Phys. Sci. 7, 1314–1320. doi:10.5897/IJPS11.1745

Unsworth, R.K.F., Taylor, J.D., Powell, A., Bell, J.J., Smith, D.J., 2007. The contribution of scarid herbivory to seagrass ecosystem dynamics in the Indo-Pacific. Estuar. Coast. Shelf Sci. 74, 53–62. doi:10.1016/j.ecss.2007.04.001

Videler, J.J., 1993. Fish Swimming. Chapman & Hall, London.

Wainwright, P.C., Bellwood, D.R., Westneat, M.W., 2002. Ecomorphology of locomotion in labrid fishes. Environ. Biol. Fishes 65, 47–62. doi:10.1023/A:1019671131001

Welsh, J.Q., Bellwood, D.R., 2014. Herbivorous fishes, ecosystem function and mobile links on coral reefs. Coral Reefs 33, 303–311. doi:10.1007/s00338-014-1124-7

Willmer, P., Stone, G., Johnston, I., 2005. Environmental physiology of animals, 2nd Editio. ed, Blackwell Publishing. Blackwell Publishing Ltd, Malden. doi:10.1007/s13398-014-0173-7.2

Winberg, G.G., 1960. Rate of Metabolism and Food Requirements of Fishes. doi:10.1017/CBO9781107415324.004

Wootton, R.J., 1985. Energetics of reproduction, in: Tytler, P., Calow, P. (Eds.), Fish Energetics: New Perspectives. Croom Helm Ltd, Sydney, pp. 231–254.

Wootton, R.J., 1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. Symp. Zool. Soc. L. 44, 133–159.

Arkin, C., Riseman, E., Hanson, A., 1987. AURA: An architecture for vision-based robot navigation. Proc. DARPA Image Underst. Work. 417–431.

Arkin, R.C., 1989. Motor Schema-Based Mobile Robot Navigation. Int. J. Rob. Res. 8, 92–112.

Bélisle, M., 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology. Ecology 86, 1988–1995. doi:10.1890/04-0923

Bellwood, D., 1995. Direct estimate of bioerosion by two parrotfish species on the Great Barrier Reef, Australia. Mar. Biol. 121, 419–429. doi:Doi 10.1007/Bf00349451

Brett, J.R., Grooves, T.D.D., 1979. Physiology Energetics, in: Hoar, W., Randall, D., Brett, J. (Eds.), Fish Physiology. Academic Press, New York, pp. 279–352.

Bruggemann, J., Begeman, J., Bosma, E., Verburg, P., Breeman, A., 1994. Foraging by the stoplight parrotfish Sparisoma viride II. Intake and assimilation of food, protein and energy. Mar. Ecol. Prog. Ser. 106, 57–71. doi:10.3354/meps106057

Catano, L.B., Rojas, M.C., Malossi, R.J., Peters, J.R., Heithaus, M.R., Fourqurean, J.W., Burkepile, D.E., 2016. Reefscapes of fear: Predation risk and reef hetero-geneity interact to shape herbivore foraging behaviour. J. Anim. Ecol. 85, 146–156. doi:10.1111/1365-2656.12440

Choat, J.H., Carpenter, K.E. Clements, K.D., Rocha, L.A., Russell, B., Myers, R., Lazuardi, M.E., Muljadi, A., Pardede, S., Rahardjo, P., 2012. Chlorurus sordidus. The IUCN Red List of Threatened Species 2012 [WWW Document]. World Wide Web Electron. Publ. version.

Clifton, K.E., 1995. Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish Scarus iserti. Mar. Ecol. Prog. Ser. 116, 39–46. doi:10.3354/meps116039

Codling, E.A., Plank, M.J., Benhamou, S., 2008. Random walk models in biology. J. R. Soc. Interface 5, 813–834. doi:10.1098/rsif.2008.0014

Connell, J.H., 1990. Minimalist Mobile Robotics. Academic Press, San Diego.

Dill, L., 1983. Adaptive flexibility in the foraging behaviour of fishes’. Can. J. Fish Aquat. Sci. 40, 398–408. doi:10.1139/f83-058

Dudek, G., Jenkin, M., 2010. Computational Principles of Mobile Robotics, 2nd editio. ed. Cam, Cambridge. doi:10.1016/S0005-1098(02)00083-3

El-Sayed Ali, T., Osman, A.M., Abdel-Aziz, S.H., Bawazeer, F.A., 2011. Growth and longevity of the protogynous parrotfish, Hipposcarus harid, Scarus ferrugineus and Chlorurus sordidus (Teleostei, Scaridae), off the eastern coast of the Red Sea. J. Appl. Ichthyol. 27, 840–846. doi:10.1111/j.1439-0426.2010.01566.x

Froese, R., Pauly, D.E., 2015. FishBase [WWW Document]. World Wide Web Electron. Publ. version.

Gotanda, K.M., Turgeon, K., Kramer, D.L., 2009. Body size and reserve protection affect flight initiation distance in parrotfishes. Behav. Ecol. Sociobiol. 63, 1563–1572. doi:10.1007/s00265-009-0750-5

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J., White, A.T., 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol. Rev. 90, 1215–1247. doi:10.1111/brv.12155

Hagelbäck, J., 2012. Potential-field based navigation in StarCraft. 2012 IEEE Conf. Comput. Intell. Games, CIG 2012 388–393. doi:10.1109/CIG.2012.6374181

Hart, P., 1993. Teleost foraging: facts and theories, in: Pitcher, T.J. (Ed.), The Behaviour of Teleost Fishes. Chapman & Hall, London, pp. 253–284.

Helfman, G., 1993. Fish behaviour by day, night and twilight, in: Pitcher, T. (Ed.), The Behaviour of Teleost Fishes. Chapman & Hall, London, pp. 479–512.

Hölker, F., Breckling, B., 2005. A spatiotemporal individual-based fish model to investigate emergent properties at the organismal and the population level. Ecol. Modell. 186, 406–426. doi:10.1016/j.ecolmodel.2005.02.010

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. Curr. Biol. 17, 360–365. doi:10.1016/j.cub.2006.12.049

Jopp, F., Reuter, H., 2005. Dispersal of carabid beetles—emergence of distribution patterns. Ecol. Modell. 186, 389–405. doi:10.1016/j.ecolmodel.2005.02.009

Khatib, O., 1986. Real-Time Obstacle Avoidance for Manipulators and Mobile Robots. Int. J. Rob. Res. 5, 90–98.

Korsmeyer, K.E., Steffensen, J.F., Herskin, J., 2002. Energetics of median and paired fin swimming, body and caudal fin swimming, and gait transition in parrotfish (Scarus schlegeli) and triggerfish (Rhinecanthus aculeatus). J. Exp. Biol. 205, 1253–1263.

Letcher, B.H., Rice, J.A., Crowder, L.B., Binkowski, F.P., 2011. Size-Dependent Effects of Continuous and Intermittent Feeding on Starvation Time and Mass Loss in Starving Yellow Perch Larvae and Juveniles. Trans. Am. Fish. Soc. 8659, 1–5. doi:10.1577/1548-8659(1996)125<0014:SDEOCA>2.3.CO;2

Lima, S.L., Dill, L.M., 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Lima, S.L., Zollner, P.A., 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. 11, 131–135. doi:10.1016/0169-5347(96)81094-9

Lokrantz, J., Nyström, M., Thyresson, M., Johansson, C., 2008. The non-linear relationship between body size and function in parrotfishes. Coral Reefs 27, 967–974. doi:10.1007/s00338-008-0394-3

McCormick, M.I., Lönnstedt, O.M., 2013. Degrading habitats and the effect of topographic complexity on risk assessment. Ecol. Evol. 3, 4221–4229. doi:10.1002/ece3.793

McIlwain, J.L., Taylor, B.M., 2009. Parrotfish population dynamics from the Marianas Islands, with a description of the demographic and reproductive characteristics of Chlorurus sordidus 61pp.

Milinski, M., 1993. Predation risk and feeding behaviour, in: Pitcher, T.J. (Ed.), The Behaviour of Teleost Fishes. Chapman & Hall, London, pp. 285–306.

Ogden, J.C., Buckman, N.S., 1973. Movements, Foraging Groups, and Diurnal Migratons of the Striped Parrotfish Scarus Croicensis Bloch (Scaridae). Ecology 54, 589–596. doi:10.2307/1935344

Ohlberger, J., Staaks, G., Hölker, F., 2006. Swimming efficiency and the influence of morphology on swimming costs in fishes. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 176, 17–25. doi:10.1007/s00360-005-0024-0

Polunin, N.V.C., Harmelin‐Vivien, M., Galzin, R., 1995. Contrasts in algal food processing among five herbivorous coral‐reef fishes. J. Fish Biol. 47, 455–465. doi:10.1111/j.1095-8649.1995.tb01914.x

Raja, P., Pugazhenthi, S., 2012. Optimal path planning of mobile robots: A review. Int. J. Phys. Sci. 7, 1314–1320. doi:10.5897/IJPS11.1745

Unsworth, R.K.F., Taylor, J.D., Powell, A., Bell, J.J., Smith, D.J., 2007. The contribution of scarid herbivory to seagrass ecosystem dynamics in the Indo-Pacific. Estuar. Coast. Shelf Sci. 74, 53–62. doi:10.1016/j.ecss.2007.04.001

Videler, J.J., 1993. Fish Swimming. Chapman & Hall, London.

Wainwright, P.C., Bellwood, D.R., Westneat, M.W., 2002. Ecomorphology of locomotion in labrid fishes. Environ. Biol. Fishes 65, 47–62. doi:10.1023/A:1019671131001

Welsh, J.Q., Bellwood, D.R., 2014. Herbivorous fishes, ecosystem function and mobile links on coral reefs. Coral Reefs 33, 303–311. doi:10.1007/s00338-014-1124-7

Willmer, P., Stone, G., Johnston, I., 2005. Environmental physiology of animals, 2nd Editio. ed, Blackwell Publishing. Blackwell Publishing Ltd, Malden. doi:10.1007/s13398-014-0173-7.2

Winberg, G.G., 1960. Rate of Metabolism and Food Requirements of Fishes. doi:10.1017/CBO9781107415324.004

Wootton, R.J., 1985. Energetics of reproduction, in: Tytler, P., Calow, P. (Eds.), Fish Energetics: New Perspectives. Croom Helm Ltd, Sydney, pp. 231–254.

Wootton, R.J., 1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. Symp. Zool. Soc. L. 44, 133–159.