How do fragmented seascapes influence fish movement behaviour?

Insights from an individual-based model (IBM) using potential fields

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by **Maren Kruse**

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Reviewers: **Dr. Hauke Reuter**
Leibniz Centre for Tropical Marine Research
Bremen, Germany

Prof. Dr. Matthias Wolff
Leibniz Centre for Tropical Marine Research
Bremen, Germany

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Advisory Committee

Reviewers: **Dr. Hauke Reuter**
Leibniz Centre for Tropical Marine Research
Bremen, Germany

Prof. Dr. Matthias Wolff
Leibniz Centre for Tropical Marine Research
Bremen, Germany

Examiners: **Prof. Dr. Juliane Filser**
University of Bremen
Bremen, Germany

Dr. Broder Breckling
University of Bremen
Bremen, Germany

Disputation colloquium on 12 December 2019

To my family

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Abbreviations

Abbreviation	Description
BL	Body length
DW	Dry weight
C. sordidus	*Chlorurus sordidus* (Forsskål, 1775)
IP	Initial phase
JUV	Juvenile
MPA	Marine protected area
RMR	Resting metabolic rate
SD	Standard deviation
SL	Standard length
TL	Total length
TP	Terminal phase
WW	Wet weight

Abstract

Analysing animal movement is essential for understanding processes such as the dynamics and spatial distribution of populations and has strong implications for the design and management of natural reserves. In tropical coastal ecosystems the movement patterns of fishes are particularly important as many fish species undertake diel migrations to utilize resources from different habitats. These small-scale movement patterns play an important role in the energy transfer between habitats and connect coastal systems like seagrass beds and coral reefs. To identify essential habitat properties for key species and anticipate their behavioural responses to changing environmental conditions is therefore critical to successful conservation. As fish behaviour is also known to be influenced by natural cycles such as tidal or diel phases it is further important to distinguish the different causes of their behavioural variation in order to correctly evaluate how environmental change may affect population distributions across space.

Despite the relevance of fish movements, guidance mechanisms for fish moving between habitats are not well understood and studies investigating possible environmental drivers of movement patterns are still scarce. In this study we thus aim to broaden our knowledge of potential causal mechanisms and spatiotemporal patterns of reef fish movements and space use. To this end, we first investigate a tropical reef system to identify a suitable model organism (the diurnal parrotfish *Chlorurus sordidus*) and its susceptibility to natural cycles. We then simulate its movement decision-making by linking it with two main functional landscape features (food availability and predation risk) in a novel approach combining individual-based modelling (IBM) with so-called potential field methods. Potential field methods are based on the analogy to physical force fields and consist of attracting and repelling potentials (gradients of the scalar field) and have the potential to steer an object. In our IBM a model fish can evaluate (via motivation-specific weighing factors) the perceived (via a perception range) risk and benefits of the surrounding landscape features and adapt its movement direction and speed accordingly taking into account its internal state (energy budget). By explicitly integrating a fish’s perceptional abilities into the movement decision-making process our model allows us to evaluate how a fish may perceive (energetic) costs and benefits of habitat features and how much impact relatively sophisticated behavioural rules have on predictions of overall population dynamics and viability in fragmented landscapes.

Our model may further assist in determining how specific landscapes are (ecologically) connected. This organism-based emergent property of the landscape, also referred to as (landscape) connectivity, is often considered to have strong implication for MPA site selection. However, this concept is equally known for its ambiguities and has been used inconsistently throughout the literature. We here discuss possible improvements to make landscape connectivity a more comparable and quantifiable concept and conclude that in order to become a more unifying framework the concept has to be (i) extended to include passive movement and transport mechanisms, (ii) used solely according to its strict and organism-centred definition, and (iii) divided into three main categories (‘potential connectivity’, ‘area connectivity', ‘effective connectivity’) relating to different spatio-temporal scales and integration levels.

Results of our model simulations show that individual movement patterns and the resulting spatial distributions of the population are more irregularly distributed among coral reef patches the more the coral reef habitat becomes fragmented and reduced. The spatial configuration of the underlying seascape thus influences the spatial exploitation of microhabitats, which may have far-reaching consequences on the ecosystem level depending on the functional role of the species under consideration. By shaping individual space use patterns, the physical features of the environment may also impact encounter rates between individuals and in the long-term the overall social structure of a population.

Based on our findings and its ability to provide detailed population dynamics over long time periods (years) and at a high spatial ($1m^2$) and temporal resolution (up to 1 s) we believe our model can provide valuable insights into the spatio-temporal variability of local herbivore fish populations. Moreover, the integration of potential field methods into IBMs seems a promising strategy to represent the complexity of dynamic decision-making of animals in applied models. Also, by being easily adaptable to different species and habitat settings as well as extendable with additional modules the model can readily be adjusted to specific questions and study systems. It may therefore provide a basic framework to process and summarize, visualize and analyse fish movement data and predict potential consequences of changing habitat structures. Eventually, the gained information may help to design effective reserves and efficiently manage and protect reef fish populations.

Zusammenfassung

Die Analyse von Bewegungsmustern bei Tieren leistet einen wesentlichen Beitrag, Prozesse wie räumliche Verteilungen oder Populationsdynamiken besser zu verstehen und hat zugleich großen Einfluss auf die Gestaltung und Bewirtschaftung von Naturschutzgebieten. In tropischen Küstenökosystemen kommt vor allem den Bewegungsmustern von Fischen eine besondere Bedeutung zu, da viele Fischarten tageszeitabhängige Wanderungen durchführen, um Ressourcen aus verschiedenen Habitaten zu nutzen. Diese kleinskaligen Bewegungen spielen zudem eine wichtige Rolle im Energietransfer zwischen den Habitaten und verbinden Küstensysteme wie Seegraswiesen und Korallenriffe. Für einen erfolgreichen Schutz ist es daher unerlässlich, die Anforderungen von Schlüsselarten an ihren Lebensraum zu bestimmen und ihre Verhaltensreaktionen auf sich ändernde Umweltbedingungen abzuschätzen. Da das Verhalten von Rifffischen bekanntlich auch durch natürliche Zyklen wie Gezeiten oder Tageszeit beeinflusst wird, ist es zudem erforderlich, die verschiedenen Ursachen für Verhaltensänderungen zu differenzieren, um Auswirkungen von Umweltveränderungen auf die räumliche Verteilung der Fischpopulationen beurteilen und einordnen zu können.

Trotz der Relevanz von Fischbewegungsmustern sind die Mechanismen, die die Wanderungen zwischen verschiedenen Habitaten steuern, bisher wenig bekannt, und es existieren nur vereinzelt Studien, die beeinflussende Umweltfaktoren untersuchen. In dieser Studie wollen wir daher das Verständnis möglicher kausaler Zusammenhänge bei der Entstehung raumzeitlicher Bewegungsmuster von Rifffischen erweitern. Zu diesem Zweck führen wir zunächst empirische Untersuchungen in einem tropischen Riffsystem durch, um einen geeigneten Modellorganismus (den tagaktiven Papageifisch *Chlorurus sordidus*) zu identifizieren und eine mögliche Beeinflussung seines Bewegungsverhaltens durch natürliche Zyklen zu bestimmen. Im Anschluss simulieren wir den Entscheidungsprozess seiner Bewegungen, indem wir diesen Prozess mit zwei wesentlichen Landschaftseigenschaften (Nahrungsverfügbarkeit und Prädationsrisiko) in einem neuartigen Ansatz verknüpfen, der individuenbasierte Modellierung (IBM) mit sogenannten Potentialfeldmethoden kombiniert. Potentialfeldmethoden basieren auf der Analogie zu physikalischen Kraftfeldern, die sich aus anziehenden und abstoßenden Potentialen (Gradienten des Skalarfelds) zusammensetzen und so ein Objekt lenken können. In unserem IBM kann ein Modellfisch das über seinen ‚perception range‘ wahrgenommene Risiko sowie den Nutzen der umgebenden Landschaft über motivationsspezifische Gewichtungsfaktoren bewerten sowie seine Bewegungsrichtung und Geschwindigkeit unter Berücksichtigung seines inneren (energetischen) Zustands anpassen. Indem wir das Wahrnehmungsvermögen eines Fisches explizit in den Entscheidungsprozess integrieren, erlaubt unser Modell eine Beurteilung, wie ein Fisch (energetische) Kosten und Nutzen von Habitateigenschaften bewertet und inwieweit vergleichsweise differenzierte Verhaltensregeln Vorhersagen allgemeiner Populationsdynamiken in fragmentierten Lebensräumen beeinflussen.

Darüber hinaus kann unser Modell bei der Analyse helfen, inwiefern bestimmte Landschaften (ökologisch) miteinander verbunden sind. Diese organismen-basierte emergente Eigenschaft der Landschaft, auch als ‘(landscape) connectivity’ bezeichnet, wird oft als Kriterium bei der räumlichen Planung von Meeresschutzgebieten herangezogen. Da dieses Konzept jedoch in der Literatur nach wie vor uneindeutig definiert und verwendet wird, diskutieren wir im Rahmen dieser Arbeit ebenfalls mögliche Verbesserungen, die eine leichtere Quantifizierung und Vergleichbarkeit von ‘landscape connectivity’ erlauben.

Um einen standardisierten Rahmen zu bieten, sollte unserer Meinung nach das Konzept (i) um passive Bewegungs- und Transportmechanismen erweitert, (ii) ausschließlich gemäß seiner ursprünglichen organismus-zentrierten Definition verwendet und (iii) in drei Hauptkategorien (‘potential connectivity’, ‘area connectivity', ‘effective connectivity’) unterteilt werden, dies sich auf verschiedene räumlich-zeitliche Skalen und Integrationsebenen beziehen.

Die Ergebnisse unserer Modellsimulationen zeigen, dass individuelle Bewegungsmuster und die daraus resultierenden räumlichen Verteilungen der Population umso unregelmäßiger auf Korallenriffflächen verteilt sind, je stärker das Korallenriff fragmentiert ist und dessen Fläche reduziert wird. Die räumliche Konfiguration der Meereslandschaft kann somit nicht nur die räumliche Nutzung von Mikrohabitaten und deren Ressourcen maßgeblich beeinflussen, sondern auch – je nach funktionaler Rolle der jeweiligen Arten – weitreichende Auswirkungen auf das gesamte Ökosystem haben. Durch die Beeinflussung der Raumnutzung auf Ebene der Individuen wirken sich die physikalischen Umwelteigenschaften zusätzlich auf die Häufigkeit aus, mit der sich Individuen begegnen, wodurch langfristig auch die soziale Struktur auf Populationsebene geprägt wird.

Basierend auf unseren Erkenntnissen und der Fähigkeit unseres Modells, detaillierte Populationsdynamiken über lange Zeiträume (Jahre) und in hoher räumlicher (1m^2) und zeitlicher Auflösung (bis zu 1 s) abbilden zu können, sind wir der Auffassung, dass unser Modell wertvolle Einblicke in die räumlich-zeitliche Variabilität lokaler herbivorer Fischpopulationen liefern kann. Zudem erscheint uns die Integration von Potentialfeldern in IBMs eine vielversprechende Strategie, um die Komplexität dynamischer Entscheidungsprozesse bei Tieren in angewandten Modellen darzustellen. Da unser Modell darüber hinaus leicht an verschiedene Arten und Habitatkonfigurationen angepasst und mit zusätzlichen Modulen erweitert werden kann, lässt es sich ohne weiteres auf spezifische Fragestellungen und lokale Systeme anwenden. Es bietet daher eine einfache Rahmenanwendung für die Verarbeitung, Visualisierung und Analyse von Fischbewegungsdaten und ermöglicht die Vorhersage möglicher Konsequenzen von Veränderungen der Habitatstruktur. Die so gewonnenen Informationen können schlussendlich dazu beitragen, effektive Meeresschutzgebiete zu planen und Rifffischpopulationen erfolgreich zu schützen.

1 Preface

Movement of organisms is a key issue in ecology, especially in naturally fragmented landscapes (Turchin 1991; Zollner et al. 1999) like tropical coastal habitats, and an important link between individual life history and population dynamics (Nathan et al. 2008; Morales et al. 2010; McClintock et al. 2014). Also, animal movement is intrinsic to all behavioural processes (Liedvogel et al. 2013) and one of the primary ways that mobile organisms can adapt to changing environments (Railsback et al. 1999; Smouse et al. 2010). This makes movement at all different spatial scales relevant to most current environmental concerns in the marine realm like coastal development, overexploitation of natural resources or increasing degradation of habitats (Nathan et al. 2008). These anthropogenic activities often result in degradation, fragmentation and/or loss of (coastal) habitats (Kindlmann and Burel 2008; Nathan et al. 2008) and can affect ecological systems in many different ways (Martinson and Fagan 2014). Increasing habitat fragmentation, for instance, is known to restrict movements of fish (Chapman and Kramer 1999; Eristhee and Oxenford 2001; Turgeon et al. 2010) and can possibly lead to local extinction of selected species. Depending on the fish`s functional role e.g. as a structuring force for benthic communities its loss can have severe adverse effects on ecosystem functioning (Nyström and Folke 2001; Bellwood et al. 2004; Welsh and Bellwood 2014).

1.1 Why are small-scale fish movements important?

Movement patterns of fish are diverse including ontogenetic shifts, spawning migrations, or diel feeding movements and occur over a wide range of spatial and temporal scales (see Green et al. (2015) for review). The latter are a common feature among reef fishes and mostly take place at rather small scales of tens of metres to a few kilometres (Helfman 1993; Green et al. 2015). They may thus not have a large impact on stock ranges, but they can greatly influence ecological interactions like the outcome of prey-predator interactions (Lima and Dill 1990). Furthermore, diel movements are important vectors for cross-habitat energy and nutrient transfer when fish use resources from different habitat types during their daily routines (Nagelkerken et al. 2000, 2008; Clark et al. 2009; Hitt et al. 2011). This nutrient input may be particularly important in oligotrophic environments like coral reef systems and can e.g. facilitate coral as well as seagrass growth (Meyer et al. 1983; Peterson et al. 2013). Moreover, diel migrations are often predictable in space and time (Helfman 1993) and are thereby also relevant for fisheries-related catchability (Bartholomew et al. 2008).

Another important aspect of diel movement patterns is their relevance for successful conservation of fish stocks (Curley et al. 2013). Due to their economic and ecological importance, fish are often a target group for conservation and nowadays, a widely recommended management tool for fisheries is the implementation of marine protected areas (MPAs, (Grober-Dunsmore et al. 2007)). The ability of a MPA to provide protection largely depends on the consistent use, both during day and night, of the protected area by individual fish (Chapman and Kramer 1999; Eristhee and Oxenford 2001; Beets et al. 2003; Grüss et al. 2011). If not planned correctly, a MPA can even be counter-productive (Hinrichsen et al. 2008). It is therefore critical for the effectivity of a reserve to consider diel movement patterns of the target species and to enclose appropriate habitats (Meyer et al. 2007; Afonso et al. 2008; Semeniuk et al. 2011). This shift to spatially explicit management presents new challenges for ecologists as well as marine resource managers (Sale and Kritzer 2008; Botsford et al. 2009) and has led to an increasing need to understand the nature and extend of small-scale movement patterns of mobile (juvenile and adult) fishes and how they may be affected by environmental conditions.

1.2 How does the seascape influence fish movements?

Animal movement behaviour is further notorious for its complexity and possible involvement of many different environmental factors. In general, movements result from interactions between the organisms and their environments (Johnson et al. 1992; Schick et al. 2008) and can be considered as directed responses to social and environmental cues (Davis et al. 2017b). Aquatic biota such as fish, for instance, is long known to be responsive to the physical structure and complexity of the underlying (benthic) seascape (Hart 1993; Chapman and Kramer 1999; McClanahan and Arthur 2001; Grober-Dunsmore et al. 2007; Gullström et al. 2008; Grüss et al. 2011; Fuller 2013).

Topographic complexity can modulate interactions among individuals such as predation by influencing encounter rates between predators and prey, the likelihood of an attack, and the escape probability of prey (Lima and Dill 1990; Overholtzer-McLeod 2006; McCormick and Lönnstedt 2013; Catano et al. 2016). Prey organisms may therefore be reluctant to leave their preferred substratum and cross large gaps of habitats of low structural complexity such as sand (Chapman and Kramer 2000). Some reef fishes, for example, have been shown to be hesitant to cross gaps in shelter of more than 20 m (Turgeon et al. 2010) and prefer to stay close to high complexity structures provided by the reef. This behaviour leads to a continuum of risky and safe areas within a prey's environment, also referred to as the 'landscape of fear' (Laundré et al. 2001, 2010), and has been demonstrated in terrestrial (Gorini et al. 2012) as well as marine ecosystems (Wirsing et al. 2008; Madin et al. 2011; Matassa and Trussell 2011; Catano et al. 2016). Consequently, the habitat composition (i.e. presence and diversity of habitats) and configuration (i.e. area, shape and isolation of habitats) can regulate and restrict fish movement (Nemeth and Appeldoorn 2009) and thus affect spatio-temporal dynamics in fish populations and assemblages.

Additionally, by constraining a fish's movements the seascape may force a foraging fish to not always take the shortest possible path from shelter to food and vice versa (Hart 1993). As locomotion is metabolically costly for fish (Brett and Groves 1979; Calow 1985) the habitat structure therefore has implications not only on the population level but also on the level of the individual by influencing its energy budget. Resulting space use patterns hence represent trade-offs between energy acquisition, survival, and reproduction (Davis et al. 2017b). These organism-seascape linkages are likely to be of particular importance in coral reefs systems as typically heterogenous environments with a patchy distribution of different habitat types.

1.3 What part does seascape connectivity play?

Not only can the seascape influence animal movements, it also has the potential to exercise a species-specific control: The same environment can be perceived and used differently across species and nowadays unique organism-habitat relationships have been observed across a wide range of taxa and spatial scales (Chittaro 2004; He et al. 2019). Hence, animal space use patterns are more likely to result from the interaction between movement behaviour and the characteristics of the environment in which the animals are embedded, rather than being completely random or uniform in space and time (He et al. 2019). As a consequence, when foraging in heterogenous habitats animals may distribute themselves among habitat patches not solely in proportion to available resources (as predicted by the ideal free distribution) but also constrained by other factors and habitat characteristics like competition, risk of predation or availability of refuges (Tootell and Steele 2016). Depending on the species' ecological role, the resulting spatial distribution can have important impacts on community structure and ecosystem function.

The identification of habitats that are primarily used by a target organism and how such habitats are ecologically connected by the organism's movements – also referred to as 'landscape connectivity' (Taylor et al. 1993, 2006) – is a critical issue in ecosystem-based management (Appeldoorn et al. 2009). Connectivity is, for instance, considered a key determinant of meta-population dynamics (Lima and Zollner 1996) with strong implication for MPA site selection as it may greatly enhance reserve performance by promoting fish abundance (Olds et al. 2012a, 2012b). However, despite its potential relevance for many ecological processes as well as its frequent usage, the definition and measurement of connectivity remain inconsistent throughout the literature regarding scales, dimension, and scope.

This ambiguity can largely be attributed to the fact that in spite of being originally defined for animals in a terrestrial context, the term 'connectivity' has been applied to a variety of organisms and their larval stages in both terrestrial and aquatic ecosystems. Furthermore, an increasing number of studies use 'connectivity' with regard to gene flow or transfer of information, matter or energy between populations (see Kool et al. (2013) for review). Although many authors have recognized the inconsistent use of this concept (Tischendorf and Fahrig 2000; Moilanen and Hanski 2001; Taylor et al. 2006; Kool et al. 2013), limited progress has been made to unify its definition and quantitative use (but see (Calabrese and Fagan 2004; Bélisle 2005; Kindlmann and Burel 2008; Lindenmayer et al. 2008; Grober-Dunsmore et al. 2009)). A clear formulation, taking the concept to its logical conclusion but at the same time delimiting its application, is still missing. Moreover, some important aspects are not yet included in its definition (despite being applied), such as passive transportation which can be an important process for plant dispersal or dispersal of marine species via larval stages. Thus, for landscape connectivity as a decidedly useful concept for ecological theory and applied biology, to become a reliable management criterion, we believe a trade-off has to be made between applicability and being all-encompassing in scope.

1.4 Why individual-based modelling (IBM)?

To date, general patterns of organismal movements and migrations are well documented, but surprisingly little has been done yet to explicitly explore the linkages between habitat structure and behavioural characteristics of organisms like adult fishes (Beets et al. 2003; Holyoak et al. 2008). This is true for marine habitats in general and coral reefs in particular (Levin et al. 2000; Fuller 2013; Welsh and Bellwood 2014) and relates to empirical as well as modelling studies (Williams et al. 2010). Hence our understanding of the fish-seascape link among tropical coastal ecosystem and the effects of seascape heterogeneity on movement behaviour is still fairly limited. This is further compounded by the lack of advanced techniques to measure fish movements over full 24-h cycles at high spatio-temporal resolution (for most species still not available (Curley et al. 2013)), although modern techniques like hydro-acoustic telemetry can provide valuable quantitative data on precise movement pathways of individual animals (see e.g. (Simpfendorfer et al. 2002; Chateau and Wantiez 2008; Heupel et al. 2010; Meyer et al. 2010; Hitt et al. 2011)).

Moreover, individual movement behaviour and the resulting spatial dynamics of fish populations are complex (Botsford et al. 2009) making it difficult to empirically capture the full range of spatial and temporal variability (Reuter et al. 2005; Curley et al. 2013) or measure how environmental changes such as increasing habitat fragmentation may impact the physiology and viability of individual organisms (Nisbet et al. 2012). Added to this is a disadvantage that all empirical investigations have in common: If an ecological response is simply measured, it has to be re-measured when the environment changes as they can only provide a snapshot view of movements at a given time point (Sutherland 1998; Avgar et al. 2013; Davis et al. 2017b). For effective protection, however, it is not only important to be able to analyse observable patterns but also to anticipate what will happen to fish populations as a result of current or future environmental changes (Sutherland 1998; Stillman et al. 2015).

It thus seems that empiricism alone does not offer a practical way to disentangle potential driving forces and simulation models may build a bridge between experimental studies and management decisions. If based on behavioural decisions these models can account for adaptive behaviour like phenotypic plasticity (Reuter et al. 2008) and thus elucidate potential consequences of habitat loss and fragmentation on individual movement and species distribution in space and time (Sutherland 1998; Semeniuk et al. 2011). Since animal movement is inherently an individual-level process (Tracey et al. 2011) and inter-individual variation omnipresent (Semeniuk et al. 2011), individual-based models (IBMs) are particularly suitable to study small-scale movement behaviour in heterogenous environments.

IBMs in general are a relatively recent category of ecological models mostly constructed with object-oriented programming techniques (e.g. SIMULA, Smalltalk, C++, Java), although early IBM applications go back to the 1970s (Grimm 1999; Breckling et al. 2006). IBMs largely emerged in the context of computer science and were a response to the requirements to include more biological realism and explicit spatial representations into ecological models (Reuter et al. 2008, 2011).

In an IBM the considered organisms are represented not only as countable entities (i.e. objects) but also as organisms with one or more additional features that specify the particular state of each individual (Breckling 2002). Thus, differences among individuals are not levelled out and the described ecosystem is composed of a collection of autonomous decision-making objects (bottom-up approach, (Semeniuk et al. 2011)). The programme structure itself is sufficiently flexible to capture organismic development and behaviour, environmental conditions, and the interaction of both (Reuter et al. 2011). Properties at the population and community levels (e.g. size, age distribution, and space use) will then emerge as a result of the behavioural traits and interactions (e.g., decision rules, behaviour, physiology) of all constituent individuals (DeAngelis and Mooij 2005), also referred to as emergent properties (Breckling et al. 2005). Due to this potential to represent detailed biological knowledge and small-scale mechanisms, IBMs tend to have a complex model structure. However, the description level of these models is very close to the information level of empirical results enabling the integration of observations directly into the model (Grimm 1999; Breckling 2002) and making interpretation of model results simple and straightforward.

Owing to this bottom-up design IBMs have therefore the ability to disintegrate populations into individuals and re-integrate individual events into population processes (Huse and Giske 2004; Breckling et al. 2006; Mumby 2006; Mumby and Hastings 2007). Thereby they allow researchers to study functional connections which are difficult or impossible to observe in the field, e.g. how system level properties arise from the behaviour of individuals or how feedbacks from the system affect the behaviour of individuals (Railsback and Harvey 2001; Reuter et al. 2008). The examination of cross-level effects of a biological system also enables the identification of ecological thresholds particularly in relation to habitat loss and fragmentation or may show unexpected consequences of adaptive individual behaviour. Hence, spatially explicit IBMs can reveal which spatial patterns facilitate or impede movements across a landscape (Grober-Dunsmore et al. 2009) and therefore have the potential to highlight causal links of the organism-landscape relationship (Nathan et al. 2008; Semeniuk et al. 2011).

Moreover, recent studies have established the importance of explicitly considering individual differences in movement and space use (Spiegel et al. 2017), particularly with regard to successful spatial management and ecosystem-based management of fisheries (Pillans et al. 2014). IBMs further offer two essential advantages necessary to simulate realistic spatial distributions: Firstly, by operating on the lowest organisational level considered in ecology (i.e. activities of individuals) they can be readily linked with field observations (Breckling 2002; DeAngelis and Mooij 2003; Reuter et al. 2005; Breckling et al. 2006; Kubicek et al. 2015). Secondly, they can provide the required spatial resolution of the underlying landscape. This is vitally important in this context as natural habitats are seldom evenly distributed across space and time and population dynamics are generally guided by the detailed irregularity of a landscape rather than by its average value (DeAngelis et al. 2004).

1.5 What do we want to achieve with our IBM? And how?

To accurately estimate population dynamics, it is critically important to ensure that individuals in the model are reacting in a way that results in realistic distribution patterns. To date, model assumptions of movement processes often lack a great deal of realism or models do not incorporate condition-depending movement strategies, which can yield inaccurate and costly predictions (Grüss et al. 2011). Thus far one of the most common methods for incorporating movement into ecological models has been simple or correlated random walk based on probabilistic jumps into the adjacent cell of a grid (Tischendorf and Fahrig 2000; Bartumeus et al. 2005; Codling et al. 2008) although the implementation of complex movement behaviours is beginning to occur (see (Hölker and Breckling 2005; Jopp and Reuter 2005; Botsford et al. 2009) with very few modelling attempts having been made in marine ecosystems. IBMs dealing with fish movements in coastal habitats have largely focused on larval dispersal (Hinckley et al. 1996; Hermann et al. 2001; Cowen 2006) and rarely include small-scale migration patterns of juvenile and adult fishes or more sophisticated vector-based movement rules in relation to landscape features (Tracey et al. 2011).

Against this background, our aim is to examine the relationship between seascape structure and diel movement patterns of herbivorous parrotfishes in coral reef systems to broaden our understanding of the factors that influence the abundance and distribution of this functional group. Parrotfishes are of great ecological and economic importance in tropical coastal ecosystems (Hughes et al. 2007; Unsworth et al. 2007; Lokrantz et al. 2008; Bonaldo et al. 2014; Welsh and Bellwood 2014) and found on almost every coral reef worldwide (Hoey and Bonaldo 2018). Furthermore, due to their ecological functions in coral reef systems, especially with regard to the mediation of coral-algal dynamics (Mumby et al. 2006; Hughes et al. 2007; Russ et al. 2015; Roff et al. 2019), they are being increasingly valued and have become the focus of management actions in many areas (Davis et al. 2017b).

To allow for an exploration of causes and mechanisms of small-scale movements we deem it essential to model and integrate (i) individual rule-based movement behaviour with (ii) a spatially explicit representation of the benthic habitats under consideration of (iii) the energetic trade-offs that are involved in the movement decision-making process regarding costs (risk of predation and/or starvation) and benefits (food, survival, and/or reproduction). To this end we propose a spatially-explicit IBM that links the movement decision-making process of the individual fishes with two main functional aspects of the seascape we assume to be most relevant in this context: the habitat-dependent food availability (as a bottom-up control) and risk of predation (as a top-down control) due to changing topographic complexity.

Conceptually we follow the framework proposed by Nathan and colleagues (2008), which provides a conclusive mechanistic description of the basic processes involved in individual movement (Revilla and Wiegand 2008). Model fishes are therefore characterized by three main components (Fig. 1):

(1) an internal state, which is directly related to the reasons behind the individual movement decision (*why move?)*

(2) a navigation capacity (*where and when to move?*), which is the individual ability to perceive and use movement-related information of the environment,

(3) and a motion capacity (*how to move?*), which is the inherent ability to move with some properties modulated by the navigation capacity.

The individual's movement path is then generated over time by the dynamic interaction of these components with the fourth element,

(4) the external factors, i.e. the surrounding environment.

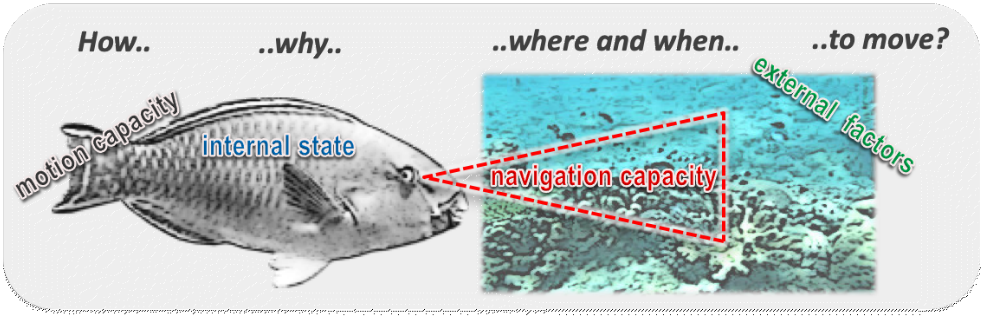

Fig. 1 The four basic elements of individual movement following Nathan et al. (2008) the internal state of an individual, its navigation, and motion capacity interact with the external factor(s) in question generating the movement path over time.

Specifically in our model this entails the individual fish with (1) its energetic state and the need 'to feed effectively yet safe and reproduce' (Holbrook and Schmitt 1988) as the most relevant motivational aspects for movement, (2) its swimming activity determining its energetic costs, and (3) its perception range allowing the fish respond to (4) the external factors or potential drivers ‘food availability’ and ‘predation risk’, both traits of the underlying seascape. The dynamic interaction between the fish and the seascape arises from a fish`s ability to sense changes in food availability and predation risk in different habitats ((Werner et al. 1983; Colgan 1993) and adjust its velocity accordingly (Milinski 1993). A fish’s motion capacity is thus directly related to food intake and habitat changes and affect the fish`s energy budget (internal state) by determining the swimming costs (Ohlberger et al. 2006). Combined with the habitat-dependent food availability, which controls the possible energy gain, both habitat features ultimately decide on the fish`s growth and survival.

To be able to capture the dominant features of small-scale diel movements of mobile (post-settlement) reef fishes within this framework and answer the questions of the “how, why, where and when” it is important to know how fish make decisions about moving across (patchy) seascapes. Movement generally implies many decisions like leave an area or adjust course and rate of travel (Bélisle 2005), and may serve one or more needs like energy gain and growth (Hughes and Dill 1990; Hughes 1998), predation avoidance (Milinski 1993) or reproduction. Also, these needs may vary between individuals due to different internal states regarding energy demand or maturity (Bélisle 2005). Thus, in nature prey animals, a classification that relates to the majority of all fish species, constantly make (behavioural) decisions to alter when, where and how they forage or reproduce reflecting the trade-offs between predation risk and benefits to be gained from other activities like feeding (Werner et al. 1983; Lima and Dill 1990; Manassa et al. 2013). When making a movement decision a fish must therefore weigh the importance of multiple sensory inputs, such as the presence of food, risk from predators, and environmental conditions (Krebs et al. 1993). The extent, to which an individual fish can sense its surroundings, i.e. the distance from which it can detect suitable habitat patches, is defined by its perceptual range and determined by its sensory abilities. The perceptual range is a consequential trait for animals inhabiting fragmented habitats like coastal ecosystems in order to minimize energy-costly searches (Lima and Zollner 1996) and functions as the interface between fish behaviour and the underlying seascape in our model.

To account for relevant trade-offs in decision-making and realistically simulate landscape-related movement we incorporate a vector-based movement algorithm that uses artificial potential fields. Potential field approaches are commonly used in computer games and mobile robotics, where they were first introduced by (Khatib 1986) and made popular by (Arkin et al. 1987; Arkin 1989). Based on a physics analogy, these methods treat an (moving) agent as a charged particle acting under the influence of a magnetic (potential) field representing the structure of the spatial environment (Connell 1990; Dudek and Jenkin 2010). By assigning charges of various magnitudes to all other objects and/or locations in this environment (based on prior knowledge), attractive and repulsive forces are computed navigating an agent in a particular direction. Analogous behaviour can also be perceived in nature, when e.g. reef fishes avoid moving through areas of high predation risk as if “repelled” resulting in the above mentioned ‘landscape of fear’. Combined with their mathematical elegance and simplicity (Raja and Pugazhenthi 2012) this similarity makes artificial potential fields an appealing approach for the exploration of organismic reactions to landscape structure and its heterogeneity.

With our model, in which the external factor food availability acts as an attractive force, while predation risk is implemented as a repulsive force, we mainly address the following questions:

(i) How do small-scale behavioural decisions affect key life history traits such as energy budgets, survival, and reproduction of the model species?

(ii) How do these individual decisions influence population dynamics and the spatial distribution as self-organized spatial structures of model species?

(iii) What are potential responses on the individual as well as the population level to changing environmental conditions like an increasing habitat fragmentation?

(iv) How does the spatial configuration affect energetic gains and costs (e.g. growth and survival)?

(v) Where are critical configurations or thresholds with respect to the life history of fish (e.g. different susceptibilities) and movement behaviour?

1.6 Outline of the chapters

The central part of the work presented here is the development of the individual-based model (IBM) and its exemplary application to a parrotfish species. Our model integrates the results of our field experiments conducted beforehand to investigate movement patterns of parrotfishes and facilitate model parametrization. As both model results and field observations relate to the connectedness of habitats in a given seascape, we further discuss the concept of ‘landscape connectivity’ as a relevant and increasingly popular framework in spatial ecology.

More specifically, Chapter 2 gives an overview of the relevance of natural (i.e. lunar, diel, and tidal) cycles on fish assemblages and how they influence community composition in tropical coral reef habitats on Zanzibar, Tanzania (published paper). The obtained results help discern potential driving factors for small-scale fish movements and provide important information for the structure and development of the IBM presented in Chapter 3.

Chapter 3 describes the IBM in detail and summarizes the findings of model simulations using different habitat maps (with increasingly fragmented seascapes) to identify patterns and linkages between fishes and their surrounding environment. It further provides insights into potential consequences of habitat degradation with regard to individual growth and development as well as population distribution and its long-term survival (manuscript in preparation).

Chapter 4 discusses the concept of landscape connectivity, which is frequently used in both marine and terrestrial spatial ecology. Despite its frequent usage, it is also a much-debated framework due to its ambiguities and different interpretations when applied to marine or terrestrial systems. Moreover, it is of particular interest in the context of habitat-related fish movement behaviour as resulting space use patterns will strongly depend on how a species perceives certain landscape features as corridors or barriers, which ultimately determine the accessibility of habitat patches in the surrounding environment. In this chapter a potential solution to unify the framework for an application to both realms is presented (manuscript in submission).

Chapter 5 provides a synopsis of the findings of Chapter 2 to 4, their relevance in the context of coral reef sciences and an outlook to potential future developments.

2 Lunar, diel, and tidal changes in fish assemblages in an East African marine reserve

Kruse M, Taylor M, Muhando CA, Reuter H (2016). Lunar, diel, and tidal changes in fish assemblages in an East African marine reserve. Regional Studies in Marine Science 3: 49-57.

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https://www.sciencedirect.com/science/article/abs/pii/S2352485515000134;

DOI: 10.1016/j.rsma.2015.05.001

3 Best places to go in a heterogenous seascape: How potential field methods can help to simulate trade-offs in fish movement behaviour

(Manuscript in preparation)

3.1 Abstract

In nature fish are seldom evenly distributed across a heterogenous seascape like coral reef systems and their space use patterns will largely result from the interactions between individual movement behaviour and the characteristics of the environment in which the fishes are embedded. When foraging, herbivorous parrotfishes, for instance, are likely to be constraint by habitat characteristics like the availability of resources and different levels of predation risk. As parrotfish play an important role in structuring benthic communities, the resulting spatial distribution of the fish population can have severe impacts on community composition and ecosystem resilience.

Motivated by this increasing awareness of the importance to study organisms at the individual level and in order to limit model biases due to over-simplified movement patterns we aim at a more realistic representation of fish movements and their decision-making process: By combining individual-based modelling (IBM) with potential field methods in a novel approach we hope to take a step forward in this direction. Potential fields, which are frequently used in robotics and computer gaming, represent environments as a field of repellent and attracting forces making them an appealing approach for the exploration of organismic reactions to landscape structure and its heterogeneity.

In our model, the biotic components represented are individual parrotfishes, food availability and predation risk, while abiotic factors include the diel cycle as well as the underlying habitat structure of a coral reef system. By coupling the fish's bioenergetics with a navigation capacity using the potential field we provide a mechanistic basis for better understanding and predicting how changes in the habitat structure and fragmentation may cause shifts in population dynamics and space utilization.

Model results indicate that movement patterns and the resulting spatial distributions of the population are more irregularly distributed among coral reef patches the more the coral reef habitat becomes fragmented and reduced. On the individual level the process of reproduction seems most susceptible to changes in habitat configuration and composition. Based on our findings we believe that the integration of potential field methods into IBMs is a promising strategy to represent the complexity of dynamic decision-making of animals in applied models.

Keywords: individual-based modelling, potential fields, decision-making, fish bioenergetics, diel movements, habitat fragmentation

3.2 Introduction

Movement of organisms is a key issue in ecology, especially in naturally fragmented landscapes (Turchin 1991; Zollner et al. 1999) like tropical coastal habitats, and an important link between individual life history and population dynamics (Nathan et al. 2008; Morales et al. 2010; McClintock et al. 2014). Also, animal movement is one of the primary ways that mobile organisms can adapt to changing environments (Railsback et al. 1999; Smouse et al. 2010). This makes movement at all different spatial scales relevant to most current environmental concerns in the marine realm like coastal development, overexploitation of natural resources or increasing degradation of habitats (Nathan et al. 2008).

Animal movement behaviour is further notorious for its complexity and generally considered to consist of directed responses to social and environmental cues, resulting in space use patterns that represent trade-offs between energy gain, survival, and reproduction (Davis et al. 2017b). Also, the possible involvement of many different environmental factors such as predation and habitat complexity as top-down controls or food availability as bottom-up drivers (Roff et al. 2019) complicate the analysis of potential driving forces and causal interconnections. Ultimately, animal distribution is often the result of individual compromises between (habitat-related) resource availability, predation risk, and competition (Tootell and Steele 2016). Understanding the relative influence of these factors, in particular of different habitat and landscape arrangement, has been a long-standing goal of ecologists (Gilby et al. 2016).

With regard to habitat features, fish, for instance, are known to be responsive to the physical three-dimensional structure and spatial arrangement (i.e. configuration) of the underlying seascape and the diversity and extent of the associated benthic habitats (Hart 1993; Chapman and Kramer 1999; McClanahan and Arthur 2001; Grober-Dunsmore et al. 2007; Gullström et al. 2008; Grüss et al. 2011; Fuller 2013). Ample evidence exists that greater complexity of reef structures correlates with higher fish abundances and species richness suggesting that topographic complexity is a key component of habitats and habitat configuration an important driver for space utilization patterns (Chittaro 2004; Welsh and Bellwood 2012a; Gilby et al. 2016; He et al. 2019).

The central mechanism by which topographic complexity influences population level processes is based on the modulation of interactions among individuals: Encounter rates between prey and predators, the likelihood of an attack or the escape probability of prey are altered in dependence of the habitat structure, e.g. by providing more or less suitable refuges (Lima and Dill 1990; Jones and Syms 1998; Overholtzer-McLeod 2006; Pratchett et al. 2008; McCormick and Lönnstedt 2013; Catano et al. 2016; Roff et al. 2019). Prey organisms may therefore be reluctant to leave their preferred substratum and cross large gaps of habitats of low structural complexity such as sand (Chapman and Kramer 2000; Turgeon et al. 2010). This behaviour leads to a continuum of risky and safe areas within a prey's environment, also referred to as the 'landscape of fear' (Laundré et al. 2001), which has been demonstrated in terrestrial (Gorini et al. 2012) as well as marine ecosystems (Wirsing et al. 2008; Madin et al. 2011; Matassa and Trussell 2011; Catano et al. 2016). When making movement decisions habitat features may thus present physical barriers while others facilitate movement and an increasing fragmentation may severely impact how animals use their space.

By regulating and restricting movement patterns of the individuals the configuration of the seascape shapes at the same time the global structure of fish populations, in particular with regard to their spatio-temporal dynamics and distributions (Hart 1993; Bellwood and Hughes 2001; Nemeth and Appeldoorn 2009). However, by constraining a fish's movements the seascape has yet another, important effect on their inhabitants: depending on the degree of fragmentation the seascape may force a foraging fish to not always take the shortest possible path from shelter to food and vice versa (Hart 1993). As locomotion is metabolically costly for fish (Brett and Groves 1979; Calow 1985) these detours may have a severe impact on a fish's energy budget. All these organism-seascape linkages are likely to be of particular importance in coral reef systems as typically heterogenous environments with a patchy distribution of different habitat types from highly complex reef structures to open flat sandy bottoms (Gil et al. 2017).

To date, general patterns of organismal movements and migrations are well documented, but surprisingly little has been done yet to explicitly explore how habitat structure and behavioural characteristics of organisms like adult fishes are interlinked (Beets et al. 2003; Holyoak et al. 2008). This is true for marine habitats in general and coral reefs in particular (Levin et al. 2000; Fuller 2013; Welsh and Bellwood 2014) and relates to empirical as well as modelling studies (Williams et al. 2010). Due to its complexity, however, it is difficult to empirically capture the full range of spatial and temporal variability of movement behaviour (Reuter et al. 2005; Curley et al. 2013) or measure how environmental changes such as increasing habitat fragmentation may impact the physiology and viability of individual organisms (Nisbet et al. 2012). Moreover, for effective protection it is not only important to be able to analyse observable patterns but also to anticipate what will happen to fish populations as a result of current or future environmental changes (Sutherland 1998; Stillman et al. 2015).

It thus seems that empiricism alone does not offer a practical way to disentangle potential driving forces and simulation models may build a bridge between experimental studies and management decisions. If based on behavioural decisions these models can account for adaptive behaviour like phenotypic plasticity (Reuter et al. 2008) and thus elucidate potential consequences of habitat loss and fragmentation on individual movement and species distribution in space and time (Sutherland 1998; Semeniuk et al. 2011). Since animal movement is inherently an individual-level process (Tracey et al. 2011) and inter-individual variation omnipresent (Semeniuk et al. 2011), individual-based models (IBMs) are particularly suitable to study small-scale movement behaviour in heterogenous environments.

To accurately estimate population dynamics, it is critically important to ensure that individuals in the model are reacting in a way that results in realistic distribution patterns. To date, model assumptions of movement processes often lack a great deal of realism or models do not incorporate condition-depending movement strategies, which can yield inaccurate and costly predictions (Grüss et al. 2011). Thus far one of the most common methods for incorporating movement into ecological models has been simple or correlated random walk based on probabilistic jumps into the adjacent cell of a grid (Tischendorf and Fahrig 2000; Bartumeus et al. 2005; Codling et al. 2008) although the implementation of complex movement behaviours is beginning to occur (see (Hölker and Breckling 2005; Jopp and Reuter 2005; Botsford et al. 2009) with very few modelling attempts having been made in marine ecosystems. IBMs dealing with fish movements in coastal habitats have largely focused on larval dispersal (Hinckley et al. 1996; Hermann et al. 2001; Cowen 2006) and rarely include small-scale migration patterns of juvenile and adult fishes or more sophisticated vector-based movement rules in relation to landscape features (Tracey et al. 2011).

Against this background, our aim is to examine the relationship between seascape structure and diel movement patterns of herbivorous parrotfishes in coral reef systems to broaden our understanding of the factors that influence the abundance and distribution of this functional group. Parrotfishes are of great ecological and economic importance in tropical coastal ecosystems (Hughes et al. 2007; Unsworth et al. 2007; Lokrantz et al. 2008; Bonaldo et al. 2014; Welsh and Bellwood 2014) and found on almost every coral reef worldwide (Hoey and Bonaldo 2018). Furthermore, due to their ecological functions in coral reef systems, especially with regard to the mediation of coral-algal dynamics (Mumby et al. 2006; Hughes et al. 2007; Russ et al. 2015; Roff et al. 2019), they are being increasingly valued and have become the focus of management actions in many areas (Davis et al. 2017b).

To allow for an exploration of causes and mechanisms of small-scale movements we deem it essential to model and integrate (i) individual rule-based movement behaviour with (ii) a spatially explicit representation of the benthic habitats under consideration of (iii) the energetic trade-offs that are involved the movement decision-making process regarding costs (risk of predation and/or starvation) and benefits (food, survival, and/or reproduction). To this end we propose a spatially-explicit IBM that links the movement decision-making process of the individual fishes with two main functional aspects of the seascape we assume to be most relevant in this context: the habitat-dependent food availability (as a bottom-up control) and risk of predation (as a top-down control) due to changing topographic complexity (Christensen and Persson 1993; Colgan 1993).

Conceptually we follow the framework proposed by (Nathan et al., 2008) and implement four basic components (internal state, motion capacity, navigation capacity, and external factors) to capture the relevant processes of a parrotfish's movement ecology: the individual fish with (1) its energetic state and the need 'to feed effectively yet safe and reproduce' (Holbrook and Schmitt 1988) as the most relevant motivational aspects for movement, (2) its swimming activity, and (3) its perception range allowing a fish respond to (4) the external factors or potential drivers 'food availability' and 'predation risk', both traits of the underlying seascape (see graphical abstract). The dynamic interaction between the fish and the seascape arises from a fish`s ability to sense changes in food availability and predation risk in different habitats (Werner et al. 1983; Colgan 1993) and adjust its velocity accordingly (Milinski 1993). A fish's motion capacity is thus directly related to food intake and habitat changes and affect the fish`s energy budget (internal state) by determining the swimming costs (Ohlberger et al. 2006). Combined with the habitat-dependent food availability, which controls the possible energy gain, both habitat features ultimately decide on the fish`s growth and survival.

To realistically simulate landscape-related movement we incorporate a vector-based movement algorithm that uses artificial potential fields. Potential field approaches are commonly used in computer games and mobile robotics, where they were first introduced by Khatib (1986) and made popular by Arkin and colleagues (Arkin et al. 1987; Arkin 1989). Based on a physics analogy, these methods treat an (moving) agent as a charged particle acting under the influence of a magnetic (potential) field representing the current structure of the spatial environment (Connell 1990; Dudek and Jenkin 2010). In case the environmental structure changes, the potential field can easily and dynamically be updated. By assigning charges of various magnitudes to all other objects and/or locations in this environment (based on prior knowledge), attractive and repulsive forces are computed navigating an agent in a particular direction. Analogous behaviour can also be perceived in nature, when e.g. reef fishes avoid moving through areas of high predation risk as if “repelled” resulting in the above-mentioned ‘landscape of fear’ (Laundré et al. 2001; Catano et al. 2016). Combined with their mathematical elegance and simplicity (Raja and Pugazhenthi 2012) this similarity and flexibility makes artificial potential fields an appealing approach for the exploration of organismic reactions to landscape structure and its heterogeneity. In our model the external factors are implemented as attractive (food availability) and repulsive forces (predation risk) thereby acting as the environmental stimuli of the benthic seascape for a fish to move in a particular direction.

With our model, in which the external factor food availability acts as an attractive force, while predation risk is implemented as a repulsive force, we mainly address the following questions: (i) How do small-scale behavioural decisions affect key life history traits such as energy budgets, survival, and reproduction of the model species? (ii) How do these individual decisions influence population dynamics and the spatial distribution as self-organized spatial structures of model species? (iii) What are potential responses on the individual as well as the population level to changing environmental conditions like an increasing habitat fragmentation? (iv) How does the spatial configuration affect energetic gains and costs (e.g. growth and survival)?

3.3 Material and Methods

In this section we briefly describe the proposed IBM following the ODD protocol (Grimm et al. 2006, 2010) while detailed model flows, equations and all parameters as well as model validation and the results of the sensitivity analysis are summarized in Appendix A1 and A2, respectively. Our model has been developed using the object-oriented programming language Java (version 1.8) with the MASON multi-agent simulation toolkit (see https://cs.gmu.edu/~eclab/projects/mason/) and it is available at gitlab (https://gitlab.leibniz-zmt.de/ecomod/kitt). Subsequent data analysis of model outputs is performed using Python 3 with Jupyter Notebook 5.7.4. The model is designed and parametrized based on our own field observations of the study system and target organism (unpublished data) as well as the comprehensive literature data available regarding the life cycle, bioenergetics and general ecology of parrotfishes, in particular the Daisy parrotfish (*Chlorurus sordidus* (Forsskål, 1775)) as an ubiquitous and well-studied member of this functional group.

3.3.1 **Purpose**

Our model is designed to spatially-explicitly simulate diel movement behaviour and resulting population dynamics of herbivore parrotfishes in various habitat settings in order to better understand how the underlying seascape influences small-scale movement decisions (Fig. 2).

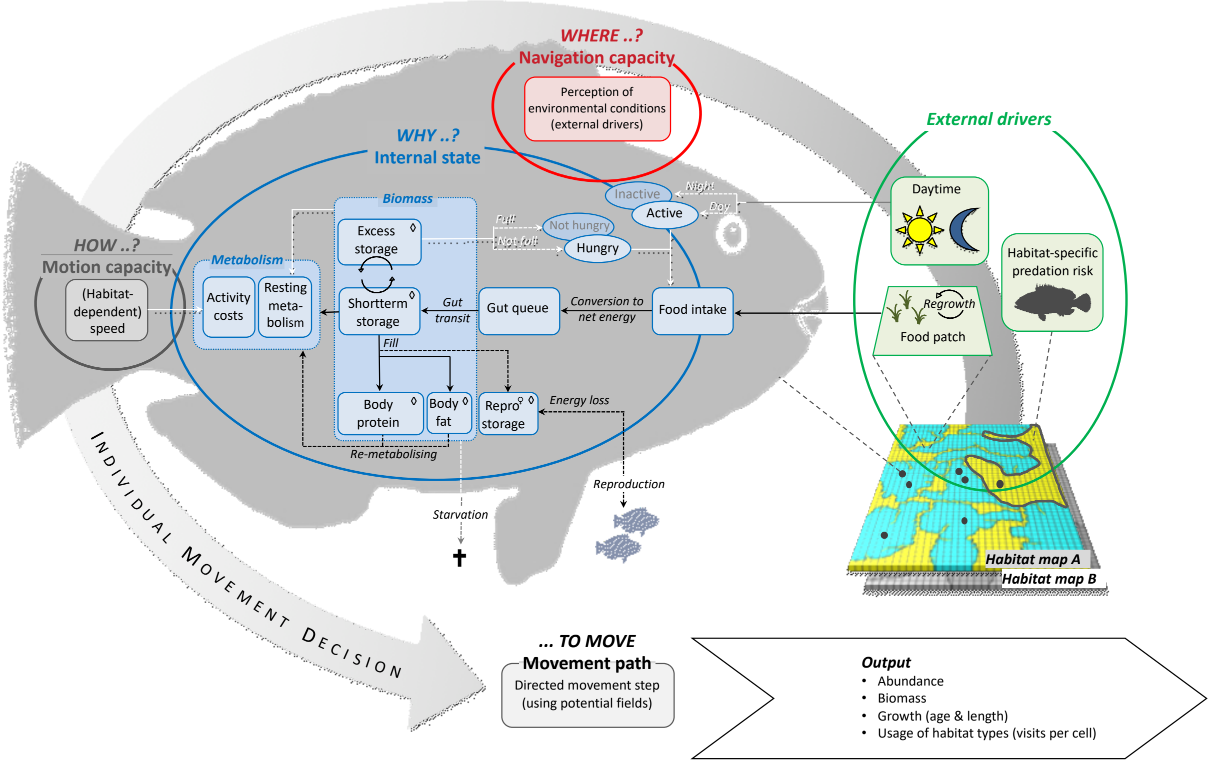
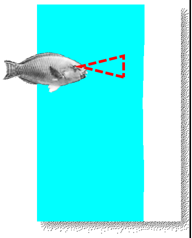
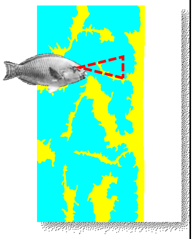
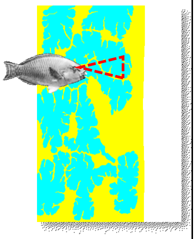
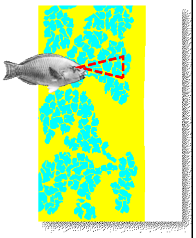
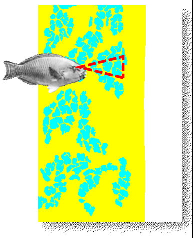
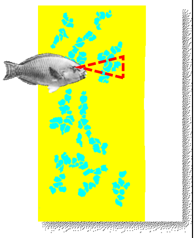


Fig. 2 Overview of basic model processes and linkages between model compartments.

⟶	Flow of energy
⇨	Flow of information
- - -➔	Conditional fluxes of energy or information
◊	Compartment size depending on individual body length
♀	Applies solely to female individuals

Our specific goals in this study are to assess (i) how trade-offs between effectively foraging and avoiding risk of predation on the individual level may affect individual growth and energy budgets, as well as the spatial distribution of a population and its (long-term) survival and (ii) whether different habitat configurations with a varying degree of fragmentation may have the potential to enhance or alleviate any of the observed effects. To this end we simulate six different scenarios with varying spatial compositions and configurations of the benthic seascape (Table 1).

Table 1 Overview of tested scenarios with six alternative seascape settings (I-VI). Habitat types are indicated in blue = coral reef, yellow = sand, and white = mainland (to simulate coastlines).

Movement strategy *PERCEPTION* (movement algorithm based on potential fields)					
Basic assumptions: - Behavioural explicit with adaptive movement decision-making, i.e. individuals are able to navigate in space and time and can adapt their behaviour (i.e. direction of next movement step and/or swimming speed) to changing environmental conditions (i.e. food availability and predation risk) Individuals can sense and respond to (changing) habitat features via their perception range, which serves as an informational window to the surrounding seascape					
I. Scenario *Default*	**II. Scenario *Connected***	**III. Scenario *Patchy_80***	**IV. Scenario *Patchy_60***	**V. Scenario *Patchy_40***	**VI. Scenario *Patchy_20***
					
Continuous coral reef habitat of 0.1 km^2 along a coastline of 0.035 km^2	Coral reef habitat of 0.07 km^2 surrounded by sandy bottom patches of 0.03 km^2 along a coastline of 0.035 km^2	Coral reef patches of 0.056 km^2 separated by sandy bottom habitat of 0.044 km^2 along a coastline of 0.035 km^2 representing a loss of coral reef habitat of 20 %	Coral reef patches of 0.042 km^2 separated by sandy bottom habitat of 0.058 km^2 along a coastline of 0.035 km^2 representing a loss of coral reef habitat of 40 %	Coral reef patches of 0.028 km^2 separated by sandy bottom habitat of 0.072 km^2 along a coastline of 0.035 km^2 representing a loss of coral reef habitat of 60 %	Coral reef patches of 0.014 km^2 separated by sandy bottom habitat of 0.086 km^2 along a coastline of 0.035 km^2 representing a loss of coral reef habitat of 80 %

3.3.2 Entities, state variables, and scales

Our model encompasses two kinds of entities (see Appendix A1.1 and A1.2) and three hierarchical levels: the individuals of a common group of diurnal reef fishes as one entity, the population comprising all individual fishes, and the underlying benthic seascape as the second entity and spatial environment, in which the fish (inter-)acts.

Individual fishes are parametrized to represent (post-settlement) herbivorous parrotfishes with their (coarse) life cycle and bioenergetics defined by relevant components and key processes following (Hölker and Breckling 2005). The modelled life cycle comprises all life stages from recently settled post-larval juveniles to adult terminal phases. Larval stages are excluded because larvae are part of the plankton and thus subject to different mechanisms and drivers. Individual fish are characterized by 17 state variables such as *biomass* (g wet weight), *length* (standard length in cm), *age* (years; *age*), *position* (spatial coordinates), *sex* (female or male) and *phase* (juvenile, initial phase, or terminal phase) which are updated according to a set of rules (behavioural repertoire). The behaviours of each individual include all main activities a fish exhibits during a 24 h cycle such as moving, feeding, growing, reproducing, and resting and are each associated with different energetic gains and costs (in kJ, as the model's 'currency' following (Hart 1993)). A full description of all state variables as well as execution flows can be found in Table A1.1 and sections A1.1.1 – A1.1.9.

The virtual environment consists of four principal components we deem essential to represent the fish-seascape link with its potential key drivers (i.e. risk of predation and food availability) for movement decision-making at the spatio-temporal scale of diel movement behaviour. As the spatial base for the simulation we use two overlapping 2D grids of identical size and resolution to depict (i) the seascape with different habitat types (*HabitatMap*) and (ii) the habitat-dependent food resources (*FoodMap*). The *HabitatMap* also holds (iii) information on the habitat-dependent predation risk (*PredationRiskFactors*) while (iv) the abiotic factor daytime (*TimeOfDay*) functions as the main controlling force for a fish's daily activities (Helfman 1993; Bellwood 1995). Detailed descriptions, state variables and parameter settings for all environmental components appear in Table A1.3 and sections A1.2.1 – A1.2.4.

In short, the *HabitatMap* is composed of at least one of two different habitat types (coral reef or sandy bottom; *habitatType*) whose distribution is based on an artificial habitat map designed to represent typical habitat configurations in tropical coastal environments. The six variants of this map used in our simulations have different habitat configurations and compositions with a decreasing amount and size of coral reef patches and an increasing separation by sandy bottom areas. The order of magnitude of the reduction rate of coral reef habitat between scenarios (-20 %) is based on reported destruction rates of corals, which can be as high as 69 % in one year as recently measured on the Great Barrier Reef after a major bleaching event (Schaffelke et al. 2016). Associated with each habitat type is a (habitat-dependent) risk of predation, one of the two external drivers we explicitly consider in our model. Due to a lack of empirical values with regard to habitat-related mortality rates as well as computational constraints we model the risk of predation as an increment of the natural mortality rate, which changes in dependence of the topographic complexity of each habitat type (Pratchett et al. 2008; Welsh and Bellwood 2012a; McCormick and Lönnstedt 2013).

The *FoodMap* holds all relevant information on food availability as the second external driving factor considered in our model. Food availability is implemented as an abstract calorific value for epilithic algal turf, which we consider to be sufficient to model relevant population dynamics. Algal turf, which is ubiquitous on coral reefs and one of the largest sources of primary production in these systems (Tootell and Steele 2016), is one of the main food sources of many parrotfishes (Polunin et al. 1995). It is also, however, a food source of low energetic value and parrotfish must therefore continuously feed throughout the day to satisfy their daily energy demands (Chen 2002). To incorporate feedback processes between individual fishes and the algal food resources we add a regrowth function (following Kelly et al. (2017)). We further assume conditions to be uniform within one grid cell regarding habitat type, predation risk, and food resources.

Since the main goal of our model is to capture the movements of each fish as well as its interaction with the surrounding environment, the finest resolution process considered is the foraging process. The appropriate spatial scale has therefore to reflect the size of a patch that a parrotfish may use in one feeding bout as well as the typical scale comprising a fish's choice of movement to a new food patch. Based on these assumptions and field observations of short-term foraging ranges of parrotfishes (Nash et al. 2012; Tootell and Steele 2016) we set the spatial resolution (size of spatial grid cells) to 1 m so that 1 pixel of both the *HabitatMap* and the *FoodMap* correspond to 1 m^2. At this resolution we also believe it possible to represent the essential spatial details like habitat patchiness or changing spatial distribution of local resources, which are needed to address our research questions. With a map size of 450 x 300 pixel the simulated landscape equals a total area of 0.135 km^2 encompassing typical home range sizes of < 500 m^2 of diurnal herbivores like parrotfishes (Welsh and Bellwood 2012b; Green et al. 2015). Time proceeds in discrete time steps at a high resolution of 1 s to allow for the emergence of habitat-related movement patterns which have been suggested to only be discernible at a narrow range of temporal resolutions (Avgar et al. 2013).

3.3.3 Process overview and scheduling

Process overview. Our model considers five main processes with four of them related to a fish's lifecycle (moving, growing, reproducing, and feeding) and one involving the regrowth of food sources (Fig. **3**). All fish-related processes are executed every time step and include an evaluation system to decide which part of the behavioural repertoire will be performed. Thereby each fish can individually evaluate which behaviour is appropriate to the local surroundings and its energy demands to allow for short-term behavioural responses to its internal energetic state. The decision process is followed by the execution of the chosen behaviour and the updating of the respective state variables. All fish-related modules execute in the same sequence, while the fish entities themselves are processed in a randomized order. The regrowth of food resources occurs only once at the beginning of a 24 h cycle and both the modules *Daytime* and *Predation risk* do not carry out any active processes.

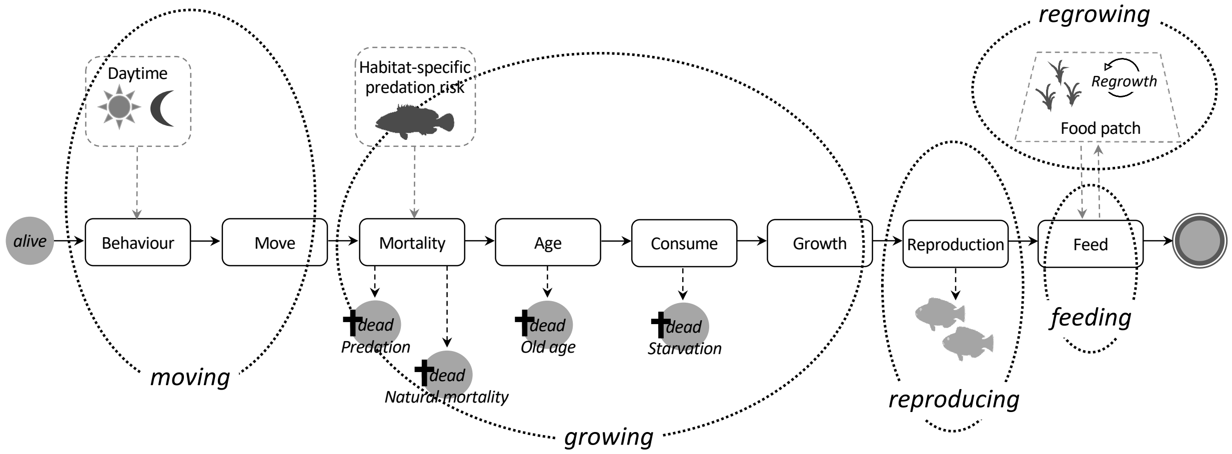


Fig. 3 Schematic overview and execution order of main modules and model processes (in italics). Dotted black lines indicate which modules of a fish's life loop are part of a certain process. Dashed grey lines and arrows illustrate influencing environmental factors.

Scheduling. In our model the scheduling of a fish's activities and processes is intended to follow a biologically meaningful yet computationally practical order to mimic a fish's natural behaviour during a 24 h cycle. In order to reflect the overriding and predictable constraint the diel cycle imposes on the behaviour and activity of fishes (Helfman 1993) we implement a factor called *TimeOfDay* (Appendix A1.2.4) which primarily controls a fish's behaviour (Appendix A1.1.2). As a consequence of this natural controlling force, most (tropical reef) fishes are known to be either diurnal or nocturnal with an active phase characterized by feeding and an inactive one by cover-seeking and resting (Hobson

1972). The changeover behaviour between these two phases typically occurs in the intermediate twilight periods. Parrotfishes like *C. sordidus* as diurnal herbivores spend on average about 90 % of daylight hours foraging with abruptly starting and stopping to feed at dawn and dusk (Bellwood 1995). At dusk they move to boulders or rocks on the reef slope to sleep (Bellwood 1995). Thus, depending on *TimeOfDay* our diurnal model fish is set to either forage (if daytime = *DAY*), rest (*NIGHT*) or migrate from resting to feeding habitats (*SUNRISE*) or vice versa (*SUNSET*).

If a model fish is scheduled as active and hungry, it will move to search for food based on a spatially informed movement algorithm using potential fields (see below and Appendix A1.1.3 for a full description). Once a fish has moved to its next position it will deplete the food resources on the current food cell based on its body-size dependent feeding rate (*meanIngestionRate*) until it has gained enough energy to meet its energetic demands (Appendix A1.1.9). As fish are further known to be able to increase their average feeding rate with increased hunger levels (Godin 1981) a model fish can adapt its feeding rate between a minimum (*minIngestionRate*) and a maximum (*maxIngestionRate*) (order of magnitude following (Polunin et al. 1995)) based on its current energy budget.

Following the paradigm that all energy acquired by any animal through the ingestion of food is ultimately either used in metabolic processes, deposited as new body tissue (including reproduction), or lost as waste products (Willmer et al. 2005) the model uses individual energy budgets for each fish to describe the partitioning of the ingested energy into these components. To realistically depict relevant bioenergetic processes we implement five different body compartments with specific functions following (Hölker and Breckling 2005): (1) the gut to mimic digestion, (2) an excess storage to regulate the fish's hunger state, (3) a short-term storage representing carbohydrates, (4) body fat as a medium-term energy storage, and (5) body protein as a long-term storage. Female individuals also possess a reproduction compartment to account for the dynamics and energetic costs of the reproduction process (Hölker and Breckling 2005) including spawning, which is one of the most metabolically demanding activity in the lives of fishes (McBride et al. 2015). Energy requirements associated with the maturation of male gonads, on the other hand, are usually substantially lower (Wootton 1979; Miller and Kendall 2009; Berg and Fleming 2017) and are therefore not considered here.

Since the prime demand for food, before any energy storage or somatic growth can occur is to meet maintenance requirements (Brett and Groves 1979) our model fish first covers all energy costs due to its resting metabolism needed to keep it alive, followed by all energetic losses caused by its movement activity (Appendix A1.1.6). Any remaining energy is then used for growth (i.e. increase in biomass and body length) and allocated to the different body compartments following the approximate body composition of a parrotfish (Karakoltsidis et al. 1995). In case, however, more energy is consumed then assimilated the fish will eventually die due to starvation. All assumptions underlying the allocation and conversion of energy is detailed in Appendix A1.1.6-A1.1.9 with all related parameters listed in Table A1.2.

Apart from starvation a model fish can also die due predation (Appendix A1.2.3), senescence (Appendix A1.1.5) or due to natural mortality (Appendix A1.1.4), which comprises any mortality-inducing factor other than starvation, predation or senescence, such as sickness, diseases or pollution. All types of mortality are implemented to approximate a total annual mortality rate of 0.3 to 0.4 year^{-1} without fishing as mortality due to fishing is not (yet) implemented in our model.

Depending on biomass, body length, and age individual fishes are either referred to as juveniles (considered as non-reproductive females), females or males. We include protogynous (female-to-male) sex change in our model because it is a common life history pattern in parrotfishes such as *C. sordidus* and ignoring life history variation in assessing stock dynamics has been demonstrated to lead to an overestimation of spawning biomass (Alonzo et al. 2008). As a protogynous hermaphrodite a model fish can therefore change from the juvenile life phase to the female initial phase and then to the male terminal phase depending on its biomass and length (Appendix A1.17). To account for reproductive processes female fishes in their initial phases are able to spawn once they have acquired enough energy resources in their reproduction storage (Appendix A1.1.8). Due to the assumption of low energy costs regarding the maturation of testes male individuals have no functional role in the modelled reproduction but still contribute to processes related to population densities and food depletion. Spawning can occur during each time step since 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). Following (Lewis 1997; Miller et al. 2001; Miller and Kendall 2009) and to ensure a stable (self-recruiting) model fish population over time we assumed that two juvenile individuals per female and spawning event (*NumRecruits*) settled within the population after the timespan of a post-settlement age of 120 days had passed (following (McIlwain and Taylor 2009)). Stock-recruitment relationships are generally difficult to establish for coral reef fishes (Roberts 1996) due to larval dispersal over long distances and the high temporal variability of post-recruits immigration (Lewis 1997). It is likely, however, that recruitment is at least partly controlled by local reproduction (Green et al. 2015) and local populations of *C. sordidus* seem to be mainly affected by the recruitment of larvae and less by post-recruits inputs (Lewis 1997). We therefore consider recruitment to be determined solely by the local population and without any post-recruit immigration.

Movement. As we put special emphasis on the analysis of spatial interactions and their influence on movement behaviour a model fish can make an informed movement decision based on perceived environmental conditions regarding food availability and predation risk to navigate through its surroundings. At each time step the actual movement step is modelled discretely using a vector-based walking algorithm based on the step length (defined by the current speed) and the turning angle (direction). As described below the direction (in degree) is computed using potential field methods and constrained by a maximum turning range and a spatial perception range, while the actual speed value (in cm s^{-1}) is determined by the fish's current activity and the underlying habitat type.

To compute the direction of a fish's next movement step we use vector field path planning based on artificial potential fields (Khatib 1986; Arkin et al. 1987; Arkin 1989; Connell 1990; Dudek and Jenkin 2010). Treating the pathfinding of an 'intelligent' model fish as a flow field problem allows us to integrate the motivational basis of a fish to move: Depending on a fish's behavioural mode (*FORAGING*, *RESTING*, or *MIGRATING*) different landscape features are considered relevant and function as attractive or repulsive forces, which are individually weighted and then added to compute the most favourable direction. Thereby a fish can adapt its behaviour to its movement goal as well as respond to a changing environment. The set of environmental stimuli a diurnal fish considers during daytime (i.e. when in *behaviourMode FORAGING*) are food availability (attraction) and predation risk (repulsion). During dusk, however, a fish's motivation to move changes from safely finding food to safely migrating to the appropriate habitat type for resting and during dawn to safely migrating to suitable feeding areas. Thus, instead of food density the appropriate habitat type of the benthic seascape becomes the relevant attractive force when a fish is *MIGRATING*. As soon as a fish reaches the target habitat, it will switch to the next scheduled behaviour mode (*FORAGING* or *RESTING*). While *RESTING* the sole motivation of a fish is to survive while resting, which is why only predation risk is considered as a relevant landscape feature during this behaviour mode.

To realistically depict a fish's response towards the above-mentioned seascape characteristics we incorporate a perception radius for each relevant habitat feature. This radius functions as a spatial range, in which a fish will react to a certain feature and include it into its movement decision. For the risk of predation, we set the perception range (*perceptionRadiusPredation*) to 10 m based on the knowledge that vision is of the main sensory systems involved in prey – predator interactions of coral reef fishes (Myrberg and Fuiman 2002) such as escape responses (Domenici 2002) and most fishes thus have well developed visual capabilities with a high spatial and temporal resolution that match those of other vertebrates (Guthrie 1986; Rosa Salva et al. 2014). Furthermore, parrotfish live in relatively shallow and clear-water environments around coral reefs in which an average visibility of 10 m can be expected (Roy and Smith 1971; Aerts and van Soest 1997). For computational reasons the inclusion of the dynamic habitat feature food availability in the decision-making process is limited to the next eight directly adjacent cells representing a perception range (*perceptionRadiusFood*, [m]) with a reactive distance of 1 m (see Appendix A1.1.3 for further details).

The direction of the next step is further constrained by a fish's maximum turning range (*maxTurnSpeed*, [° s^{-1}]), which delimits the maximum angle a fish can turn at each time step at high temporal resolutions (1 s) to ensure the emergence of realistic changes of direction at a lower time resolution (Jopp and Reuter 2005). The range is parametrized based on field studies by (Davis 2016), in which movements of individual *C. sordidus* were tracked over 20 min time periods with a time resolution of 15 s. The recorded movement trajectories suggest convoluted foraging paths for *C. sordidus* with a high tortuosity (i.e. having many directional changes within a small area) and which result in paths with a start-finish distance much shorter than the total distance travelled (Fulton and Bellwood 2002).

Moreover, fishes are not only known to be able to sense changes in predation risk or food availability in different habitats but also to adapt their velocity accordingly (Milinski 1993). Therefore, a model fish will not only adapt its movement direction according to the perceived surroundings but also increase its speed in riskier (i.e. topographically less complex) and/or low-food habitats (*SANDYBOTTOM_SPEED_FACTOR*) and become slower under more favourable conditions, i.e. habitats with high structural complexity (Nash et al. 2012, 2016; Tootell and Steele 2016) . Changes in speed can have a considerable impact on a fish's energy budget because locomotion, which generally constitute a large proportion of an animal's energy budget (Alexander 2005; Ohlberger et al. 2005), is metabolically costly for fish (Brett and Groves 1979). To integrate the level of activity of a model fish with its energetic state our model computes metabolic costs of swimming using a relationship between oxygen consumption, fish mass and average swimming speed (Hölker and Breckling 2005) and adds these additional costs to a fish's resting metabolism (Appendix A1.1.6). Details on the exact computation of movement steps appear in Appendix A1.1.3.

3.3.4 Design concepts

In this section we describe all concepts identified by the ODD protocol that apply to our IBM. Concepts such as *Learning*, *Prediction*, *Interaction*, and *Collectives* are not employed and therefore omitted.

3.3.4.1 Emergence

Population dynamics (i.e. changes in size, length-, age- and life-phase distributions) as well as its spatial distribution arise from the properties of the individual fishes regarding their ontogenetic development and somatic growth as well as their movement behaviour(s) and direct interactions with the underlying seascape structure. Also, traits of the individual such as mortality are not modelled explicitly but emerge in our model depending on a fish's current age (mortality due to senescence), its failure to keep a minimum energetic level (mortality due to starvation) as well as its choice of habitat and the habitat-related predation risk combined with the time spent on a particular habitat (mortality due to predation).

3.3.4.2 Adaptation

While individual fish behaviour is largely imposed via empirical rules, fish can make adaptive decisions with regard to their feeding rates. The more imminent the threat of starvation becomes the more food a fish will try to assimilate (up to a certain maximum) as fish are known to be able to increase their average feeding rate with increased hunger levels (Godin 1981). Furthermore, fish are able to adapt their direction of the next movement step to the most favourable position perceived with regard to predation risk and/or food availability (see above) and thus enhance their chance of survival.

3.3.4.3 Objectives

The foremost goal of each fish is to ensure its survival by meeting its energetic requirements. To achieve this objective a model fish will try to reach the (theoretical) biomass it would have gained at its current age under ideal conditions based on the species-specific Von Bertalanffy Growth Function, one of the most widely used growth curve in fisheries science (Appendix A1.1.6).

3.3.4.4 Sensing

Individuals can obtain information about their internal and external environment as they are assumed to know their own energetic and reproductive state as well as food levels and predation risks in their vicinity and consider this information in their decisions. Information of the surroundings, however, is restricted to the local environment via the fish's perception range: A fish on one habitat patch can sense and correctly evaluate the resource levels as well as the associated predation risk of all potential destinations within its perception range.

3.3.4.5 Stochasticity

Stochastic events in our model include whether a fish will die due to predation or natural causes like diseases, which are represented as probability rates, while mortality due to starvation or old age are emergent properties of our model. Life phase transitions are also implemented as probabilities, and therefore stochastic.

Furthermore, our model uses stochasticity during the initialization of the population to assign each individual fish its initial age and its position on the habitat grid as well as to allocate the initial standing crop (within a pre-defined habitat-specific minimum and maximum value) to each cell of the food map (Appendix A1.2.2). Any new recruit that enters the simulation after a spawning event will also be placed randomly on the simulation grid. Also, if a fish is located at the currently most favourable position, the direction for the next movement step is chosen randomly using a uniform distribution on all directions (360°) to restrain the fish from getting stuck in local minima.

To create intrinsic variation among individuals a random component is added to the following variables using a uniform distribution: (i) *SPEED,* (ii) the limits of the reproduction compartment, which determine if spawning occurs (*UPPER_LIMIT*) and how much energy is remaining after spawning (*LOWER_LIMIT*), (iii) the threshold determining if a fish enters the next life phase (*Length_InitialPhase, Length_TerminalPhase)* and (iv) the maximum age (*MAX_AGE*) a fish can reach.

3.3.4.6 Observation

On the level of the individual our model traces the fate of each fish in the population from birth to death by tracking its location and noting its velocity as well as its energetic state. On the population level the model logs the total abundance and biomass, the abundances and biomass grouped by life phase (juveniles, females, males), as well as age- and size-frequency distributions at regular pre-defined intervals. On the environmental level it records the number of fish visits that occur in each habitat cell over a predefined time period to allow for an analysis of habitat use patterns and spatial distributions of fishes across the simulated seascape (Table A1.3).

To facilitate the observation of individual movement trajectories as well as to monitor the spatial distribution of the population at a high temporal resolution and thus address the questions our model is designed for, a graphical user interface (GUI) is implemented. The GUI shows the structure of the underlying seascape by representing the habitat type of each grid cell via pre-defined colours and displays all fish agents of the population and their current location as different-sized diamond shapes (depending on maturity state). To closely follow the movement path as well as energetic and ontogenetic development of a single individual it is further possible to inspect a specific fish entity by displaying its movement trail and the values of all relevant key life history features.

3.3.5 Initialization

Our model first initializes the habitat grid as the environment or ‘model world’, in which all fish entities spend their entire life loop: Each grid cell is assigned a habitat type based on an external input file, which is designed to represent a typical tropical coastal environment, and is then initialized with a random food value within the limits of its habitat type. The initialization of the environment is followed by the computation of the individual fish entities. Due to computational constraints the habitat grid is initially occupied with a population of 50 randomly placed individuals (*InitialNum)*, whose initial age distribution is derived stochastically from (arbitrary) probabilities given for each maturity state (*AgeDistribution*): 0.4 for juveniles, 0.5 for initial and 0.1 for terminal phases. All other state variables like biomass and body length are then computed accordingly based on the implemented formulas and assumptions summarized in Appendix A1.1. A simulation starts at 8 hrs and DAYTIME as *TimeOfDay,* when parrotfish usually start feeding.

The implementation of the *AgeDistribution*, the stochastic allocation of individuals to the grid and of initial food values to each grid cell allow for variation between simulation runs. Reproducibility of a particular run, however, is guaranteed by means of a seed value (*Seed*) which fixes its random state. All (default) parameter values and initial settings are listed in Table A1.4.

3.3.6 Input data

Our model includes one external data source (*.png* image file) to spatially-explicitly represent the habitat configuration of the underlying seascape. The image file depicts a benthic habitat map identifying different habitat types by means of a pre-defined colour code. The file can be replaced by any image file, that satisfies the required colour coding, and thus allows for representations of different local scenarios and habitat settings.

3.3.7 Model validation

Our model is parametrized, tested, and validated following a hierarchically structured validation approach (Reuter et al. 2011; Kubicek et al. 2015). For parametrization we mainly use information from three different sources: Experimental data, expert knowledge including own field observations of the study system and target organism (unpublished data), and calibration. Most of the parameter values are directly obtained from published field studies on parrotfish and reef ecosystems, while parameters concerning the recruitment rates and habitat-dependent predation risks are estimated based on available literature regarding general reproduction patterns of reef fish and overall natural mortality rates, respectively. We further set the values of the pathfinding weighing factors, for which presently no data is available, based on studies regarding the relative importance of different habitat-related drivers for fish movement and our expert knowledge of the study system gathered during several years of field research. To assist parametrization and calibration of parameter values which are highly uncertain (no data available or known to be difficult to estimate) or to which we suspect model outputs to be highly sensitive we conduct a sensitivity analysis (Reuter et al. 2011). To do this, we identify the most susceptible parameters of each main model process (food availability, movement, energy gain and loss, reproduction and survival), cover the biologically plausible range of each of these parameters by varying each parameter one at a time by ± 10 %, and simulate all potential combinations with three different seeds each (i.e. three replicates per parameter combination). We then evaluate the effects of changing parametrization on population metrics like total biomass, abundance and life-phase ratios as critical model outputs.

To assess the validity of our model and its parameter settings, i.e. the robustness, precision and reliability of model results (Reuter et al. 2011) we inspect the energetic state of the individual fish process by process and by defined variables that can be compared to available independent data such as the body weight and length. These quantities contain information relative to growth, reproduction and survival we aim to interpret with regard to habitat-dependent movement behaviour and space use patterns**.** On the population level we assess the (long-term) population structure that emerge from the interactions of the individuals with regard to abundances, biomass, age-distributions, life phase composition and reproduction frequency and compare them to published field observations. Our model validation is further assisted by an appropriate choice of output plots monitoring population dynamics.

By performing this consistency check of key processes and dynamics on different hierarchical levels we ensure that the system behaviour we intend to represent has been captured correctly and results are reliable within the applied conceptual system (Reuter et al. 2008). Based on this data reconciliation and visual inspection of model outputs with results from the literature we then choose the parameter set that is able to reproduce a realistic population structure for our subsequent simulation experiments. Details on model validation and results of our sensitivity analysis can be found in Appendix A2.

3.3.8 Simulation experiments

To assess whether and how individual development and population dynamics are influenced by individual capabilities to interact with the environment and/or habitat settings (habitat configuration and level of fragmentation) we conduct a series of simulation experiments: We test four different scenarios (Table 1) with each factor combination replicated three times. Each replicate simulation is run for a time limit of 30 years and a maximum population size of 175 individuals (for computational feasibility). The time period modelled encompasses several generations thereby allowing for conclusions on a population level. The evaluation of a simulation run starts from year 10 as the first year in which the number and life-phase ratios of model fishes is comparable to those of parrotfish populations observed in field studies (see Appendix A2 for details).

3.4 Results

3.4.1 Fish abundances, biomass, and life phase composition

There is substantial variability in the total abundance, biomass, and life phase compositions of model fish populations among simulations under different scenarios (Fig. 4). While the two scenarios *Connected* (connected reef habitat of 0.07 km^2) and *Patchy_80* (reef habitat patches of 0.056 km^2) differ relatively little compared to model results of the *Default* scenario (continuous reef habitat of 0.1 km^2), both the scenarios *Patchy_40* (reef habitat patches of 0.028 km^2) and *Patchy_20* (reef habitat patches of 0.014 km^2) show a high and increasing decline in fish abundance (*Patchy_40* = ~40 %, *Patchy_20* = ~90 %, Fig. 4 a) and biomass (*Patchy_40* = ~45 %, *Patchy_20* = ~85 %, Fig. 4 b). Fish populations under the scenario *Patchy_60* (reef habitat patches of 0.042 km^2) initially develop similarly to the *Default* scenario but begin to decline in biomass and abundance from year 15 onwards and level off at a value of 85 % (abundance and biomass).

Of all simulated scenarios the IP:TP ratio varies strongest in scenario *Patchy_20* with values as high as 4.3:1 and as low as 0.2:1 (Fig. 4 c). Populations thus change from being strongly female-dominated to more male-dominated during the simulation period and eventually oscillate between 3.2:1 to 1.1:1. In all other scenarios the IP:TP ratio is rather stable throughout the simulation period and settles at a value of about 1.4:1 indicating a balanced ratio between female and male model fishes with a slight tendency to an increased number of females. Initial-phase females, which control recruitment and thus have a key function in regulating model population dynamics, have a mean body length of about 16.0 cm (Fig. 4 d). Again, the value varies most strongly in the *Patchy_40* and *Patchy_20* simulations but is similar across all other simulations suggesting that in these scenarios female fishes can still acquire enough energy to maintain their individual growth.

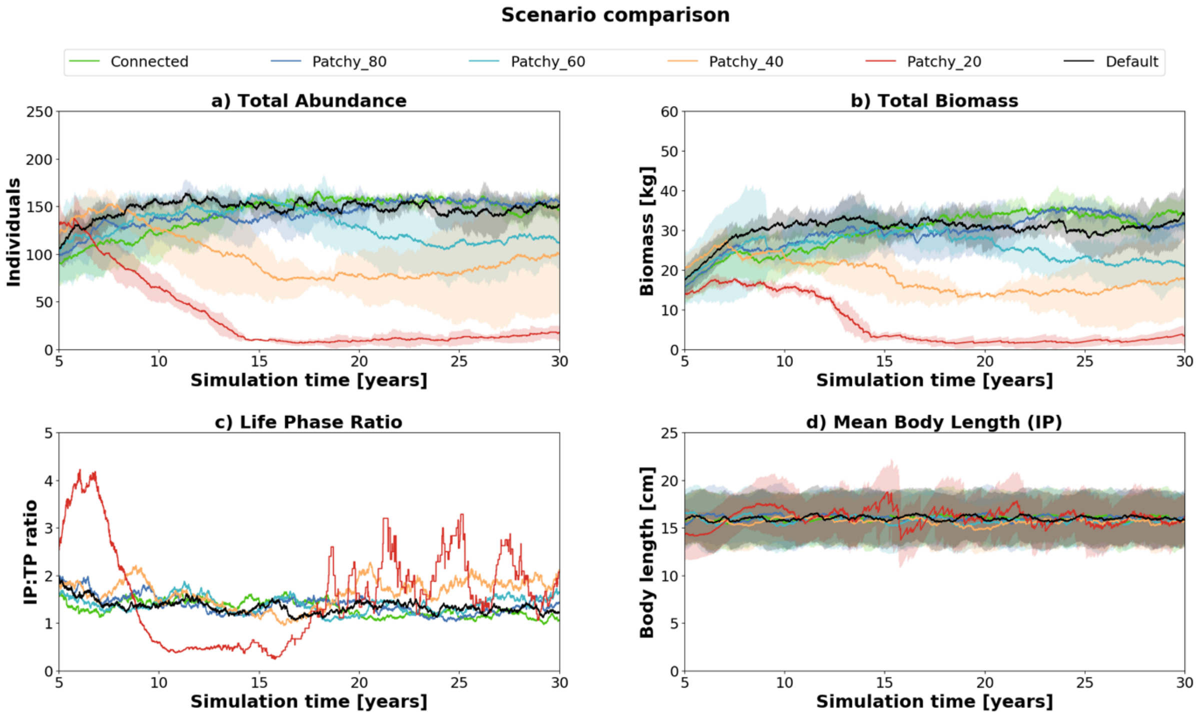


Fig. 4 Comparison of key population characteristics of simulation runs under different scenarios: **a)** total abundance, **b)** total biomass **c)** life phase composition (IP:TP), and **d)** mean body length of (female) fishes in their initial phase (IP).

Total abundances in the *Default* scenario with on average 150 ± 10 fishes (Fig. 5 a) are comparable to those of the scenarios *Connected* (150 ± 9 fishes, Fig. 5 b) and *Patchy_80* (148 ± 14 fishes, Fig. 5 c), but approximately 15 % higher compared to *Patchy_60* from year 15 onwards (125 ± 31 fishes, Fig. 5 d), about 2-fold higher compared to *Patchy_40* (88 ± 38 fishes, Fig. 5 e), and about 9-fold higher than under scenario *Patchy_20* (17 ± 6 fishes, Fig. 5 f).

As mentioned above life phase compositions vary little throughout the simulation period under the *Default* scenario with on average 28 ± 6 fishes in the juvenile phase, 69 ± 7 in their (female) initial phase (IP), and 53 ± 10 in their (male) terminal phase (TP). Very similar compositions can be found in simulations under the scenario *Connected* (28 ± 6 juveniles, 69 ± 7 IPs, 54 ± 8 TPs) and *Patchy_80* (29 ± 7 juveniles, 68 ± 8 IPs, 52 ± 9 TPs). Ratios under the scenario *Patchy_60* start to deviate from the Default scenario after ~15 years (23 ± 10 juveniles, 58 ± 19 IPs, 43 ± 9 TPs) with a tendency to more female dominated populations as fewer individuals reach their terminal phase. Proportionally even fewer male fishes are present in the simulations under scenario *Patchy_40* (16 ± 10 juveniles, 44 ± 22 IPs, 28 ± 10 TPs). As mentioned above under scenario *Patchy_20* proportions of life phases are highly variable with on average 3 ± 2 juveniles, 6 ± 3 IPs, and 8 ± 3 TPs.

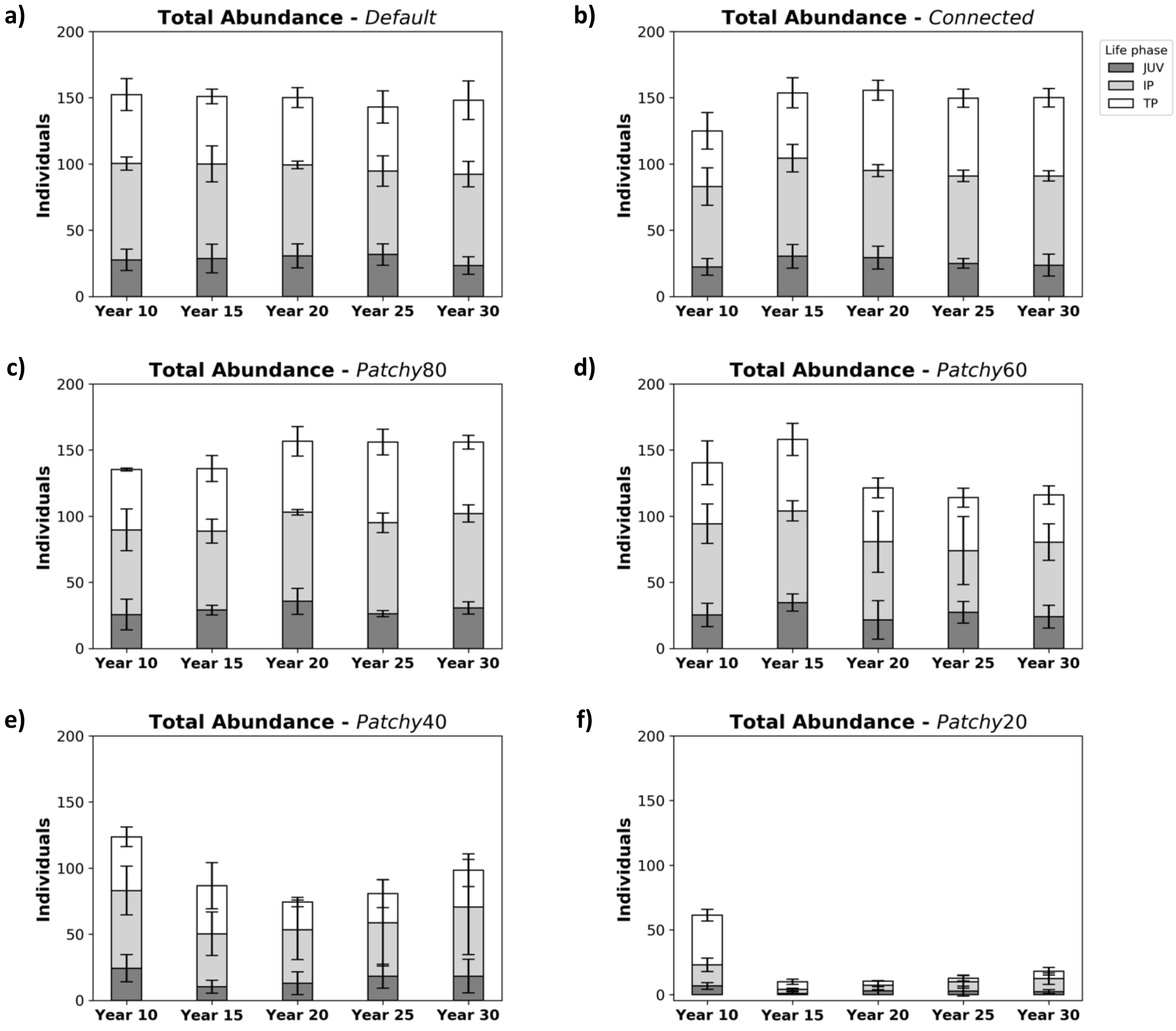


Fig. 5 Abundances and life phase composition of model fish populations at different points in time during a simulation under different scenarios: **a)** scenario *Default*, **b)** scenario *Connected*, ***c)*** scenario *Patchy_80*, **d)** scenario *Patchy_60*, **e)** scenario *Patchy_40*, and **f)** scenario *Patchy_20*. Bars indicate mean values (± standard deviation (SD)) and are subdivided into life phases (JUV = juveniles, IP = (female) initial phases, TP = (male) terminal phases).

3.4.2 Mortality rates and reproduction frequencies

Total annual mortality rates (Fig. 6 a-f) change little between scenarios (*Default* = 0.278 ± 0.071, *Connected* = 0.259 ± 0.065, *Patchy_80* = 0.271± 0.067, *Patchy_60* = 0.270 ± 0.080, *Patchy_40* = 0.272 ± 0.104), except for scenario *Patchy_20* with 0.347 ± 0.248. Also, little variability can be observed in the relative contribution of the different types of mortality, which range on average between 0.105-0.131 (M_{nat}), 0.116-0.130 (M_{pred}), and 0.032-0.085 (M_{age}). This outcome is as expected since individual fishes are able to sense the risk of predation in each habitat cell, include this information in their movement decision and thereby reduce the time spent on riskier habitats. In contrast to mortality rates, there is considerable variation in the reproduction frequency among the different scenarios from on average 20 to 24 reproduction events per year (*Default* = 24.0 ± 4.1, *Connected* = 23.7 ± 4.4, Patchy_80 = 23.5 ±5.6, *Patchy_60* = 20.7 ± 8.8,) to values as low as 2 to 12 (*Patchy_40* = 11.5 ± 6.8, *Patchy_20* = 2.1 ± 1.2). This decrease can be caused by both the reduced total number of females and a decrease in energy gain due to the reduction of food-rich coral reef habitat. With relatively stable mortality rates across scenarios and declining reproduction frequencies, which can compensate losses due to mortality, populations will inevitably collapse and eventually become extinct. As female fishes are mostly able to maintain their individual growth (with the exception of scenario *Patchy_20*, see above), but increasingly lack the energy to reproduce, the modelled systems seemingly become more and more food-limited. Moreover, reproduction seems to be the model process most susceptible to an increasing fragmentation and loss of habitat, rather than affecting population survival due to a growing risk of predation.

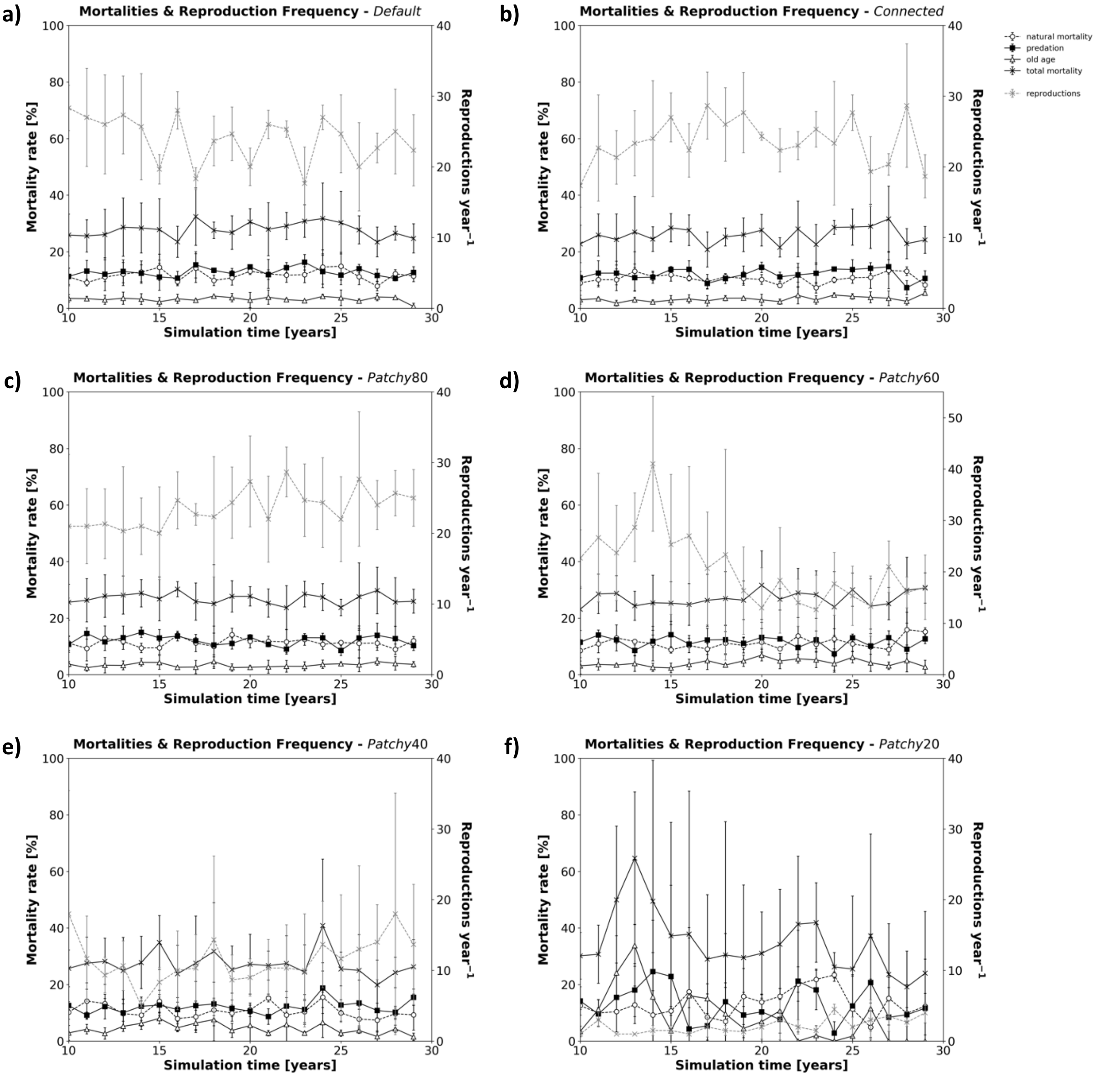


Fig. 6 Annual mortality rates (in black) and reproduction frequency (grey dashed line) of model fishes during a simulation under different scenarios: **a)** scenario *Default*, **b)** scenario *Connected*, **c)** scenario *Patchy_80*, **d)** scenario *Patchy_60*, **e)** scenario *Patchy_40*, and **f)** scenario *Patchy_20*. Values are mean values (± standard deviation (SD)) of replicated simulation runs.

3.4.3 Individual space use and spatial distribution of the fish population

Individual movement trajectories over a time period of 20 min differ noticeably across scenarios (Fig. 7) and the shape of the short-term foraging range changes in relation to the availability and distribution of coral reef habitat: As the coral reef habitat increases the more circular the movement becomes (Fig. 7 a). Consequently, the linear distance travelled increases in dependence of the area of sandy bottom, a fish has to cross in order to reach more favourable coral reef habitat patches (Fig. 7 b-f). In the examples shown in Figure 7 a) and f) the distances travelled during a 20 min time period increases from approximately 40 m in continuous reef habitat to 75 m in a highly fragmented reefscape, which corresponds to an increase of ~190 %. This behaviour is also found in nature as, when habitat fragmentation increases, individual fishes will have to travel over larger areas per unit time to reach suitable foraging sites, to maintain their energy intake rates.

The emerging patterns of the spatial distribution of modelled fish populations is not uniform among the tested scenarios (with the exception of the *Default* scenario with only one habitat type, Fig. 8 a), but clearly reflect the distribution and configuration of the coral reef patches of the underlying seascape (outlined in light grey, Fig. 8). While the monthly space use pattern under the scenario *Connected* (Fig. 8 b) appears relatively homogenous among coral reef patches, the frequency of visits are concentrated among certain patches in all other scenarios. Under the scenario *Patchy_60*, for instance, some patches in the upper region are heavily frequented (Fig. 8 d) with > 8000 visits per cell, a tendency that is even more pronounced under scenario *Patchy_40* with values of > 9500 visits per cell (Fig. 8 e). Interestingly, under all scenarios except *Default* and *Connected* some of the coral reef patches are hardly visited at all throughout the time period of one month. In general, however, space use patterns seem to be clearly driven by the characteristics of the underlying habitat structure.

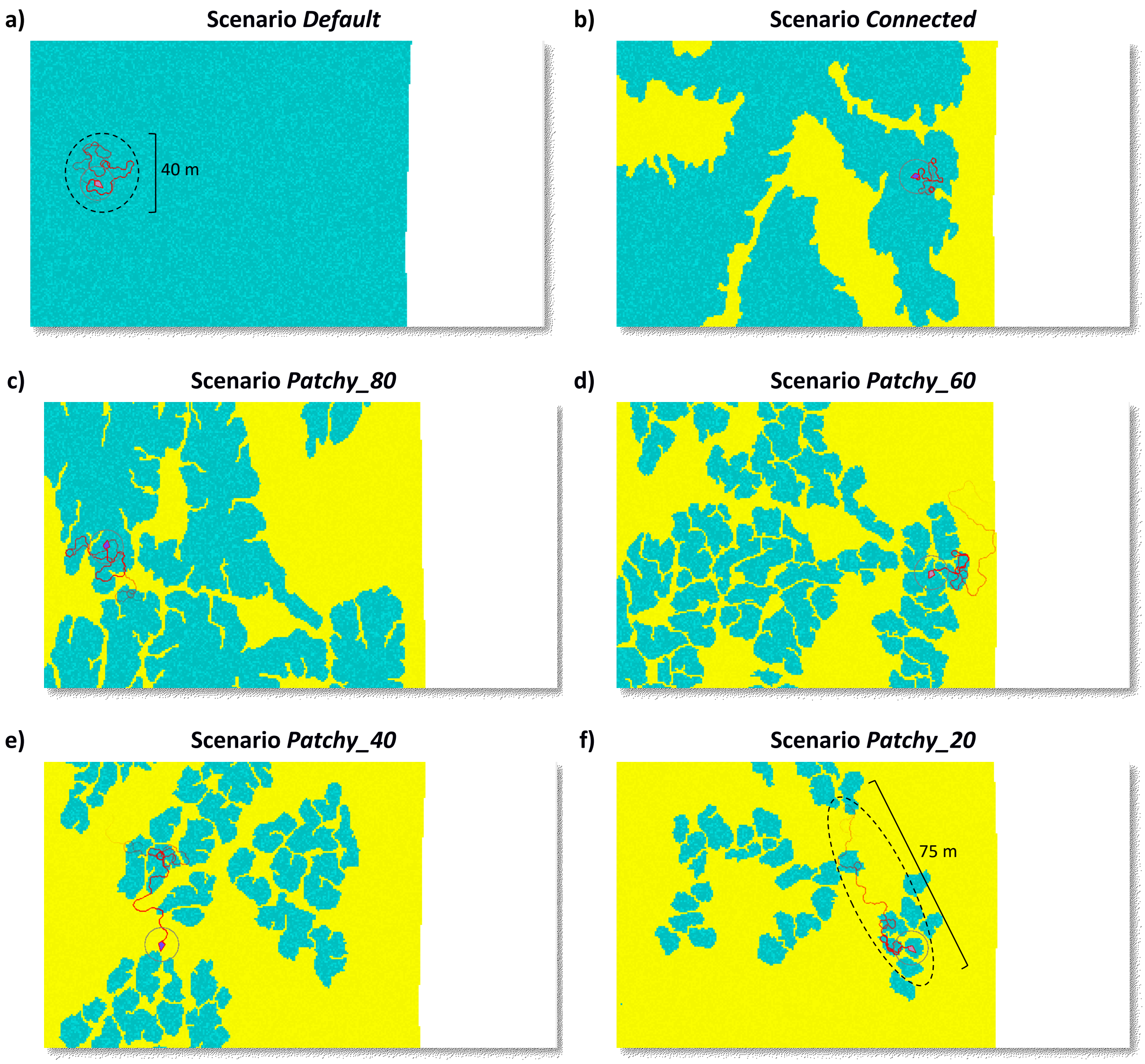


Fig. 7 Individual movement trails of a (female) model fish in its initial phase over a 20 min time period and under different scenarios: **a)** scenario *Default*, **b)** scenario *Connected*, **c)** scenario *Patchy_80*, **d)** scenario *Patchy_60*, **e)** scenario *Patchy_40*, and **f)** scenario *Patchy_20*. Blue areas = coral reef habitat, yellow = sandy bottom, white area = coastline. Darker shades of a colour indicate higher food availability and circular areas illustrate the fish's perception radius.

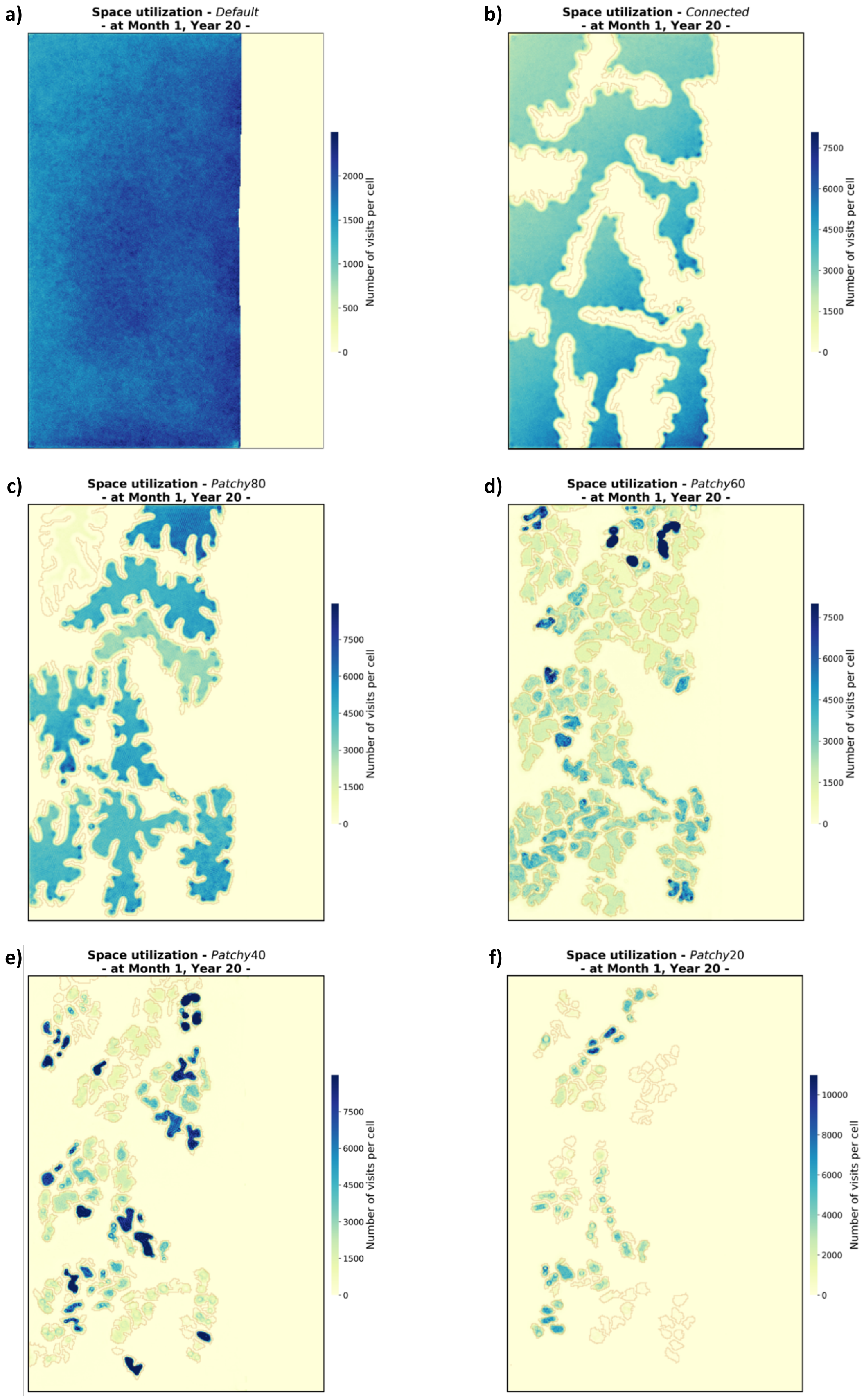


Fig. 8 Cumulated visits of fishes to each habitat cell illustrating the monthly space use patterns on the population level. Shown are representative data of Month 1 at Year 20 of the simulation period. The underlying patches of coral reef habitat are outlined in light grey.

3.5 Discussion

Our simulation experiments reveal substantial differences on both the individual and population level between the six scenarios tested (*Default*, *Connected*, *Patchy_80*, *Patchy_60*, *Patchy_40*, and *Patchy_20*), in which the underlying coral reef habitat is increasingly fragmented and successively reduced by a rate of 20 %. Based on annual rates of coral reef destruction, which can be as high 69 % (Schaffelke et al. 2016), our scenarios thus represent situations, that may occur in coral reef systems throughout relatively short time periods of a few years or less. While the scenarios *Default*, *Connected*, and *Patchy_80* show similar developments, the scenarios *Patchy_40* and *Patchy_20* deviate strongly in their results with *Patchy_60* exhibiting intermediate trends. In general, our findings reflect outcomes of empirical studies in various aspects and elucidate the potential of seascape characteristics to guide and constrain movement of herbivorous fishes.

Population dynamics. The modelled fish populations respond as expected to the manipulation of habitat configurations and degree of fragmentation with regard to abundance, biomass and overall survival. Population size declines gradually among scenarios along with food-rich and safer coral reef habitat. A loss of reef habitat by 80 % (scenario *Patchy_20*) corresponds to a reduced fish abundance by almost 90 % compared to the scenarios *Default* and *Connected*. Apart from the loss of the coral reef itself, the subsequent decline in parrotfishes may have further adverse effects for the ecosystem functioning as parrotfishes are important bioeroders and structuring force for benthic communities (Bellwood 1995; Bonaldo et al. 2014; Welsh and Bellwood 2014). By keeping turf algae in a cropped state parrotfish provide open substrata for enhanced coral recruitment and thereby have the potential to mediate coral-algal dynamics (Mumby et al. 2006; Hughes et al. 2007; Russ et al. 2015; Tootell and Steele 2016; Roff et al. 2019). A change in these complex interrelations may further alter an ecosystem’s ability to respond to disturbances (Bellwood et al. 2004).

Interestingly, the decline in model population size is mainly caused by a reduced reproduction frequency rather than an increase in predation mortality (except scenario *Patchy_20*) and/or starvation. As predation mortality in our model is determined by habitat complexity combined with the time spent on risky habitats and a fish is able to react to changing predation risk by changing its movement direction, it seems plausible that predation mortality does not increase significantly among scenarios. However, as indicated by predation mortality rates under scenario *Patchy_20* increasing distances moved over low complexity and riskier habitats will inevitably result in an increased exposure to predation, as was also demonstrated in field experiments of different herbivore fishes including *C. sordidus* (Madin et al. 2010, 2011).

In general, total annual mortality rates, which change relatively little between scenarios and vary between averages of 28 % (scenario *Default*) and 35 % (scenario *Patchy_20*), compare very well to those reported by (Gust et al. 2002) with annual mortality estimates ranging from 28 % to 43 % for *C. sordidus* populations.

The reason that model fishes do not experience mortality from starvation (as an emergent property) in our simulation experiments is likely to be caused by the low density of the model population, which is 4- to 6-fold lower than observed in the field (due to computational constraints, see Appendix A2.2). However, model results clearly show that even though female fishes can maintain their individual growth, they increasingly lack the energy reserves to be able to reproduce indicating a growing food limitation of the model system. As reproduction is known to be the most metabolically demanding activity in the lives of fishes (McBride et al. 2015) it is not surprising that reproduction proves to be the model process most susceptible to changes in habitat configuration and composition, and hence food availability. These findings are in accordance with field studies of *C. sordidus* made by (Tootell and Steele 2016), in which individual energy reserves decreased with algal turf resources suggesting that resource availability is an important factor determining the physiological condition of this species. Moreover, a decreased reproductive output will not only have implications for the persistence of the local population but may also negatively affect neighbouring population by a reduced supply of recruits. Apart from having a direct influence on the number of offspring a female may produce empirical evidence exists that the amount of energy a female has available to invest into egg production will also affect egg quality and this in turn the offspring's' fitness (Bagenal 1969; Crespi and Semeniuk 2004; Berg and Fleming 2017).

Movement behaviour and space use patterns. To better understand the consequences of population distributions and the constraints on ecosystem functions it is important to determine how individual fishes use the space when foraging and what factors may influence their movement decisions and hence their mobility (Nash et al. 2012). In the scenarios examined linear distances travelled per unit time grow longer (up to 190 %) and the shape of the foraging range is more elongated the more fragmented the coral reef habitat becomes. These findings are in accordance with field studies of parrotfish foraging behaviour by (Nash et al. 2012), in which high levels of coral cover corresponded to more compact and circular short-term foraging ranges for two common parrotfish species, *Scarus niger* and *S. frenatus*.

The implications of this change in foraging behaviour can be 2-fold. Firstly, the longer the distances an individual fish has to swim the higher are its energetic costs. Moreover, a fish will also increase its swimming speed when moving over unfavourable habitat (Milinski 1993), which further adds to its energy expenditure. With more energy spent for swimming activities, the fish has less energy left to invest into somatic growth and/or reproduction. Differences in surplus energy may also have consequences for processes such as tissue repair and maintenance or defence against predators and the trade-offs between movement, growth, and reproduction are often at the expense of the reproductive output (Goldstein et al. 2017). Thus, habitat fragmentation is most likely to strongly influence the energy budgets of female fishes and their spawning frequency as shown by our model results and discussed above.

Secondly, with changing spatial dimension of their foraging range individual fishes will cover different areas during their daily routines. Hence, parrotfishes seem to be able to make small-scale changes in their movement behaviour in response to loss of coral reef habitat and their control of algal turf growth might be reduced and/or occur over different spatial ranges. This has also been observed in the field by (Gil et al. 2017), who showed in their investigation of herbivory in French Polynesia that the fragmentation of refuge habitat resulted in a reduction of the consumer's control of food resources.

With regard to the structuring force of herbivore organisms a change in individual space use patterns becomes even more relevant on the level of the population as the consequences of grazing depend in part on spatial abundance patterns (Mumby et al. 2006; Paddack et al. 2006). Model outputs reveal that the spatial distributions of fish populations (emergent as the cumulative behaviour of the individuals and illustrated above as the average number of visits per cell cumulated over one month) closely reflect the seascape arrangement. By concentrating their foraging activity within the coral reef patches model fishes graze in a spatially constrained manner. Model results are thus in accordance with recent findings over similar spatial scales by (Madin et al. 2019): Their daytime remote video surveys demonstrated that herbivorous fishes spend dramatically more time closer to the shelter of reef patches than in the adjacent sand flat habitat. In their study no herbivores were observed beyond rather small distances of 7.5 m and grazing intensity was hence highest close to the reef. By 15 m from the reef, no grazing by herbivores could be recorded. As indicated by our simulation results these field observations also suggest the existence of a behavioural constraint that spatially restricts herbivore foraging patterns.

Intriguingly, our simulation experiments also show that with an increasing habitat fragmentation coral reef patches are less equally frequented with an intensified foraging effort on specific patches and others rarely visited throughout the duration of one month. This concentration of foraging effort again has implications for the ecosystem function provided by the parrotfishes as the grazing pressure will be more intensive in some patches and substantially lower in others. Furthermore, the irregular usage of different reef patches may also have consequences concerning the social relationships among individual parrotfishes as it can affect encounter rates with conspecifics and/or competitors. Thereby the ‘effective’ distance between individuals may be much larger than their physical distance, a landcape property detailed in the much debated concept of ‘landscape connectivity’ (Taylor et al. 1993, 2006). However, as density-related processes are not yet explicitly considered in our model further simulation experiments and model adaptations will be necessary in the future to investigate this aspect more thoroughly. Nonetheless based on our findings and as stated by others (e.g. Nash et al. (2012) it appears advisable to incorporate behavioural flexibility when representing herbivory in time and space. The more accurate our estimates the more we will be able to better understand how coral cover might be affected on a local scale or why shifts in community compositions occur.

Landscape of fear. Risk effects are known to alter habitat and space usage of prey organisms (Manassa et al. 2013; Madin et al. 2019) and can be visualized in the model of the ‘landscape of fear’ established by (Laundré et al. 2001). In this model the relative levels of predation risk that a prey organism experiences in different areas of its environment are represented as peaks and valleys (Laundré et al. 2010). We incorporate this concept in our model using a novel approach that combines individual-based modelling with potential field methods: To this end, we translate the peaks and valleys of the (habitat-related) predation risk into a potential field map in which a growing risk of predation is represented as increasingly repellent areas. As ample evidence exists that predation risk correlates with habitat types and characteristics such as topographic complexity (Lima and Dill 1990; Jones and Syms 1998; Chapman and Kramer 2000; Overholtzer-McLeod 2006; Pratchett et al. 2008; Turgeon et al. 2010; McCormick and Lönnstedt 2013; Catano et al. 2016; Roff et al. 2019), we correlate the habitat structure with the perceived risk of predation. This information is then used by the individual fishes and included in the decision-making process for the direction of the next movement step. In our simulation experiments individual fishes react to an elevated predation risk by avoiding risky areas and/or by less tortuous movement paths to minimize the time spent on riskier habitats. Our results thus support empirical studies showing that spatial areas of high risks are less likely to be grazed and areas of lower risks are at elevated risk of disproportional high grazing intensity (Madin et al. 2010). As suggested by (Laundré et al. 2001) behavioural responses to different levels of predation risk may therefore have more far-reaching consequences for the systems under consideration than the actual killing of individuals by the predators. However, evidence also exists that while the loss or fragmentation of refuge habitat reduces consumer control of resources, greater resource densities may counteract this effect by altering landscapes of fear of consumer species (Gil et al. 2017). To be able to evaluate potentially counteracting effects due to resource availability by our model, it will be necessary to include further habitat types with diverging properties as food density and predation risk change in the same direction in the two implemented habitat types *CORALREEF* and *SANDYBOTTOM*.

3.6 Conclusions

Although what a fish perceives is undoubtedly complex, in this study we focus on (habitat-dependent) food availability and predation risk as the main drivers for individual movement decisions to better understand the driving influence of the underlying seascape. Both habitat components are known to play a fundamental and important role in shaping the spatial distribution of fish populations. Model results indicate that individual space use patterns and the resulting spatial distributions of the population are more irregularly distributed among coral reef patches the more the coral reef habitat becomes fragmented and reduced. This heterogeneity can have strong implications for the delivered ecosystem functioning, e.g. by concentrating or diluting the grazing effort. Our results also highlight the importance of incorporating individual foraging-path patterns and the spatial exploitation of microhabitats into marine spatial planning: Since the ability of marine reserves to provide protection largely depends on the consistent use of the protected area by the individual fishes (Kramer & Chapman 1999) conservation strategists and managers need to identify core areas and essential habitats. They may also benefit from information about the consequences of changing landscape structures on movement behaviour to maintain effective reserves.

By providing population dynamics over long time periods (years) and at a high spatial ($1m^2$) and temporal resolution (up to 1 s) combined with the potential to simulate future scenarios we believe our model can provide valuable insights into the spatio-temporal variability of local herbivore populations. Our model further incorporates individual differences in movement behaviour and may thereby assist in understanding the interactions of individual properties and the properties of the environment. Moreover, by combining individual-based modelling with potential field methods our model integrates a more realistic and dynamic decision-making process, in which each fish weighs different rewards and risks of the environment. We thus hope that our findings can add to the disentanglement of the complex mechanisms that characterize the movement decision making processes in herbivorous fishes and that the gained information may eventually help to efficiently manage reef fish populations.

3.A Appendix

3.A1 Model description

(DW = dry weight, WW = wet weight, BL = body length, SL = standard length, TL = total length)

Our model is designed to spatially-explicitly simulate diel movement behaviour of reef fishes in a heterogenous seascape. It is composed of two main entities: the agent *fish* (A1.1) and its surrounding *environment* (A1.2), in which a fish agent spends its entire life loop. At present, the model implements two contrasting movement strategies (*PERCEPTION* and *RANDOM*), which the user can select prior to each simulation run to analyse mechanisms of spatial behaviour and its potential consequences in different habitat settings. The *RANDOM* mode simulates movement as a purely stochastic process and a model fish will travel without drifting in any particular direction or knowledge of its surroundings and has therefore no capabilities to respond to any environmental stimuli. As random walk 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) this move mode may serve to highlight differences between different modelling strategies of fish movement behaviours. In the present study, however, we focus on the move mode *PERCEPTION* and only include the description of the mode *RANDOM* for the sake of completeness of the model description. The user can further adapt the model to a range of reef fish species of different functional groups by specifying key life history features such as activity patterns or feeding guilds via the species definition parameters (Table A1.3). Combined with the possibility to use custom habitat maps we hope our generic application will be useful to analyse and evaluate various local scenarios and habitat configurations.

The simulations tested and analysed in the present study are exemplified for parrotfishes as diurnal herbivores (used as default values in our model), 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 are derived from own observations (unpublished data) as well as comprehensive literature data available from empirical studies mainly of the Daisy parrotfish (*Chlorurus sordidus*), a ubiquitous and well-studied member of this functional group.

During a simulation run the model keeps track of the location and fate of each individual in the population (from recently settled post-larval juveniles to adult terminal phases) and notes its velocity and energetic state. On the population level it logs the abundances and biomass of juveniles, initial phases, and terminal phases, as well as age- and size-frequency distributions at regular pre-defined intervals (Table A1.3). On the level of the environment the model records the number of fish visits that occur in each habitat cell over a pre-defined time period to allow for an analysis of habitat use patterns.

3.A1.1 *Fish* entity

3.A1.1.1 State variables and behavioural repertoire

To allow for an analysis of individual development as well as population characteristics over time, each model fish is characterised by 17 state variables (Table A1.1). The behavioural repertoire of a model fish comprises four main lifecycle-related activities: Moving (energetic costs of activity), feeding (digestion and energetic gain based on food intake), growing (updating of energy budget based on energy gained and spent, somatic growth), and reproducing (energetic costs of reproduction and creation of offspring). All activities and related processes of a fish's life loop are executed in different modules (hereafter: systems, Fig. A1.1) described below and state variables are updated every time step unless stated otherwise.

Table A1.1 State variables and corresponding values or units for the entity *fish*

State variable	Unit or value	Description
position	(x, y)	Spatial coordinates, which are used in combination with *velocity* to depict individual movement trajectories
velocity	[m s $^{-1}$]	Composed of two vectors, *velocity.x* and *velocity.y*
age	[years]	To follow individual development as well as age distributions of the fish population
length	[SL in cm]	Calculated based on *biomass*; to allow for length-based change of sex and/or life phase and analysis of size-frequency distributions on the population level
biomass	[g WW]	Calculated based on energy values of body compartments to determine energy demand and to analyse ontogenetic development (individual level) as well as population dynamics
gut	[kJ]	Body compartments to model the fish's bioenergetics
shortterm	[kJ]	
protein	[kJ]	
fat	[kJ]	
repro storage	[kJ]	
excess	[kJ]	
behaviourMode	*FORAGING*, *RESTING* or *MIGRATING*	Determines which actions a fish executes; depends on diel cycle
sexChangeMode	*PROTOGYNOUS*	To account for reproductive strategies of parrotfishes
sex	*FEMALE* or *MALE*	Based on a fish´s *length* and used in combination with *phase* to regulate reproduction-related processes
phase	*juvenile, initialPhase* or *terminalPhase*	Determined by *sex* and *sexChangeMode*; used to account for a fish's ontogenetic development to regulate reproduction; for simplicity juveniles are considered as non-reproductive females
feedingGuild	*HERBIVORE*	Determines food source and food-related assimilation efficiencies
isHungry	*yes* or *no*	Hunger state (Boolean value) which depends on a fish's current energy level and gut fullness to regulate feeding activity

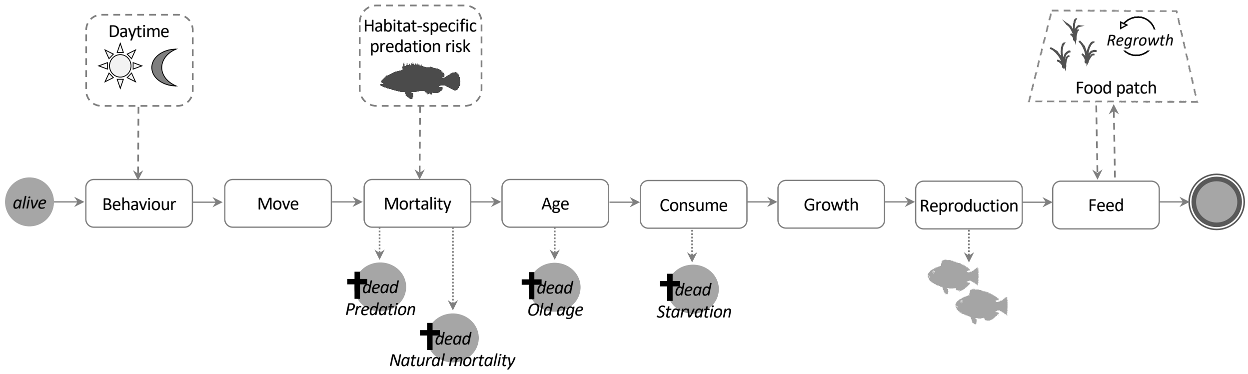


Fig. A1.1 Simplified overview of model systems and execution flow of a fish´s life loop. Influencing or interacting environmental components are indicated by dashed lines.

3.A1.1.2 *Behaviour* system

Determined by the abiotic factor daytime *(TimeOfDay*, A1.2.4) the diurnal model fish is either foraging (*DAY*), resting (*NIGHT*) or migrating from resting to feeding areas (*SUNRISE*) or vice versa (*SUNSET*). Additionally, the fish´s hunger state (*isHungry*) is set depending on its current energy level and biomass (Fig. A1.2).

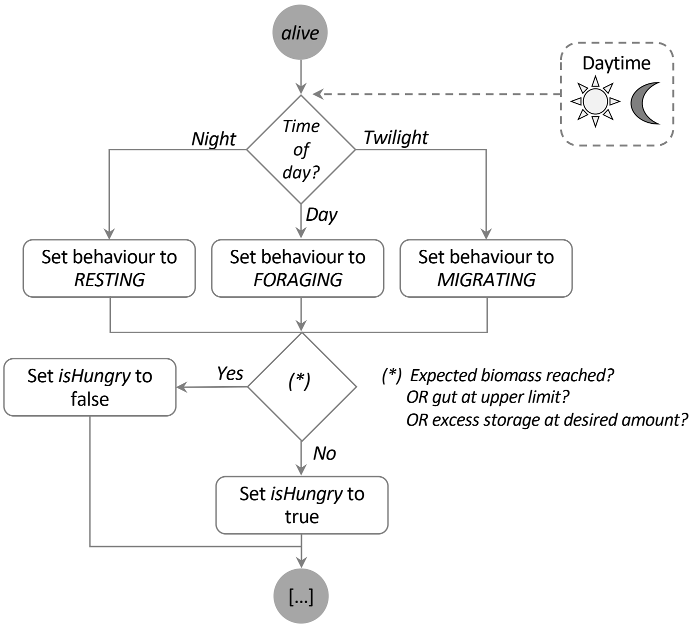


Fig. A1.2 Model flow of the *Behaviour* system and influencing environmental factors (dashed line).

3.A1.1.3 *Move* system

The three different behaviour modes (*FORAGING*, *RESTING*, and *MIGRATING*) are each associated with a different speed factor: Based on experimental studies with parrotfishes (Korsmeyer et al. 2002; Rice and Westneat 2005) the average foraging speed (*SPEED_FACTOR_FORAGING*) is set to 1.5 [BL s^{-1}] while the migration speed (*SPEED_FACTOR_MIGRATING*) is defined as 2.0 [BL s^{-1}] and speed at resting (*SPEED_FACTOR_RESTING*) as 0 [BL s^{-1}]. Parrotfishes sleep in caves or under boulders (Ogden and Buckman 1973) and are thus stationary when resting. The resulting speed value [cm s^{-1}], i.e. step length for the current time step, determines the energy costs the fish spent moving (net costs of swimming [kJ], A1.1.6). To mimic natural variation among individuals a random component (*SPEED_DEVIATION* of ± 10 % following (Korsmeyer et al. 2002)) is added to the selected speed value using a uniform distribution. We implement a uniform instead of a normal distribution to delimit both the extent of the speed variation and computational costs. The actual movement step is modelled discretely using vector-based walking algorithms based on the step length defined by the current speed value and the turning angle (direction) determined by the pre-selected move mode (*moveMode*, either *RANDOM* or *PERCEPTION,* Fig. A1.3).

For both movement strategies the direction of the next step is calculated within the fish’s maximum turning range (*maxTurnSpeed* [° s^{-1}]), which delimits the maximum angle a fish can turn at each time step at high temporal resolutions (1 s). Thereby we ensure the emergence of realistic changes of direction at a lower (minutely) time resolution (Jopp and Reuter 2005). The maximum turn range is parametrized based on field studies by (Davis 2016), in which movements of individual *C. sordidus* were tracked over 20 min time periods with a time resolution of 15 s. To reproduce the observed movement patterns at a 15 s time resolution we set the *maxTurnSpeed* to 6 [° s^{-1}].

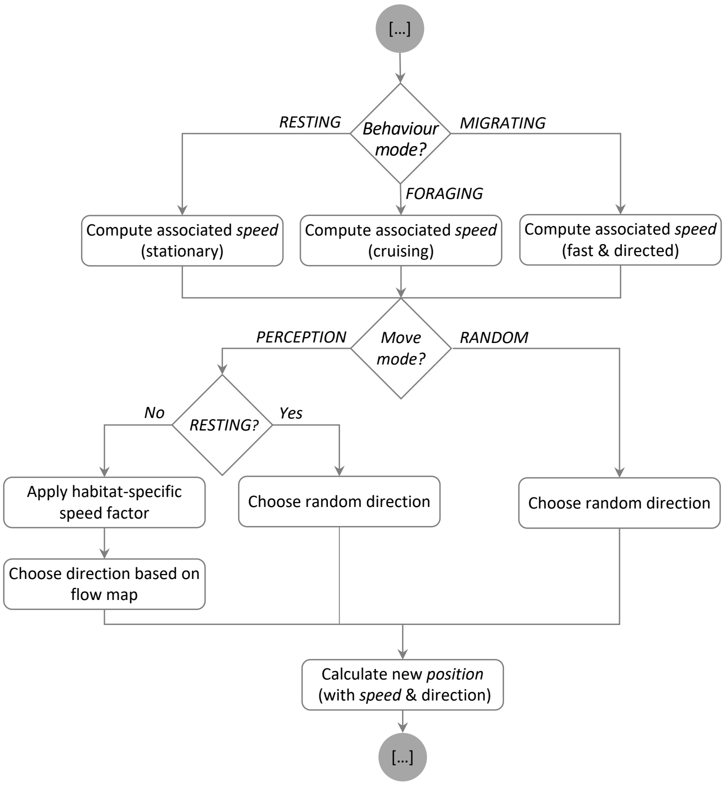


Fig. A1.3 Model flow of the *Move* system.

When applying the move mode *RANDOM*, the next direction is chosen randomly within this range based on a simple random walk algorithm and using a uniform distribution. Since individuals cannot interact with their environment, the three behaviour modes *FORAGING*, *MIGRATING,* and *RESTING* only differ in their corresponding speed factors determining the step length of each movement step. The resulting movement trajectories of fish traveling at random therefore follow a simple isotropic (unbiased) random walk model (Codling et al. 2008) meaning that a fish is equally likely to move in each possible direction and directions are uncorrelated (i.e. the direction taken at a given time is independent of the direction at all preceding times).

To compute the movement direction of a fish that can perceive and navigate through its surroundings (*moveMode PERCEPTION)* we use vector field path planning based on artificial potential fields (Khatib 1986; Arkin et al. 1987; Arkin 1989; Connell 1990; Dudek and Jenkin 2010). The attractive and repulsive forces in our model are 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 is composed of three basic steps following (Hagelbäck 2012): (1) Depending on the fish's behavioural mode different potential subfields of relevant landscape features are generated and normalized. (2) These subfields are individually weighted and then added to integrate the motivational basis of a fish to move. (3) Based on the gradients of the summed potentials, a vector-based flow field is 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 is neutral (zero vector), i.e. the fish is located at the currently most favourable position, the direction for the next movement step is chosen randomly using a uniform distribution on all directions (360°). Thereby a fish is restrained from getting stuck in local minima, a known drawback of artificial potential field methods (Raja and Pugazhenthi 2012).

To calculate the most favourable direction of movement when *FORAGING*, first, two potential subfields are generated based on food availability (*foodPotentialMap*, see A.2.2 for details on food availability) and predation risk (*riskPotentialMap*, see A.2.3 for details on predation risk). The (dynamic) *foodGrid* subfield is generated by assigning each grid cell a normalized positive (attractive) value between 0 and 1 mirroring the actual food density value of the food grid, while the (static) *riskGrid* subfield consists of normalized negative (repulsive) values between -1 and 0 displaying the habitat-dependent level of predation risk. Due to the static nature of the latter calculating the *riskPotentialMap* is a relatively simple process, which is executed once per simulation run when the first individual of a fish species to which the *riskPotentialMap* is assigned, enters the simulation. In contrast, the *foodPotentialMap* is updated globally at every time step based on changing food densities due to foraging activities of the fish and regrowth of food resources. To further incorporate the perception range of an individual fish as an informational window to its environment ('look-a-head'), we use a blurring filter (Gaussian blur kernel) on the *riskPotentialMap*, in which each grid cell in the resulting risk map has a value equal to the average value of its neighbouring cells weighted by their distance in the input map. The number of neighbouring cells considered is defined by the *perceptionRadiusPredation*, which we set to 10 m. For computational reasons the inclusion of the dynamic habitat feature food availability in the decision-making process is limited to the next eight directly adjacent cells representing a perception range (*perceptionRadiusFood*) with a reactive distance of 1 m (as part of step 3).

In the second step, the two subfields (*foodPotentialMap* and *riskPotentialMap*) are weighted by their field-specific weighing factor (*PathfindingWeights.FOOD* and *PathfindingWeights.RISK*) and added to form the aggregated potential field (1). We do not know how coral reef fishes assess the trade-off between foraging and avoiding predation, but it has been suggested that food availability may be more important than the risk of predation in structuring diel space use patterns of larger juveniles and adult parrotfishes like *C. sordidus* and other herbivorous species (Welsh et al. 2013; Gil et al. 2017). We therefore make the simplifying assumption that in the movement decision-making process food availability is weighed twice as much as the risk of predation (*weightFood* = 2, *weightRisk* = 1).

(1) $p_{total}(x, y) = \sum_{i=0}^{n} w_i \, p_i(x, y)$

where n is the number of subfields affecting position (x, y) and w_i is the weight for subfield i (Hagelbäck 2012)

Thirdly and lastly, the vector-based flow field designating the direction of movement for each grid cell as a two-dimensional normalized vector is generated based on the gradients of the summed potentials. As a fish is set to evaluate the aggregated potential in all positions within a 1 m^2 range of its own position, unit vectors for all directions (east (E), south (S), west (W), north (N) including southeast (SE), southwest (SW), northwest (NW), and northeast (NE)) pointing to the respective neighbouring cell (2), are multiplied with the potential of the indicated cell. All eight vectors are then added resulting in the final unit direction vector for the next movement step ($\overrightarrow{\mathrm{sum}}$, (3)).

(2)
$$\vec{E} = (1, 0),\ \vec{S} = (0, 1),\ \vec{W} = (-1, 0),\ \vec{N} = (0, -1),$$
$$\overrightarrow{SE} = \left(1/\sqrt{2}, 1/\sqrt{2}\right), \overrightarrow{SW} = \left(-1/\sqrt{2}, 1/\sqrt{2}\right), \overrightarrow{NW} = \left(-1/\sqrt{2}, -1/\sqrt{2}\right), \overrightarrow{NE} = \left(1/\sqrt{2}, -1/\sqrt{2}\right)$$

(3)
$$\overrightarrow{\mathrm{sum}} = \Big(\vec{E} * p_{total}(x+1, y) + \vec{S} * p_{total}(x, y+1) + \vec{W} * p_{total}(x-1, y) + \vec{N} * p_{total}(x, y-1) + \overrightarrow{SE} * p_{total}(x+1, y+1) + \overrightarrow{SW} * p_{total}(x-1, y+1) + \overrightarrow{NW} * p_{total}(x-1, y-1) + \overrightarrow{SE} * p_{total}(x+1, y-1)\Big)$$

The computation of the most favourable direction when the fish is *MIGRATING* (during twilight periods) or *RESTING* (at night) is based on the same calculation described above with the following differences: When *MIGRATING,* instead of considering food density levels, the second subfield is generated based on the habitat type of the benthic seascape (*toForagePotentialMap, toRestPotentialMap*). The potential of the target habitat(s) defined by the parameters *foragingHabitat* and *restingHabitat*, respectively, is set to 1 as the most attractive locations. Has the fish reached its target habitat, it switches to the next scheduled behaviour mode (*FORAGING* or *RESTING*), again depending on its activity pattern and time of day. If a fish is set to *RESTING*, it solely considers predation risk as a relevant landscape feature.

Based on the direction given as a unit vector ($\overrightarrow{\mathrm{sum}}$) calculated by either one of the two movement algorithms (*RANDOM* or *PERCEPTION*) and the behaviour-mode-dependent step length (i.e. the speed value as the vector length) the new velocity of a fish is calculated by multiplying the two (4).

$$(4) \qquad \overrightarrow{velocity} = \overrightarrow{\mathrm{sum}} * speed$$

Fishes are further known to be able to sense changes in food availability or predation risk in different habitats and adapt their velocity accordingly (Milinski 1993). In unfavourable habitat patches, for instance, a fish will move faster, i.e. steps will be longer, resulting in higher swimming costs. To reflect this linkage between habitat and individual energy budgets in our model, a fish in the move mode *PERCEPTION* will increase its speed (i.e. vector length) on low-complexity and low-food habitats like sandy bottoms by 50 % (*SANDYBOTTOM_SPEED_FACTOR = 1.5*) following (Tootell and Steele 2016). Fish in the move mode *RANDOM*, on the other hand, are not able to perceive their surroundings and therefore cannot adapt their speed in response to landscape features.

3.A1.1.4 *Mortality* system

To account for loss of fish in the population through death we distinguish four different types of natural mortality in our model: mortality due to (i) senescence (M_{age}), (ii) starvation (M_{starve}), (iii) predation (M_{pred}), and (iv) any other natural mortality-inducing factors such as sickness, diseases or pollution (M_{nat}). Mortality due to fishing is not (yet) implemented in our model. Both, M_{age} and M_{starve} are emergent properties of the *Age* system (A1.1.5) and the *Consume* system (A1.1.6), respectively, while M_{pred} and M_{nat} are represented as annual probability rates. Although mortality rates in coral reef fish are known to decline exponentially with increasing body size, rates tend to be rather low and change little with increased size once a certain size threshold of about 4.3 cm TL is reached (Goatley and Bellwood 2016). As our model solely considers post-settlement individuals with a body length of at least 8 cm SL we assume all three types of morality to be independent of body size. We further calibrate the model so that all mortalities considered approximate a total annual mortality rate (M_{total}, (5)) of 0.3 to 0.4 year^{-1} (Bozec et al. 2016).

$$(5) \qquad M_{total} = M_{age} + M_{starve} + M_{pred} + M_{nat}$$

The *mortality* system comprising M_{pred} and M_{nat} is applied every time step to each individual fish (Fig. A1.4) once it has reached its new position on the simulation grid. A fish survives predation if – based on the risk of predation (A1.2.3) – the next generated, uniformly distributed Boolean value evaluates to FALSE (i.e., the fish is not preyed upon). Similarly, the fish does not experience mortality from any other natural cause (M_{nat}), if the Boolean value based on the annual natural mortality rate (0.11 year^{-1}) evaluates to FALSE as well.

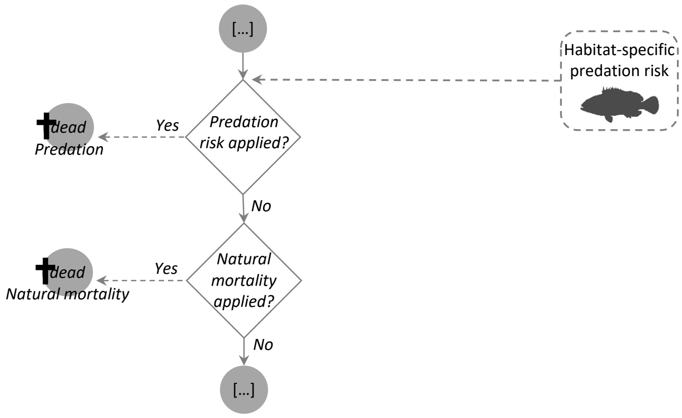


Fig. A1.4 Model flow of the *Mortality* system and influencing environmental factors (dashed line).

3.A1.1.5 *Age* system

In case of survival the fish´s age is updated and evaluated whether its new age exceeds the maximum age (*maxAgeAverage* of 9.0 years with a *MAX_AGE_DEVIATION* of ± 10.0 % following (McIlwain and Taylor 2009)). If not, the model fish continues its life loop and its bioenergetic systems are updated (consisting of the systems *Consume*, *Growth*, *Reproduction*, and *Feed*, Fig. A1.5).

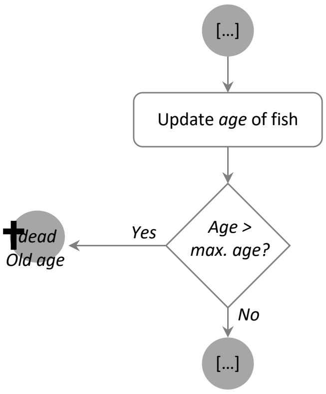


Fig. A1.5 Model flow of the *Age* system.

3.A1.1.6 *Consume* system

As mentioned above a fish´s bioenergetics are modelled by implementing different body compartments with specific functions (following (Hölker and Breckling 2005)): the gut to mimic digestion, an excess storage to regulate the fish's hunger state, a short-term storage representing carbohydrates, body fat as a medium-term energy storage, and body protein as a long-term storage. Female individuals also possess a reproduction compartment to account for the dynamics of the reproduction process (Hölker and Breckling 2005) and the high energy demand for ovarian growth (A1.1.8). Energy costs associated with the maturation of testes can often be considered as negligible compared with the costs of ovarian maturation (Wootton 1979; Miller and Kendall 2009; Berg and Fleming 2017) and even though this may vary from species to species, we assume male individuals to have neglectable reproduction costs.

Body compartments are filled or depleted in the *Consume* system (Fig. A1.6), except for the gut, which is filled in the *Feed* system (A1.1.9) when the fish is hungry and foraging. Compartments are limited by a maximum and/or minimum capacity (Table A1.2), which, with the exception of the protein compartment, depend on the fish's current biomass (*biomass* [g WW]) or its size-dependent resting metabolic rate (i.e. metabolic rate of a resting but non-fasting individual at zero speed). To ensure a realistic growth pattern, the protein compartment is limited not based on the state variable *biomass* but on the theoretical biomass (*expectedBiomass* [g WW]) a fish would have reached at the current age under ideal conditions based on the species-specific Von Bertalanffy Growth Function (6) and the allometric length-weight conversion (to convert length to biomass) (7).

(6) Von Bertalanffy Growth Function for *C. sordidus* to calculate the expected length (L_t) of a fish at a given age (t): $L_t[SL\ in\ cm] = 39.1[SL\ in\ cm] * (1 - e^{(-0.15*(t+1.25))})$ (El-Sayed Ali et al. 2011)

(7) Length-weight relationship for *C. sordidus* to calculate the expected biomass of a fish at a given length (L): $Biomass\ [g\ WW] = 0.0309 * (L[SL\ in\ cm])^{2.935}$ (El-Sayed Ali et al. 2011)

The fish is 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 120 % of the expected biomass.

Whether the compartments are filled or depleted was determined by the fish´s energy budget (energetic costs and gains) for the current time step. The fish's overall energy costs (*totalEnergyCost* [kJ]) are composed of the resting metabolism (*costRestingMetabolism* [kJ]), which is calculated based on the size-dependent resting metabolic rate (following Winberg (1960)), (8) plus the net swimming costs (*netCostSwimming* [kJ]), i.e. the energy amount the fish uses for its activities defined by its behaviour mode (see above) calculated following (Korsmeyer et al. 2002) (9). We use an oxicaloric value of 14.2 J mg O_2^{-1} (Ohlberger et al. 2006) to convert oxygen consumption rates into energy units as the model's `currency´.

(8) $costRestingMetabolism\ [ml\ O_2\ h^{-1}] = 0.307 * (biomass\ [g\ WW])^{0.81}$

Conversion to [kJ h^{-1}]: $costRestingMetabolism\ [ml\ O_2\ h^{-1}] * 1.429\ [mg\ ml\ O_2]\ * 0.0142\ [kJ\ mg\ {O_2}^{-1}]$

(9) $netCostSwimming\ [mg\ O_2\ h^{-1}] = (-1.193) + \log(speed[cm\ s^{-1}])$

Conversion to [kJ h^{-1}]: $netCostSwimming\ [mg\ O_2\ h^{-1}] * 0.0142\ [kJ\ mg\ {O_2}^{-1}]$

(10) $totalEnergyCost\ [kJ] = costRestingMetabolism\ [kJ] + netCostSwimming\ [kJ]$

Subsequently, the consumed energy (10) is subtracted from the energy surplus a fish has available due to its feeding activity (A1.1.9) from previous time steps. The surplus consists of the net energy available from the gut after digestion and all energy stored in the fish´s excess storage. In case any energy remains after subtraction of the costs, it is subsequently added to the short-term storage (until its upper limit is reached), and then in different proportions to the fat (*GROWTH_FRACTION_FAT* of 1.0 %) and protein storage (*GROWTH_FRACTION_PROTEIN* of 99.0 %) following (Karakoltsidis et al. 1995). If the fish is a reproductive female (*phase*: *initalPhase*) energy is also proportionally allocated to the reproduction compartment (*GROWTH_FRACTION_FAT* of 0.1 %, *GROWTH_FRACTION_PROTEIN* of 89.9 %, *GROWTH_FRACTION_REPRO* of 10.0 % (following (Diana 1983; Wootton 1985)) with less energy available for somatic growth and less energy stored as body fat (Calow 1985; De Troch et al. 2013). If all of compartments are filled to their upper limits, any remaining energy is added to the excess storage. If the latter reaches the desired amount (*desiredExcessRmr,* Table **A1.2**), the fish is set to be satisfied *(isHungry*: no) and it stops feeding (A1.1.9) until the energy level in the excess storage drops below the desired value again.

If, however, the available energy is not sufficient to cover all energetic demands, the lacking amount is taken from the short-term storage. In case the amount of energy consumed can still not be covered, e.g.

due to food scarcity, the energy deficit is 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 (Table A1.2). If both compartments are depleted (i.e. reaching their lower limits), the fish would die of starvation.

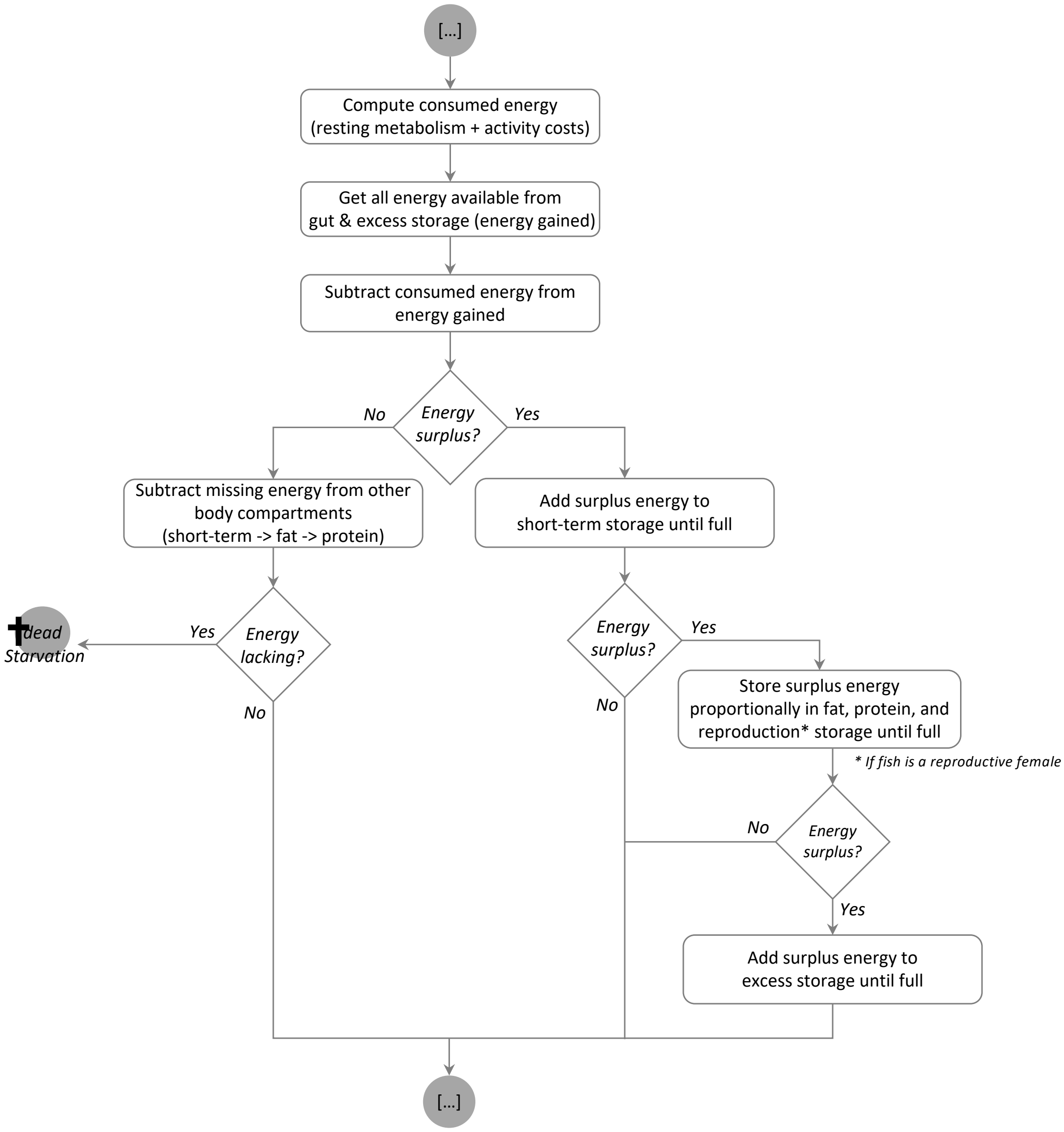


Fig. A1.6 Model flow of the *Consume* system.

Table A1.2 Applied limits of a model fish's body compartments *(GUT, SHORTTERM, EXCESS, FAT, PROTEIN, REPRODUCTION)* including conversion factors (biomass [g WW] to energy [kJ]).

Limit	***CONTSTANT*** **or** ***variable name***	Value [unit]	Description
GUT			
Upper limit	*UPPER_LIMIT_GUT_MG_DW_FOOD_PER_G_WW_BIOMASS*	17.0 [mg (DW food)* g (WW fish)$^{-1}$]	(Polunin et al. 1995)
SHORT-TERM			
Upper limit	*shorttermUpperLimitRmr*	6.0 [h]	This storage can hold the energy equivalent of up to 6 h of a fish´s resting metabolic rate
EXCESS			
Upper limit	*desiredExcessRmr*	3.0 [h]	This storage can hold the energy equivalent of up to 3 h of a fish´s resting metabolic rate. If a fish has reached this desired value, its hunger state is set to be not hungry
FAT			
Upper limit	*UPPER_LIMIT_BIOMASS_FRACTION*	1.5 [% of *biomass*]	Following the body composition of a parrotfish (Karakoltsidis et al. 1995)
Lower limit	*LOWER_LIMIT_BIOMASS_FRACTION*	0.5 [% of *biomass*]	Following the body composition of a parrotfish (Karakoltsidis et al. 1995)
Growth fraction	*GROWTH_FRACTION_FAT*	1.0 (0.1)* [% of *biomass*]	Fraction of surplus energy stored fat compartment (following (Karakoltsidis et al. 1995)); *reproductive females
Loss factor	*LOSS_FACTOR*	87.0 [%]	Loss factor for exchanging energy with this storage type, i.e. synthesising or re-metabolizing (Brett and Groves 1979)
Conversion factor	*KJ_PER_GRAM_FAT_VALUE*	39.5 [kJ g^{-1}]	Metabolizable energy from body fat (Brett and Groves 1979)
PROTEIN			
Upper limit	*UPPER_LIMIT_EXP_BIOMASS_FRACTION*	120.0 [% of *expectedBiomass*]	1.2 * expected biomass[1]
Lower limit	*LOWER_LIMIT_EXP_BIOMASS_FRACTION*	60.0 [% of *expectedBiomass*]	0.6 * expected biomass[1], i.e. starvation following (Letcher et al. 2011)
Growth fraction	*GROWTH_FRACTION_PROTEIN*	99.0 (89.9)* [% of *biomass*]	Fraction of surplus energy stored in the protein compartment (Karakoltsidis et al. 1995); *reproductive females
Loss factor	*LOSS_FACTOR*	90.0 [%]	Loss factor for exchanging energy with this storage, i.e. synthesising or re-metabolizing (Brett and Groves 1979)
Conversion factor	*KJ_PER_GRAM_PROTEIN_VALUE*	4.0 [kJ g^{-1}]	Metabolizable energy from body protein (including moisture content) (following (Brett and Groves 1979)
REPRODUCTION			
Upper limit	*UPPER_LIMIT_BIOMASS_FRACTION*	25.0 [% of *biomass*]	Following (Wootton 1985)
Lower limit	*LOWER_LIMIT_BIOMASS_FRACTION*	10.0 [% of *biomass*]	Following(Wootton 1985)
Growth fraction	*GROWTH_FRACTION_REPRO_REPRODUCTIVE*	10.0 [%]	Fraction of surplus energy stored in the reproduction storage (applies to reproductive fishes only) (Diana 1983; 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: L_t [SL in cm] = 39.1 [SL in cm]$*(1-e^{(-0.15*(t+1.25))})$ and length-weight relationship: biomass [g WW] = 0.0309*(length [SL in cm])$^{2.935}$ (El-Sayed Ali et al. 2011).

3.A1.1.7 *Growth* system

The energy sum of the short-term, fat, protein, and excess storage (converted into mass) represents the fish's *biomass* (11).

$$(11)\ Biomass\ [g\ WW] = \sum body\ compartment\ [kJ] * conversion\ factor\ \ [g\ kJ^{-1}]$$

The energy amounts in the short-term and excess storage are converted into mass using the same conversion factor as for protein (Table A1.2) while the gut and reproduction storage are not considered for somatic growth. The state variable *biomass* as well as the *biomass*-dependent *restingMetabolicRate* are updated in each time step and a fish would grow in length when the updated biomass value is greatest out of all previously calculated biomass values for this fish (Fig. A1.7). If the updated biomass also exceeded the previously calculated expected biomass the state variable *expectedBiomass* is updated as well.

A fish would not grow in length, if no energy is added to the fish's fat and protein compartments and the energy level in short-term storage remains below its upper limit. In case the energy amount in the short-term storage has dropped below its lower limit and the fish has 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 remains unchanged (growth in body length is generally considered to be unidirectional for vertebrates).

Has the fish indeed grown in body length, which is updated on a weekly basis, it might enter the next life phase (*phase*: *JUVENILE*, *INTIAL* or *TERMINAL*) and/or change its sex (*sex: FEMALE* or *MALE*) depending on the corresponding length-based thresholds (Table A1.4). The exact mechanisms that triggers sex changes in parrotfishes are still largely unknown, but life phase transitions based on body size has been suggested as a plausible process (Pavlowich et al. 2018). We therefore model transitions using a logistic function (following (Pavlowich et al. 2018)) where the probability of transitioning into the next life phase (p_{trans}) increases with body size (12) and which is applied bi-monthly to ensure the emergence of realistic patterns of phase changes on the population level.

$$(12)\quad \rho_{trans} = \frac{1}{1+\ e^{-(length\,[cm]-\ threshold\,[cm])}}$$

As most parrotfishes are protogynous hermaphrodites a model fish is set to mature from juvenile into the female initial phase when it becomes larger than 10.0 cm (*initialPhaseStartLength*) and later to the male terminal phase when exceeding a length of 15.5 cm (*terminalPhaseStartLength*) following (McIlwain and Taylor 2009). For computational reasons and due to their relatively low abundance, primary males (individuals that are already male in their initial phase) are not considered in the model.

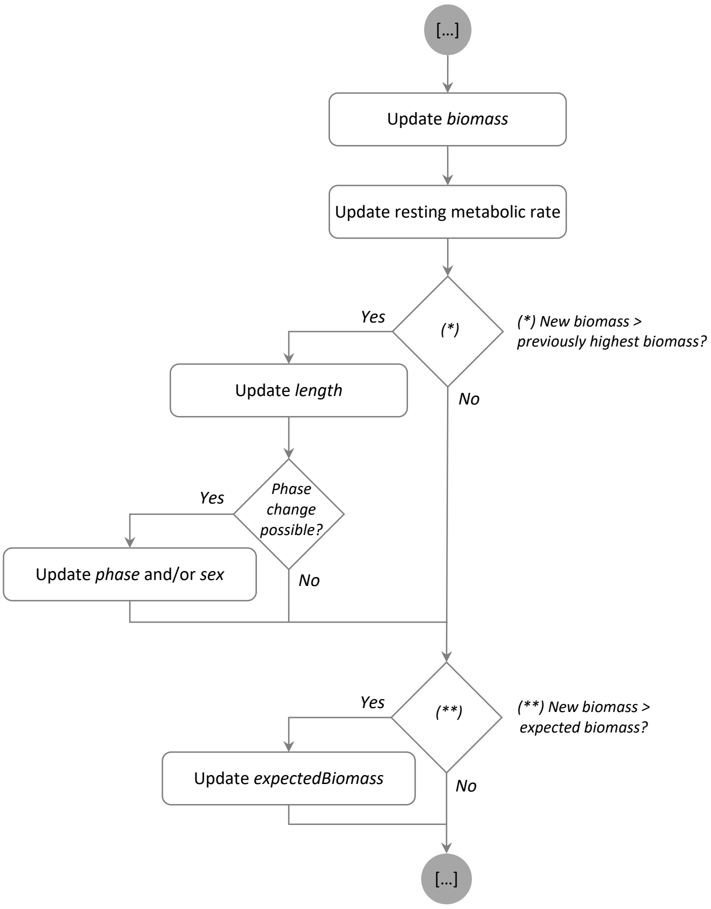


Fig. A1.7 Model flow of the *Growth* system.

3.A1.1.8 *Reproduction* system

As soon as the fish becomes a *FEMALE* in its initial phase, it starts filling its reproduction compartment according to the rules implemented in the *Consume* system (A1.1.6 above). Once the reproduction compartment reaches 25.0 ± 2.5 % (using a uniform distribution) of the fish's current total biomass, the fish has gathered enough energy supplies to reproduce (Wootton 1979). When reproducing, the reproduction compartment is set back to an energy level of 10.0 ± 1.0 % (again using a uniform distribution) of the fish's biomass (Wootton 1979) to compensate for the energetic costs of spawning (Fig. A1.8). In contrast to female model fishes, male individuals have no functional role in the modelled reproduction process but still contribute to processes related to population densities and food depletion.

Following (Lewis 1997; Miller et al. 2001; Miller and Kendall 2009) and to ensure a stable (self-recruiting) model fish population over time we assume that two individuals per female and spawning event (*numOffspring*) will survive the larval stage (which is not part of our model) and settle within the population after 120 days (*postSettlementAge* following (McIlwain and Taylor 2009)). To allow for the investigation of the dynamics of externally influenced populations, however, our model also permits the simulation of an 'open' population (*populationClosed* = FALSE) and by specifying a constant monthly recruitment rate (*monthlyNumRecruitsOpen*). In both cases each fish recruit is initialized with a biomass (*initialBiomass*), which is calculated from the Von Bertalanffy Growth Function (6) at the post-settlement age and allocated to the different body compartments following the approximate body composition of a parrotfish (Karakoltsidis et al. 1995). When these new individuals enter the simulated population, they are placed randomly on the simulation grid.

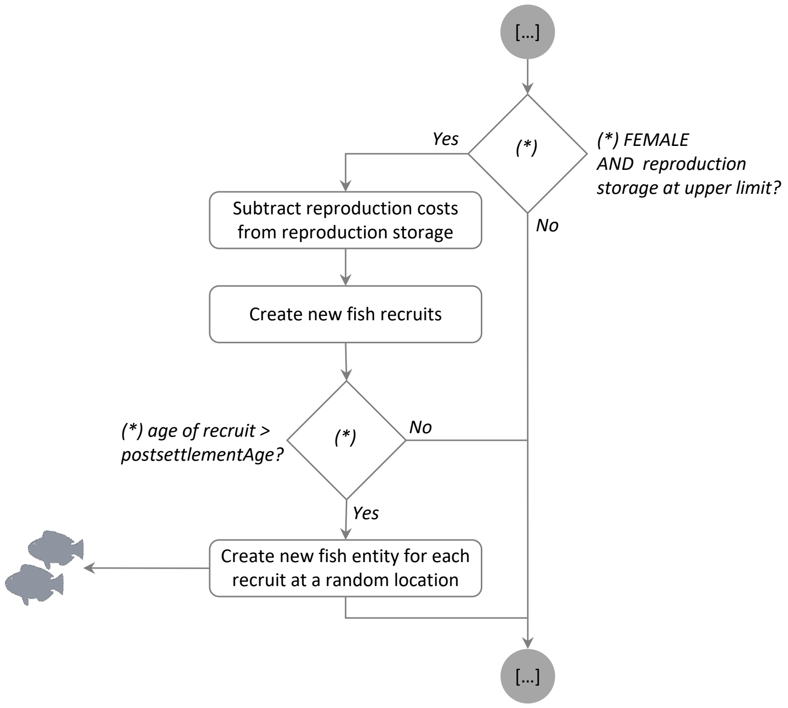


Fig. A1.8 Model flow of the *Reproduction* system.

3.A1.1.9 *Feed* system

A model fish in the behaviour mode *FORAGING* is scheduled to execute `feeding´ as the last activity in a given time step while a fish in a different behaviour mode (*MIGRATING* or *RESTING*) would skip this activity (Fig. A1.9). A *FORAGING* fish consumes food (*foodToIngest* [g DW food]) based on a biomass-dependent mean ingestion rate (13) or in case not enough food is found on the current food cell all the food that is available (*availableFood*, [g DW food], A1.2.2). However, as fish are known to be able to increase their average feeding rate with increased hunger levels (Godin 1981), a model fish can adapt its feeding rate up to a maximum of 0.4*food [g DW]*(fish biomass [g WW])$^{-1}$ day^{-1} (*maxIngestionRate*) if the energetic difference of its current to its expected biomass (*desiredFoodAmount* [g DW food]) exceeds the energy amount that would be gained based on the mean ingestion rate (*ingestionAmount*). If, on the other hand, a fish has reached an energetic level, that exceeds its expected biomass, it will reduce its feeding rate down to a minimum of 0.1*food [g DW]*(fish biomass [g WW])$^{-1}$ day^{-1} (*minIngestionRate*).

$$(13) \quad meanIngestionRate = \frac{0.236 * food\ [g\ DW]}{fish\ biomass\ [g\ WW] * day} \quad \text{(Polunin et al. 1995)}$$

The ingested food is then converted to an energy value (*energyToIngest* [kJ]) (14) based on the energy content of sparse epilithic turf algae (*energyContentFood*, 4.0 kJ g DW food^{-1} following (Bruggemann 1995)), the main food source of *C. sordidus* (Polunin et al. 1995).

$$(14) \quad energyToIngest\ [kJ] = \frac{foodToIngest\ [g\ DW]}{energyContentFood\ [kJ\ (g\ DW\ food)^{-1}]}$$

A fish feeds until it is satisfied (*isHungry*: no), i.e. it has either reached the maximum capacity of its gut or acquired enough energy to fill all its body compartments to their respective limits (Dill 1983) and has additionally stored the energy equivalent needed for 3 hours of *RESTING* in its excess storage (A1.1.6 above). Thereby it is ensured that a well-fed fish has an energy surplus for a certain amount of time to execute non-feeding activities (*RESTING* and/or *MIGRATING*) without necessarily loosing biomass.

To account for digestive processes the energy ingested in the current time step is transferred as one portion to the gut storage, which is modelled as a queue to mimic food transit. Any added energy portion is not available for the fish's metabolism until a transit duration (*HERBIVORE_GUT_TRANSIT_DURATION*) of 54 min (Polunin et al. 1995). We further assume an assimilation efficiency (*HERBIVORE_ASSIMILATION_EFFICIENCY*) of 26 % due to energy losses caused by egestion, excretion, and specific dynamic actions (following (Bruggemann et al. 1994)). The resulting net energy (*netEnergyIngested* [kJ], (15)) is then available to meet the fish's energy requirements in the following time steps.

$$(15)\quad netEnergyIngested\ [kJ] = HERBIVORE\_ASSIMILATION\_EFFICIENCY * energyIntake\ [kJ]$$

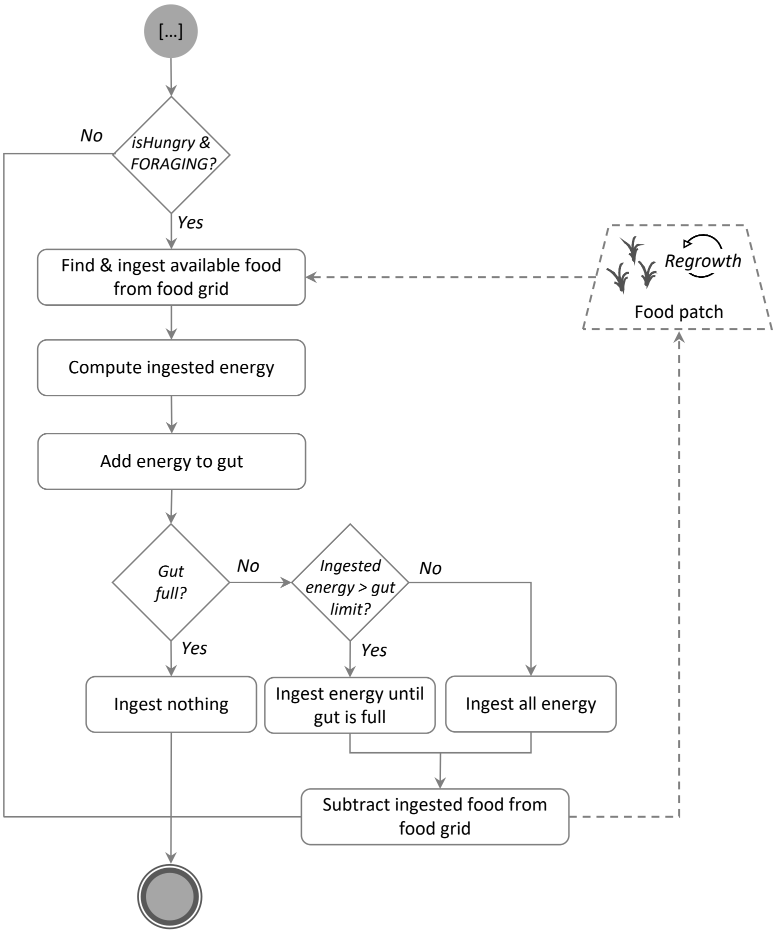


Fig. A1.9 Model flow of the Feed system and influencing environmental factors (dashed line).

3.A1.2 *Environment* entity

The virtual environment simulated in our model is represented by four main components: Two spatial grids of identical sizes (450 x 300 pixel) and resolutions (1 pixel corresponds to 1 m^2) depicting (i) the seascape with different habitat types (*HabitatMap*, A1.2.1) and (ii) the habitat-dependent food resources (*FoodMap* A1.2.2), (iii) information on the habitat-dependent predation risk for the modelled fish (*PredationRiskFactors*, A1.2.3), and (iv) the abiotic factor daytime (*TimeOfDay*, A1.2.4). The simulated area equals a total area of 0.135 km^2 and we assume conditions to be uniform within one grid cell regarding habitat type, food resources, and predation risk. All state variables for this entity appear in Table A1.3.

Table A1.3 State variables and corresponding values or units for the entity environment.

State variable	Unit or value	Description
daytime	*SUNRISE, DAY, SUNSET or NIGHT*	Relevant phases of a 24 h cycle to determine *behaviourMode* of a fish; durations are approximated for tropical regions: *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)
habitat	*CORALREEF, SANDYBOTTOM*	Relevant habitat types typically found in tropical coral reef systems
food availability	[g DW]	Amount of food available for the fish to consume in current time step
predation risk	*PredationRiskFactor***M_{nat}	Modelled as an increment of the natural mortality (M_{nat}) depending on habitat complexity

3.A1.2.1 Seascape (*HabitatMap*)

The habitat grid is based on an artificial seascape map (external image file), which is composed of at least one of two distinct habitat types typically found in any tropical coral reef system (*CORALREEF* and *SANDYBOTTOM*) as well as a type called *MAINLAND* to simulate coastlines. In the present study the habitat maps used in the different scenarios consist of (i) 0.1 km^2 *CORALREEF* plus 0.035 km^2 *MAINLAND*, (ii) 0.07 km^2 *CORALREEF* and 0.03 km^2 *SANDYBOTTOM* plus 0.035 km^2 *MAINLAND*, (iii) 0.056 km^2 *CORALREEF* and 0.044 km^2 *SANDYBOTTOM* plus 0.035 km^2 *MAINLAND*, and (iv) 0.042 km^2 *CORALREEF* and 0.058 km^2 *SANDYBOTTOM* plus 0.035 km^2 *MAINLAND* and (v) 0.028 km^2 *CORALREEF* and 0.072 km^2 *SANDYBOTTOM* plus 0.035 km^2 *MAINLAND*. For computational reasons a model fish in the move mode *RANDOM* is simply set back to its former position when attempting to move onto *MAINLAND*, while a fish in the move mode *PERCEPTION* would automatically avoid mainland borders due to the forces of the potential fields (i.e. *predationRisk.MAINLAND* is set to 1 as the highest possible value for repulsion). Independent of the move mode all individuals are 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*). To allow for an analysis of effects due to changing habitat structures as well as an adaptation of the model to different study locations the benthic map is made exchangeable.

3.A1.2.2 Food availability (*FoodMap*)

The biotic factor 'food availability' is estimated following (Kelly et al. 2017) and implemented as a grid-based, habitat-dependent amount of epilithic algal turf per unit surface area (i.e. grid cell representing 1 m^2). Depending on the underlying habitat type each food grid cell is initialized with a food value (*foodDensity* [g algal DW m^{-2}]), which is set randomly between habitat-dependent minimum and maximum values for every grid cell (*CORALREEF* = 15.0 – 45.0 and *SANDYBOTTOM* = 1.0 – 5.0 [g algal DW m^{-2}] following (Purcell and Bellwood 2001)). The minimum value for algal mass density is 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 perception radius food (*perceptionRadiusFood* [m], Table A1.4), the ingestible amount of food (*availableFood* [g algal DW m^{-2}]) is calculated at each time step using a radial neighbourhood (16) and made available for the fish, if the fish is *FORAGING* and hungry. The amount of food on each accessible food grid cell is divided by a distance-factor to decrease the available amount with increasing distance to the fish.

$$(16)\qquad availableFood\ [g\ \ algal\ DW] = \frac{\sum available\ food\ on\ accessible\ grid\ cells\ [g\ algal\ DW\ m^{-2}]}{1+(distance\ to\ a\ fish's\ position\ [m])^2}$$

The algal mass density of the current and neighbouring food cells is then depleted according to the amount actually ingested by the fish (*foodToIngest,* see above). To incorporate feedback processes between individual fishes and food resources, algal turfs in each grid cell regrow on a daily basis (i.e. every first time step of a 24 h cycle) by adding 1 % of the algal standing crop to the current food value (Tootell and Steele 2016; Kelly et al. 2017).

3.A1.2.3 Predation risk

Due to a lack of empirical values regarding habitat-related mortality rates and computational constraints we implement the habitat-dependent risk of predation (M_{pred}) as an increment of the natural mortality rate (M_{nat}, (17)). Furthermore, M_{pred} will increase in habitats with lower structural complexity such as sandy bottoms, since topographic complexity is known to moderate biotic factors like predation (Pratchett et al. 2008; Welsh and Bellwood 2012a). Though unknown for most reef fishes M_{pred} is often assumed to be considerable (Gust et al. 2002; Khan et al. 2016) and we thus assume the predation risk of sandy bottoms as riskier habitats to increase by ~35 %, i.e. we set the predation risk to equal 1.5 x M_{nat} (*PredationRiskFactors. SANDYBOTTOM*), while we suppose the risk of predation to equal 1.1 x M_{nat} (*PredationRiskFactors.CORALREEF*) in coral reef habitat, which have a high structural complexity and thus provide better refuge from predation (Pratchett et al. 2008).

$$M_{pred} = PredationRiskFactors.HABITATTYPE * M_{nat} \tag{17}$$

3.A1.2.4 Daytime (*TimeOfDay*)

Currently, abiotic factors implemented in the model are restricted to the factor daytime (*TimeOfDay*). As the main controlling force of a fish's activity (i.e. *behaviourMode*: *FORAGING, RESTING; MIGRATING,* (Helfman 1993; Bellwood 1995)), *TimeOfDay* consist of four distinct phases representing a 24 h cycle: *SUNRISE*, *DAY*, *SUNSET*, and *NIGHT* (Table A1.3). 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).

3.A1.3 Initialization values

In this study all simulations are initialized using the parameter settings listed in Table A1.4 with each factor combination replicated three times. Each replicate simulation is initialized with 50 individual fishes run for a time limit of 30 years and a maximum population size of 175 individuals (for computational feasibility).

Table A1.4 Initial parameter values for simulation runs.

Parameter name	Default value [Unit]	Description
Default parameter settings entity for 'environment'		
AlgalGrowthRate	0.001 [d^{-1}]	Proportional increase of algal turf per time unit
MapImagePath	'resources/ *filename*.png'	Path to habitat map image file. Any appropriate map file (i.e. habitat types represented by pre-defined colour values) can be loaded with the map size (in pixel) setting 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)
MaxAgentCount	175 [individuals]	Maximum number of fishes that can be 'alive' simultaneously; limited due to computational constraints
OutputAgeInterval	1 [day]	Time interval for writing age data to file
OutputLengthInterval	1 [day]	Time interval for writing length data to file
OutputPopulationInterval	1 [day]	Time interval for writing population data to file
OutputLifecyclingInterval	1 [day]	Time interval for writing life cycling related data to file

OutputStayDurationsInterval	1 [month]	Time interval for writing stay durations data to file. Larger interval chosen due to large amount of data.
Seed	23 (long)	Any value of datatype *long*. Fixes random state to ensure reproducibility of simulations: in runs with identical seeds the same sequence of pseudorandom numbers is generated
Default parameter settings for fish entity 'fish' (a diurnal herbivore parrotfish)		
General parameters		
Name	*PARROTFISH*	Identifier of modelled fish group(s)
InitalNum	50 [individuals]	Due to computational limitations 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 resemble a typical parrotfish population (probability for juvenile phase = 0.4, initial phase=0.5, terminal phase = 0.1 following (McIlwain and Taylor 2009)).
ActivityPattern	*DIURNAL*	Either *DIURNAL* or *NOCTURNAL* *DIURNAL* sets resting time = *NIGHT*, foraging time = *DAY*, migrating to feeding areas = *SUNRISE*, migrating to sleeping area = *SUNSET*; *NOCTURNAL* sets resting time = *DAY*, foraging time = *NIGHT*, migrating to feeding areas: *SUNSET*, migrating to sleeping area = *SUNRISE*
FeedingGuild	*HERBIVORE*	Functional group according to feeding habits of modelled fishes (options: *HERBIVORE*, *PISCIVORE* (including invertebrate feeders), *OMNIVORE*, *PLANKTIVORE*, *DETRIVORE*). The *feedingGuild* sets the value of the *AssimilationEfficiency*.
AssimilationEfficiency	0.26	Percentage of the digested energy, that the fish can use for its metabolism and growth (net energy). Comprises the energetic losses due to assimilation, digestion, excretion, and specific dynamic actions (SDA) and depends on the *feedingGuild*: 0.26 for HERBIVORE (Bruggemann et al. 1994) and 0.59 for all others (Brett and Groves 1979)).
PreferredHabitats. FORAGING	*CORALREEF*	Main foraging habitat(s) of modelled fish group. Used as target habitat type when fish moves from resting to feeding habitat(s) (*behaviourMode MIGRATION*)
PreferredHabitats.RESTING	*CORALREEF*	Main resting habitat(s) of modelled fish group. Used as target habitat type when fish moves from feeding to resting habitat(s) (*behaviourMode MIGRATION*)
NaturalMortalityRisk	0.11 [year^{-1}]	Order of magnitude following (Bozec et al. 2016) assuming a total mortality rate of 0.3 to 0.4 year^{-1}
PredationRiskFactors. CORALREEF	1.1	Predation risk factors used to calculate the risk of predation in the respective habitat type as an increment of the natural mortality rate (*NaturalMortalityRisk)*
PredationRiskFactors. SANDYBOTTOM	1.5	
Movement-related parameters		
MoveMode	*PERCEPTION*	Movement strategy for current simulation runs, either *PERCEPTION* or *RANDOM* with *PERCEPTION* set as default
perceptionRadiusPredation	10 [m]	Radius in which a fish perceives its surroundings and reacts regarding risk of predation, if in move mode *PERCEPTION*
maxTurnSpeed	6.0 [° s^{-1}]	Maximum turning angle of a fish (following (Jopp and Reuter 2005; Davis 2016))
SpeedFactors.FORAGING	1.5 [BL s^{-1}]	Average swimming speed of fish when in *behaviourMode FORAGING* (Korsmeyer et al. 2002; Rice and Westneat 2005)
SpeedFactors.MIGRATING	2.0 [BL s^{-1}]	Average swimming speed of fish when in *behaviourMode MIGRATING* (Korsmeyer 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)

SANDYBOTTOM_SPEED_ FACTOR	1.5	Speed increment on less complex and thus riskier sandy-bottom habitats
PathfindingWeights.FOOD	2	Weighing factor for the potential subfield *foodPotentialMap*, if in *moveMode PERCEPTION* and *behaviourMode FORAGING*
PathfindingWeights.RISK	1	Weighing factor for the potential subfield *riskPotentialMap*, if in *moveMode PERCEPTION*
PathfindingWeights. BOUNDARY	1	Weighing factor for the potential subfield *boundaryPotentialMap*, if in *moveMode PERCEPTION*
PathfindingWeights. BOUNDARY	1	Weighing factor for the potential subfield *boundaryPotentialMap*, if in *moveMode PERCEPTION*
PathfindingWeights.TO_ FORAGE	1	Weighing factor for the potential subfield *toForagePotentialMap*, if in *moveMode PERCEPTION*
PathfindingWeights.TO_REST	1	Weighing factor for the potential subfield *toRestPotentialMap*, if in *moveMode PERCEPTION*
Foraging-related parameters		
perceptionRadiusFood	1 [m]	Radius on food grid in which a fish can perceive and assess food availability, if in move mode *PERCEPTION*; Used to calculate amount of available food
energyContentFood	4.0 [kJ (g DW food)$^{-1}$]	Energy content of food resources (algal turf) following (Bruggemann 1995)
minIngestionRate	0.1 [g DW food * (g WW fish)$^{-1}$ d^{-1}]	Minimum amount of food a hungry and foraging model fish can consume daily
meanIngestionRate	0.236 [g DW food*(g WW fish)$^{-1}$ h^{-1}]	Average amount of food a hungry and foraging model fish can consume daily (Polunin et al. 1995)
maxIngestionRate	0.5 [g DW food * (g WW fish)$^{-1}$ d^{-1}]	Maximum amount of food a hungry and foraging model fish can consume daily
gutTransitDuration	54 [min]	Time span needed for food digestion (Polunin et al. 1995)
Growth-related parameters		
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)
VBGF_*AsymptoticLength*	39.10 [SL in cm]	Asymptotic average length (L_∞) of the Von Bertalanffy Growth Function (VBGF) (El-Sayed Ali et al. 2011)
VBGF_*GrowthCoeff*	0.15	Brody growth rate coefficient (*K*) of the Von Bertalanffy Growth Function (VBGF) (El-Sayed Ali et al. 2011)
VBGF_*ZeroSizeAge*	-1.25 [years]	Time (t_0) when average length is zero of the Von Bertalanffy Growth Function (VBGF) (El-Sayed Ali et al. 2011)
PostsettlementAge	120 [days]	(McIlwain and Taylor 2009)
MaxAge	9 [years]	(McIlwain and Taylor 2009)
Reproduction-related parameters		
SexChangeMode	*PROTOGYNOUS*	At present only option *PROTOGYNOUS* (sex change from female as initial phase to male as terminal phase) is fully implemented
Length_InitalPhase	10.5 [cm]	Standard length at which fish may change its life phase from *JUVENILE* (non-reproductive) to its (reproductive) initial phase (IP) (McIlwain and Taylor 2009)
Length_TerminalPhase	15.5 [cm]	Standard length at which fish may change its phase from its initial phase (IP) to its terminal phase (TP) f (McIlwain and Taylor 2009)
NumRecruits	2	Number of recruits (per spawning event) that are assumed to survive the larval stage; order of magnitude following (Miller et al. 2001; Miller and Kendall 2009)

3.A2 Sensitivity analysis and model validation

3.A2.1 Sensitivity analysis

To identify model parameters with the strongest influence on model outputs we perform a sensitivity analysis on eight model parameters (Table A2.1). These parameters are selected because they cover all main model processes (food availability, movement, energy gain and loss, survival), are uncertain and/or have proven during model development to be potentially influential. All parameters are systematically varied one at a time over three levels in a predefined range (a central value used for model calibration ± 10 %) and replicated three times, while all other parameters are kept constant. We assume a variation range of 10 % to be sufficient as most of the applied parameters are near to the represented biological processes and/or empirical data, which generally leads to a narrow and clearly definable range of plausible values (Reuter et al. 2011). All replicates are initialized with 50 individuals (40 % juveniles (JUV), 60 % initial-phase females (IP), and 10 % terminal-phase males (TP)) and population dynamics simulated for a time period of 25 years.

To evaluate model sensitivity, we examine the effects of changing parametrization on critical model outputs belonging to two hierarchical levels: 1) total abundance, 2) total biomass, 3) IP to TP life-phase ratios and reproduction frequency to assess changes in population dynamics and 4) mean body length of initial-phase females to follow individual development. The larger the deviation caused by the changed parameter value the more sensitive the model is with regard to this parameter (Reuter et al. 2011). Any parameter, that causes large effects on overall results by small variation of values, should receive high attention during parameterization in order to minimize uncertainty (Kubicek et al. 2012).

Table A2.1 Range of parameter values used to conduct the sensitivity analysis. A detailed description of all model parameters can be found in A1.

Parameter name	Lower extreme (-10%)	Default value	Upper extreme (+10%)	[Unit]
Food resources				
AlgalGrowthRate	0.0009	0.001	0.0011	[d^{-1}]
EnergyContentFood	3.6	4.0	4.4	[kJ (g DW food) $^{-1}$]
Energy budget				
MaxIngestionRate	0.45	0.5	0.55	[g DW food (g WW fish)$^{-1}$ h^{-1}]
UpperLimit (excess storage)	2.7	3.0	3.3	[h]
SpeedFactors.FORAGING	1.35	1.5	1.65	[BL s^{-1}]
Movement				
PerceptionRadiusPredation	9	10	11	[m]
MaxTurnSpeed	5.4	6.0	6.6	[° s^{-1}]
Population survival				
PredationRiskFactors.CORALREEF	0.99	1.10	1.21	Not applicable

Simulations with default parametrization. After approximately 8 years simulation time, outputs of our model with default parametrization show stable populations with a total abundance of ~ 150 individuals and a total biomass of ~ 30 kg for the simulated coral reef area of 0.1 km^2. The life phase composition (IP:TP ratio) varies during the simulation time of 25 years between values of about 1.3:1 and 1.4:1 indicating a balanced ratio between female and male model fishes with a slight tendency to an increased number of females. Initial-phase females, which control recruitment in our model and thus have a key function in regulating population dynamics, have a mean body length of about 15 cm. Spawning events (reproduction of a female model fish and creation of 2 juvenile recruits) occur on average 20-30 times per year.

Results of the sensitivity analysis (Fig. A2.1-A2.4) show that *PredationRiskFactors.CORALREEF, MaxIngestionRate, and SpeedFactors.FORAGING* are the most influential model parameters with regard to the population characteristics abundance and biomass as well as yearly reproduction frequency, while life phase compositions and on the individual level the mean body length (IP) remain rather stable for all tested combinations. Individual growth patterns and maturation processes seem thus less sensitive to changes in the tested parameter values than reproduction, overall survival, and hence population growth.

Food resources (*AlgalGrowthRate* and *EnergyContentFood*). Increasing the energy content of the food resource (algal turf) and its growth rate by 10 % result in abundance and biomass values similar to those obtained with the default parameterization (Fig. A2.1 a & b). In contrast, a decrease by 10 %, in particular of the parameter *AlgalGrowthRate* lead to a reduced population size and biomass over the first 15 years of the simulation, which, however, eventually reach values comparable to those of the other tested parameter combinations. The slower increase in abundance and biomass is mainly caused by fewer females acquiring enough energy to spawn (Fig. A2.1 c) while gaining sufficient energy to maintain their individual growth (Fig. A2.1 d). The growth phase of the population thus seems particularly affected by the change in resource-related parameter values. As algal turf production is known for its potential to strongly influence fish biomass implying that algal turf is a limited resource for *C. sordidus* (Tootell and Steele 2016) model results are consistent with field observations. Moreover, the existing data on turf biomass and production rates provide a reliable basis for model parametrization of food resource properties. Variations of both parameters *AlgalGrowthRate* and *EnergyContentFood* show similar tendencies, which is to be expected as they influence the same model processes (energy gain from food resources).

Individual energy budgets (*MaxIngestionRate*, *UpperLimit* (excess storage), and *SpeedFactors.FORAGING*). Compared to all other sensitivity analyses variation in the storage capacity (*UpperLimit*) of the excess compartment results in the least change of all considered metrices (Fig. A2.2). This indicates that model fishes are able to satisfy their energetic needs without exploiting the compartment's full capacity. In contrast, varying *MaxIngestionRate* has a strong influence particularly on population biomass throughout the entire simulation period (Fig. A2.2 b), while abundances converge towards values obtained with the default parametrization after ~15 years (Fig. A2.2 a). Surprisingly, changes in the *SpeedFactors.FORAGING* follow a very similar pattern, even though *MaxIngestionRate* influences the energetic gain of each fish at each time step while *SpeedFactors.FORAGING* controls its energetic costs. The parametrization of food intake and energy cost properties thus seems critical to model outcomes and has to be done with great care. However, good empirical estimates of ingestion rates exist for *C. sordidus* (Polunin et al. 1995) and we therefore consider the implement default values as reliable.

Individual movement behaviour (*MaxTurnSpeed* and *PerceptionRadiusPredation*). Changes in the movement-related parameters *maxTurnSpeed* and *perceptionRadiusPredation* lead to relatively small changes in overall model outcomes (Fig. A2.3). Similar to the results with changed values for food resources, total abundance (Fig. A2.3 a) and biomass (Fig. A2.3 b) increase more slowly in the beginning of the simulations but with less pronounced deviations from runs with default parametrization. After

~ 13 years simulation time all considered metrices for both *maxTurnSpeed* and *perceptionRadiusPredation* are comparable to the ones with default settings.

Population survival (*PredationRiskFactors.CORALREEF*). Increasing the parameter *PredationRiskFactors.CORALREEF* causes the highest alteration in model outcomes in particular with regard to abundance (Fig. A2.4 a), biomass (Fig. A2.4 b), and frequency of reproduction events (Fig. A2.4 c). In contrast, results of simulations with a decreased predation-based mortality are similar (with a slight increase) to those with default parametrization. Model outcomes thus differ as expected in dependence of changes in the mortality regime as mortality is a key demographic factor in fish population dynamics (Khan et al. 2016), which directly controls fish abundance. With the recruitment rate, which has a compensating effect on losses due to mortality, kept constant, fish abundance and biomass inevitably vary according to changes in mortality rates. Furthermore, increasing losses of adult fishes due to higher mortality rates will reduce local reproductive outputs (Khan et al. 2016) and is correctly reflected in our model by the changes in annual frequency of reproduction events (Fig. A2.4 c). Indicated by our analysis predation-based mortality rate is therefore a critical parameter for the outcomes of our model and has to be determined carefully.

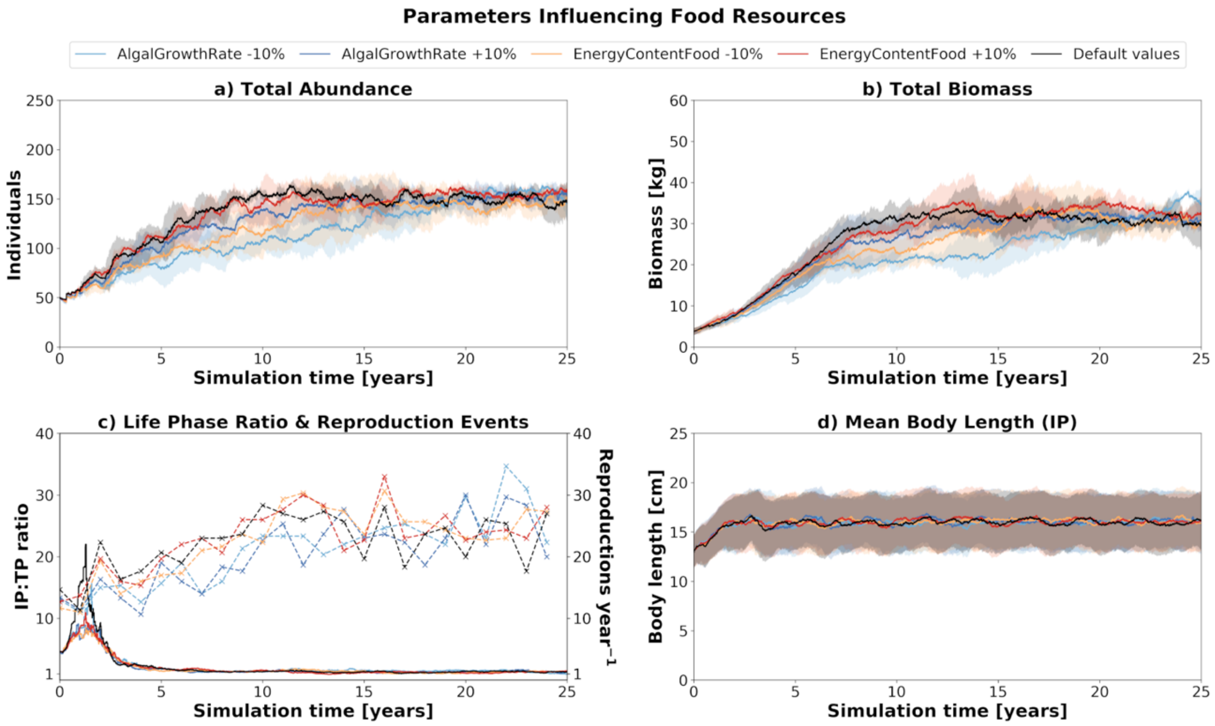


Fig. A2.1 Results of the sensitivity analysis on the parameters *AlgalGrowthRate* and *EnergyContentFood*. Model outputs are compared to simulations with default parametrization (black) with regard to **a)** total abundance, **b)** total biomass **c)** life phase composition (IP:TP) and annual reproduction frequency, and **d)** mean body length of (female) initial-phase fishes.

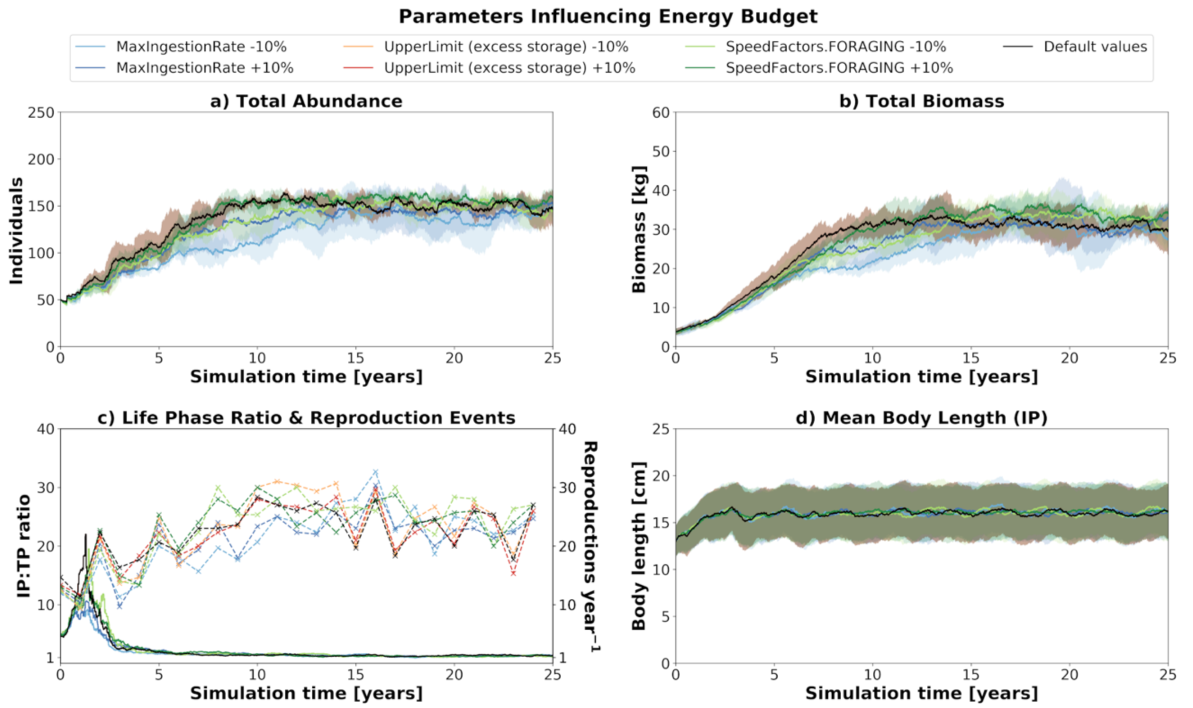


Fig. A2.2 Results of the sensitivity analysis on the parameters *MeanIngestionRate*, *UpperLimit* (excess storage), and *SpeedFactors.FORAGING*. Model outputs are compared to simulations with default parametrization (black) with regard to **a)** total abundance, **b)** total biomass **c)** life phase composition (IP:TP) and annual reproduction frequency, and **d)** mean body length of (female) initial-phase fishes.

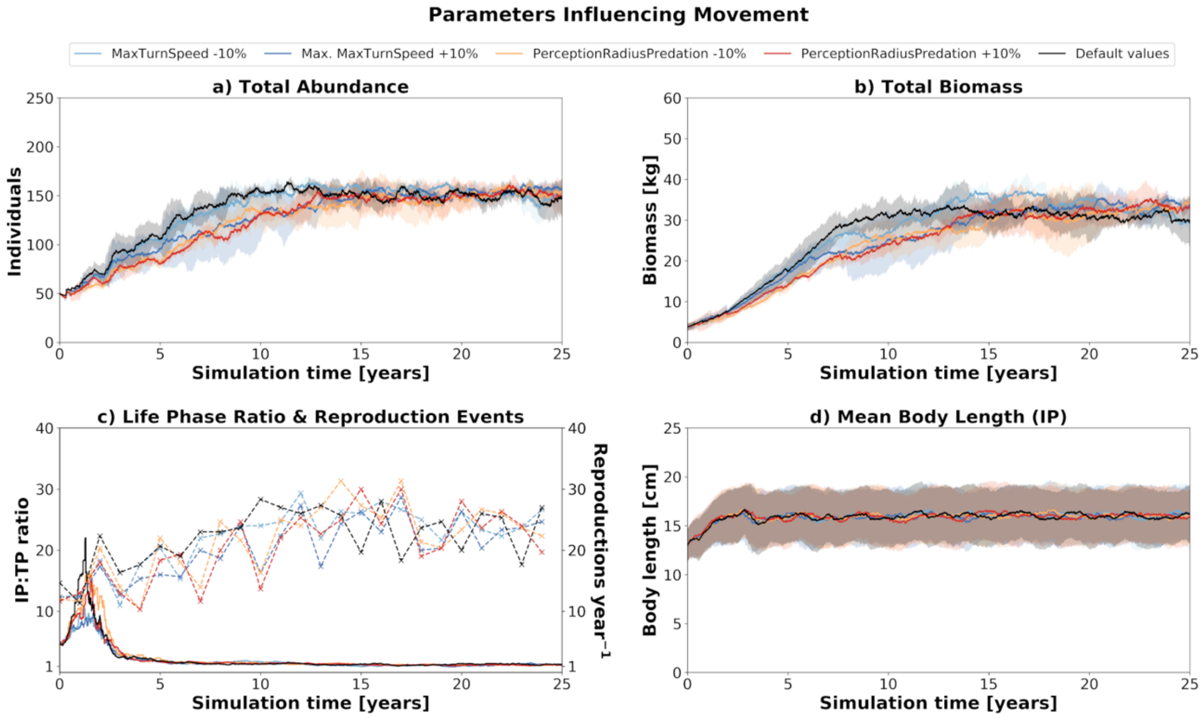


Fig. A2.3 Results of the sensitivity analysis on the parameters *maxTurnSpeed* and *PerceptionRadiusPredation.* Model outputs are compared to simulations with default parametrization (black) with regard to **a)** total abundance, **b)** total biomass **c)** life phase composition (IP:TP) and annual reproduction frequency, and **d)** mean body length of (female) initial-phase fishes.

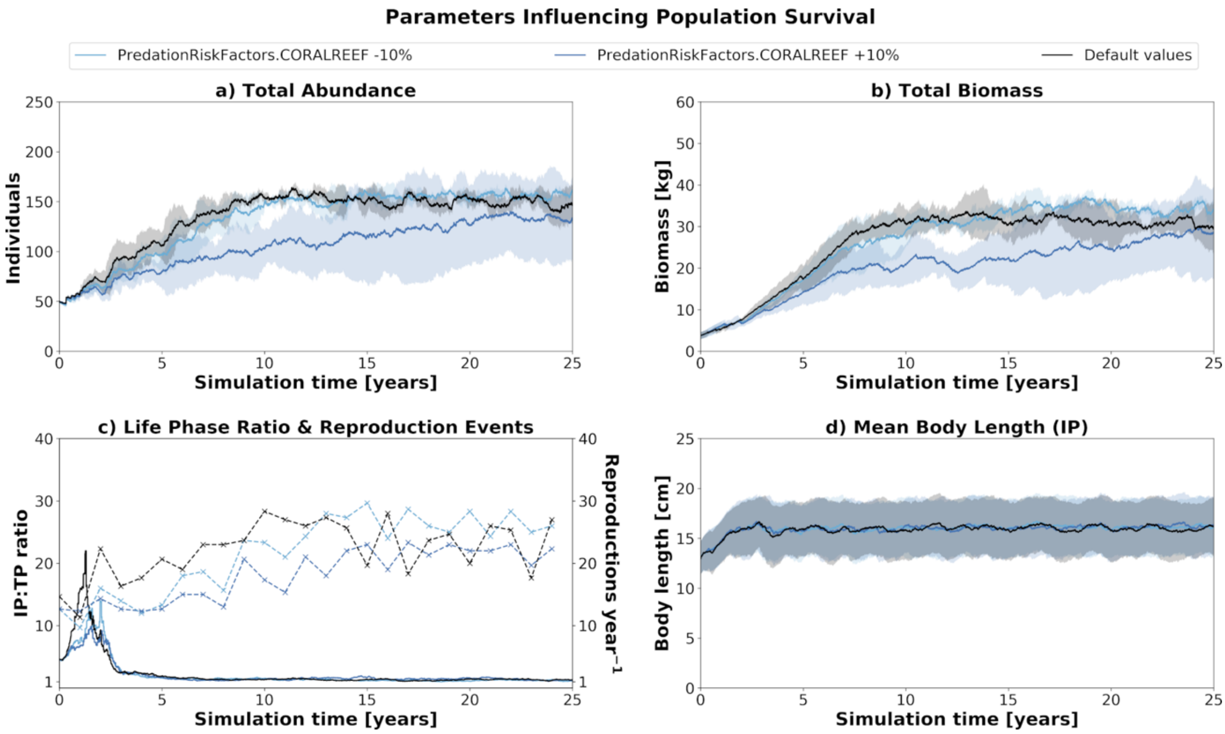


Fig. A2.4 Results of the sensitivity analysis on the model parameter *predationRiskFactors.CORALREEF*. Model outputs are compared to simulations with default parametrization (black) with regard to **a)** total abundance, **b)** total biomass **c)** life phase composition (IP:TP) and annual reproduction frequency, and **d)** mean body length of (female) initial-phase fishes.

3.A2.2 Model validation

To test whether our model is able to reproduce movement behaviour and population dynamics of parrotfishes observed in the field and thus evaluate model validity we inspect the energetic state of the individual fish process by process and by defined key variables that can be compared to available independent data such as body weight or body length (Fig. A2.5). The individual level is very close to the implemented model processes and the listed quantities contain information relative to growth, reproduction and survival we aim to interpret with regard to habitat-dependent movement behaviour and space use patterns. Furthermore, we compare individual movement trajectories as one of the key characteristics simulated by our model with published pathways of individual *C. sordidus* obtained by active tracking (Fig. A2.6). On the population level we assess the (long-term) population structure that emerge from self-organization processes and interactions of the individuals with regard to abundances, biomass, age-frequency distributions, life phase compositions and reproduction frequency (Fig. A2.7) and compare them to published field observations.

By inspecting different integration levels rather than comparing model results with specific data sets using a standard statistical approach, we follow the hierarchically structured validation approach, which is often a more meaningful means for IBMs representing complex ecological situation (Reuter et al. 2011; Kubicek et al. 2015). By ensuring a correct representation of key processes on lower hierarchical levels we also increase the probability that the system is represented correctly and results are reliable within the specified conditions and the implemented conceptual system (Reuter et al. 2011; Kubicek et al. 2012). Results of our simulations with the final (default) parametrization (Fig. A2.5-A2.7) indicate that our model is able to reproduce patterns concerning individual growth and habitat use as well as long-term population dynamics relatively well.

Individual level (mean ages, mean TP lengths, and movement trajectories). To ensure accuracy and consistency of individual life cycles we examine mean ages and mean body lengths at specific maturity states reflecting the fishes' energy budget, their individual growth and maturation. With approximately three years mean ages of model fishes (Fig. A2.5 a) are comparable to data published for *C. sordidus* populations across the continental shelf of the Great Barrier Reef of (Gust et al. 2002). In this study, reported mean ages of *C. sordidus* varied between ~1.7 and ~3.0 years. The lower variation of mean ages in the observed populations is presumably due to the stated underrepresentation of juvenile parrotfishes and young initial phases (< 10 cm body length), which are included in our model population. Mean body lengths of male terminal-phase model fishes ((Fig. A2.5 b) with approximately 25 cm are also in the range of values observed in the field by (Gust 2004) and (McIlwain and Taylor 2009). In these surveys, measured lengths for *C. sordidus* TP males were on average 20 to 25 cm and 23 to 25 cm, respectively. As age and body length at a certain life phase depend on factors such as overall energy gain and expenditure as well rules like the energy allocation to the different body compartments these outcomes confirm that our model simulates individual growth and maturation processes reasonably well.

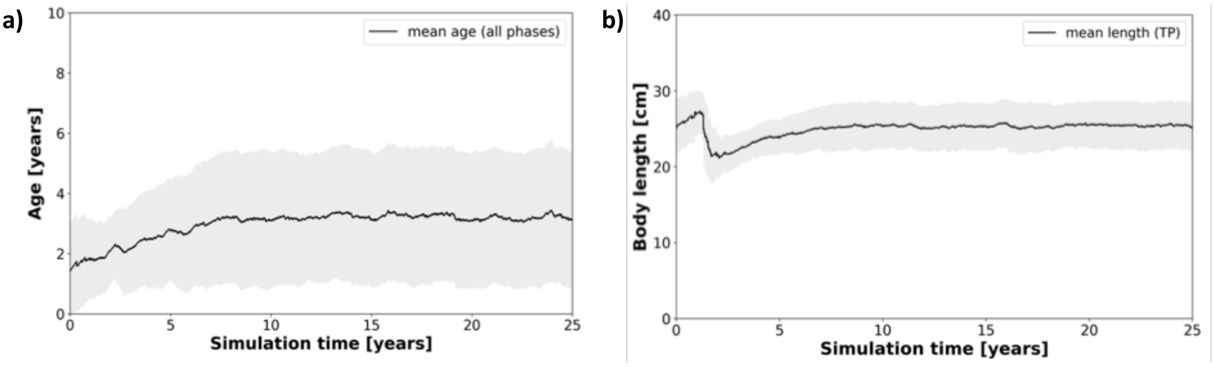


Fig. A2.5 a) Mean ages of all model fishes and **b)** mean body lengths of fishes in the terminal phase over a simulated time period of 25 years.

Guided by the implemented rules for movement behaviour, individual movement trajectories simulated over a time period of 20 min (Fig. A2.6) result in convoluted pathways with a high tortuosity and relatively small space use patterns. With a length of ~ 10 to 20 m the start-finish distances are considerably shorter than the total distances travelled and are in accordance with the range and shape of movement patterns recorded over the same time period for individual *C. sordidus* in the Northern Pacific Ocean by Davis (2016). In this investigation, the author conducted 20 min tracking trials and reported core utilization areas with a diameter of approximately 20 m. Similar short-term movement ranges have also been observed for other common parrotfish species (*Scarus niger* and *Scarus frenatus*) on the Great Barrier Reef with mean ranges of 5 to 34 m^2 and 4 to 35m^2, respectively (Nash et al. 2012).

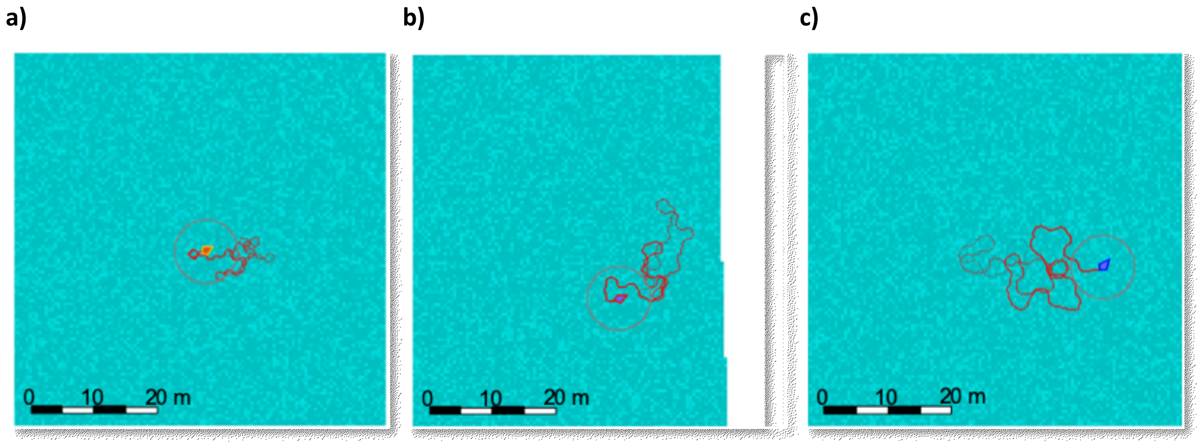


Fig. A2.6 Exemplary movement trajectories (20 min) of **a)** a juvenile model fish, **b)** a model fish in its (female) initial phase, and **c)** a model fish in its (male) terminal phase. Blue areas = coral reef habitat with darker shades indicating higher food availability, white area (in Fig. b) = coastline, and circular areas illustrate perception radius of each individual.

Population level (mean abundance and biomass, age-frequency distribution and life phase composition). To assess if individual interactions produce plausible population dynamics, which in IBMs emerge as self-organized processes, we investigate total abundance and biomass at 3 different points in the simulation period of 25 years (at year 10, 15, and 20) to allow for a comparison with empirical data. Both abundance and biomass show little difference in overall values as well as in values separated by life phase (juveniles, IP and TP adults) indicating stable population and life phase compositions (Fig. A2.7 a & b). Due to computational constraints population size was limited to 50 individuals at the start of each simulation resulting in abundances of about 150 individuals and a biomass of ~ 30 kg after ~ 8 years and a simulated area of coral reef habitat of 0.1 km^2. Compared to population densities measured by (Gust 2004) of about 500 to > 1000 individuals per 0.1 km^2 our model underestimates abundances by a factor of 4 to 6, which has to be taken into account when evaluating density-dependent effects such as use of food resources. As a consequence, also modelled biomass per unit area is lower than values observed in the field of ~200 kg per 0.1 km^2 (Friedlander and DeMartini 2002), but with a factor of ~6 in proportion to the modelled abundances.

Modelled age-frequency distributions are very similar at all three points in time (Fig. A2.7 c-e) and show a clear pattern of exponential decline in frequency with an age beyond three years. The year class 0 comprises mainly juvenile fishes (> 95 %) while females (IP) dominate the following three year classes (about 75 % in year class 1, > 98 % in year class 2 and 90 % in year class 3). Beyond an age of five years, year classes only contain male fishes (TP). These patterns are in accordance with age-frequency distributions observed for *C. sordidus* populations in Guam by (McIlwain and Taylor 2009) and at the Northern Great Barrier Reef by (Gust 2004). In these studies juveniles were observed mainly in age classes 0 and 1, while females were most abundant in the age classes 2 to 4 and males dominated the older age classes. Both studies, however, also report older, if few females (> 6 years), which are absent in our model. Modelled life phase composition, on the other hand, is again comparable to Ip to TP ratios published by (Gust, 2004) in the same study, which varied between sites from 4.75:1 and 1.48:1.

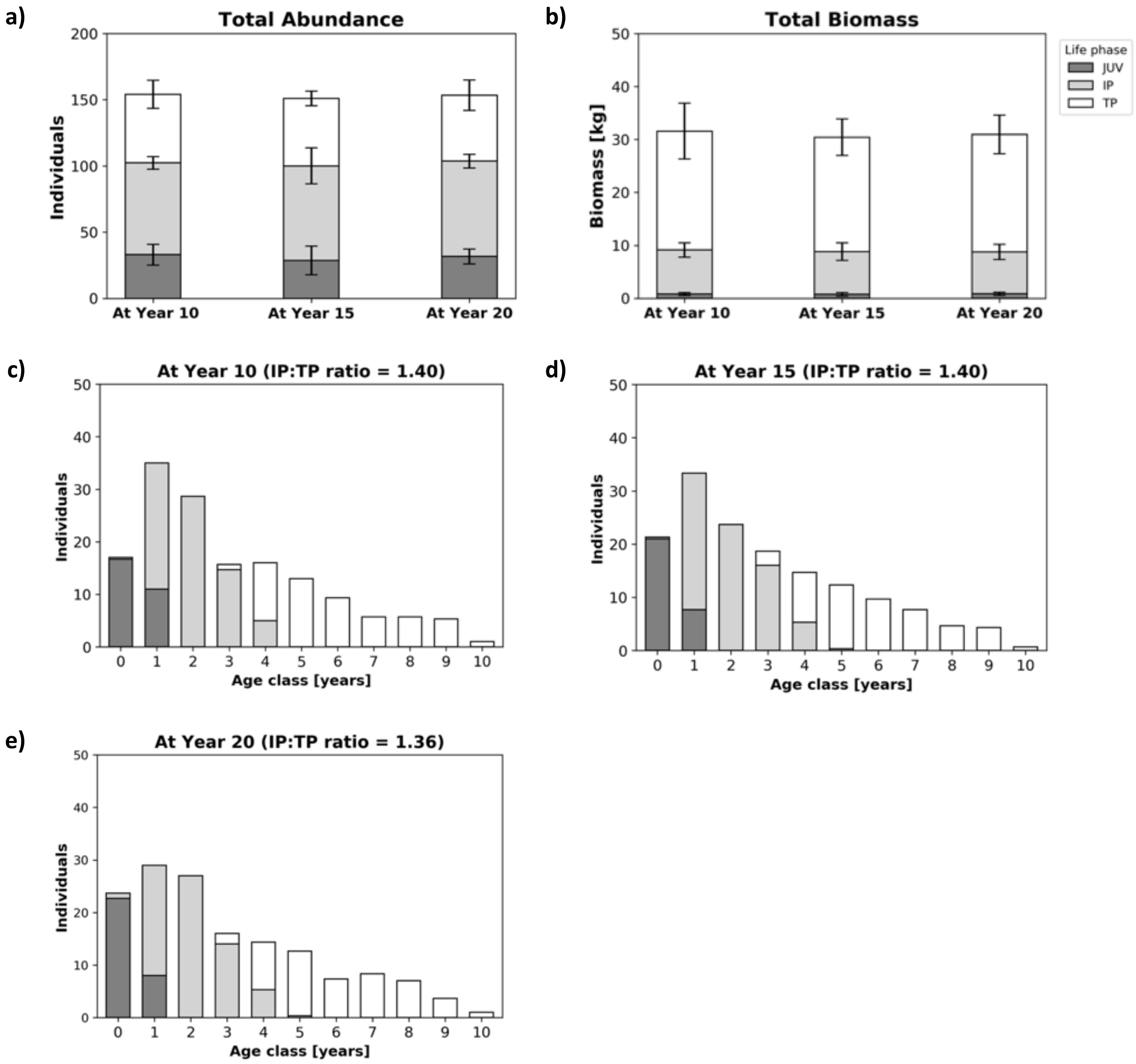


Fig. A2.7 a) Abundances, **b)** biomass and **c)-e)** life phase composition of model fish population at different points in time during a simulation with default parametrization. Bars are subdivided into life phases (JUV = juveniles, IP = (female) initial phases, TP = (male) terminal phases).

4 Landscape connectivity revisited – A unifying conceptual framework for the marine and terrestrial realm

Landscape connectivity revisited – A unifying conceptual framework for the marine and terrestrial realm

Maren Kruse[1,2]

Dr. Hauke Reuter[1,2]

[1]Department Theoretical Ecology and Modelling, Leibniz Centre for Tropical Marine Research (ZMT), Fahrenheitstr. 6, D-28359 Bremen, Germany

[2]University of Bremen, Bibliothekstr. 1, D-28359 Bremen, Germany

Email of corresponding author*: maren.kruse@leibniz-zmt.de*

Phone: +49 (0) 421 23 800 70

Fax: +49 (0) 421 23 800 30

Email of co-author*: hauke.reuter@leibniz-zmt.de*

Abstract

Context

Since its formulation more than two decades ago, (landscape) connectivity has become a frequently utilized concept in spatial ecology and conservation planning across terrestrial and marine ecosystems. However, despite its relevance for many ecological processes, its definition and measurement remain inconsistent throughout the literature regarding scales, dimension, and scope.

Objectives

We introduce a unifying framework as a step forward in overcoming the current ambiguities and shortcomings of connectivity as a concept. Importantly, our framework extends the original definition to encompass passive as well as active movement making the concept applicable to both the terrestrial and marine realm for a broad range of organisms and life stages.

Methods

We have conducted an extensive literature research covering the period from the establishment of landscape connectivity as a concept in 1993 until now to evaluate its definitions, categories and application in the different realms.

Results

Our review confirms the ambiguous usage of the landscape connectivity concept but also reveals large differences in its application between terrestrial and marine ecology regarding scale and focus of connectivity studies. Based on our findings, we suggest to use the concept strictly organism-centred, to include active and passive movement as well as appropriate temporal and spatial scales. We further denote three categories of connectivity: ‘potential’, ‘area', and ‘effective’ connectivity referring to different spatial-temporal scales and integration levels.

Conclusions

With our contribution, we hope to encourage a more consistent use of ‘landscape connectivity’ making it a more comparable and quantifiable concept.

Keywords: marine; terrestrial; dispersal, passive transport; life-history;

1 Introduction

Landscape connectivity is “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993)

Movement and dispersal of organisms has long been recognised as a key process in ecology and conservation biology (Turchin 1991; Lima and Zollner 1996; Nathan et al. 2008) and is becoming even more important in view of the advancing human-induced deterioration of the environment. Anthropogenic activities often result in drastic changes of the landscape including increasing fragmentation and/or loss of natural habitats, which are among the primary causes of global biodiversity decline (Kindlmann and Burel 2008; Haddad et al. 2015). By dispersing, motile organisms can adjust to these changing environments, making movement at all spatial scales relevant to most current environmental concerns in both the terrestrial and the marine realm (Nathan et al. 2008).

To incorporate movement as a critical component for the analysis of (animal) population’s survival into a framework of landscape processes, Taylor et al. (1993) developed the concept of ‘landscape connectivity’. They defined connectivity as one of three measures of landscape structure as “the degree to which the landscape facilitates or impedes the movement among resource patches” opposed to landscape physiognomy (distance between patches) and landscape composition (distribution of patches, Taylor et al. 1993). Hence, landscape physiognomy and composition are related to the spatial distribution of resource patches, while connectivity encompasses the organismic response to the (given) landscape structure (Taylor et al. 2006).

Ecologists and resource managers agree on the relevance of connectivity as a key element for many ecological processes, and after more than two decades it is an ever more frequently utilized concept in spatial ecology and a frequently proposed management criterion in conservation planning (Olds et al. 2012; Kool et al. 2013; Helfenstein et al. 2014; Green et al. 2015). Despite being originally defined for animals in a terrestrial context, it has been applied to a variety of organisms in both terrestrial and aquatic ecosystems ranging from plants (e.g. Murphy and Lovett-Doust 2004; Brudvig et al. 2009; Rico et al. 2012), vertebrates such as birds (e.g. Amos et al. 2014; Bellisario et al. 2014), amphibians (e.g. Stevens et al. 2005), mammals (e.g. Mueller et al. 2011; Riordan et al. 2016), and fishes (e.g. Unsworth et al. 2008; Berkström et al. 2012) to invertebrates like insects (e.g. Brückmann et al. 2010; Kennedy et al. 2013) or larval stages of various organisms (e.g. Cowen et al. 2006; Planes et al. 2009; Green et al. 2015). Furthermore, an increasing number of studies use the term ‘connectivity’ with regard to gene flow or transfer of information, matter or energy between populations (see Kool et al. 2013 for review).

However simple and straight-forward it may appear at first sight, ‘landscape connectivity’ is a complex and much debated concept which has been the source of many ambiguities – concerning its definition as well as its measurement (Moilanen and Nieminen 2002; Calabrese and Fagan 2004; Taylor et al. 2006; Kindlmann and Burel 2008; Kool et al. 2013). Functional, population, or ecological connectivity (see text box 1), to name but a few, are often defined overlapping – if at all – or used interchangeably without any consensus having been reached yet (e.g. Tischendorf and Fahrig 2000; Calabrese and Fagan 2004; Kindlmann and Burel 2008; Kool et al. 2013). Furthermore, the appropriate spatial scale for the various connectivity terms is another unresolved issue ranging from a landscape-scale property in landscape ecology (e.g. Tischendorf and Fahrig 2000) to a habitat patch-scale attribute in meta-population ecology (e.g. Moilanen and Hanski (2001), but see Kadoya (2009) for review). Thus, depending on its usage and the scale considered, connectivity can be interpreted in many different ways under different circumstances, making the concept difficult to apply and results almost impossible to compare, which aggravates a common understanding (Olds et al. 2012).

Although many authors recognized the inconsistent use of this concept (Tischendorf and Fahrig 2000; Moilanen and Hanski 2001; Taylor et al. 2006; Kool et al. 2013), limited progress has been made to unify its definition and quantitative use (but see Calabrese and Fagan 2004; Bélisle 2005; Kindlmann and Burel 2008; Lindenmayer et al. 2008; Grober-Dunsmore et al. 2009). A clear formulation, taking the concept to its logical conclusion but at the same time delimiting its application, is still missing. Moreover, some important aspects are not yet included in its definition (despite being applied), such as passive transportation which can be an important process for plant dispersal or dispersal of marine species via larval stages. Landscape connectivity is decidedly a very useful concept for ecological theory as well as applied biology, but we are convinced that a trade-off has to be made between applicability and being all-encompassing in scope to achieve meaningful and comparable results.

We further agree with Taylor et al. (2006) that connectivity itself should not be considered as inherently good or bad: through its effects it may influence population persistence in both ways, positively as well as negatively, depending on the given situation and species considered. Rather, it is important to better understand how connectivity alters as a consequence of changes in the landscape structure and for which species under what conditions connectivity is relevant (Taylor et al. 2006). This is of particular importance with regard to the increasing habitat fragmentation which interacts strongly with other components of global environmental change such as species invasions (Vilà and Ibáñez 2011), intensification of land-use and climate change (Didham 2010).

To become a reliable and meaningfully applied management criterion, more consistency in its definition and above all measurement is needed (Hodgson et al. 2009), as conservation managers are more likely to be interested in easy-to-use connectivity metrics (Kadoya 2009). Until now, the choice of how to define and assess connectivity is often arbitrary and prone to uncertainty of human decision-making (Kool et al. 2013). To unify the conceptual framework in the ecological context, it requires (i) a species-centred approach, as well as information on (ii) how the organisms of interest interact with the landscape and (iii) how those interactions differ as a function of scale-dependent influences (Taylor et al. 2006; Kool et al. 2013). We thus again share the opinion of Taylor et al. (2006) that, although complicating its assessment, landscape connectivity cannot be captured “simply by an index of landscape pattern but must be determined based on the organisms’ perception of, and interaction with the structure and heterogeneity of the landscape”.

In this article, we recommend using connectivity as a strictly organism-centred concept as it results from the interactions between the landscape and the organism making connectivity a species-specific property for any given landscape and time considered. We further propose an important step towards a more general framework that (i) extends the definition of landscape connectivity to encompass passive as well as active movement making the concept thereby (ii) applicable to both the terrestrial and marine realm for a broad range of organisms, that (iii) includes appropriate temporal as well as spatial scales, (iv) simplifies it into an accessible and applicable form, and (v) makes it a quantitative approach. We are convinced this will contribute to a more consistent use of ‘landscape connectivity’, making it a more comparable and quantifiable concept.

2 The ambiguity of the landscape connectivity context

Landscapes are complex spatial structures essentially characterized by the heterogeneity of their elements (Wiens 1995) and in which different types of habitats are patchily distributed. In this article, we refer to habitat in its functional meaning, i.e. as “the suite of resources (food, shelter) and environmental conditions (abiotic and biotic) that determine the presence, survival and reproduction of a population” (Gaillard et al. 2010). Thus, habitat is a species-specific property of the landscape and frequently, individuals of a species will have to move among suitable habitat patches across a matrix of unsuitable patches to reproduce and obtain food and other resources (Schooley and Wiens 2003).

Movement between habitat fragments in a heterogeneous landscape is commonly accepted as a key process driving population dynamics and also facilitating (re)colonization of empty habitats (Lima and Zollner 1996). Movement behaviour is a species-specific property, and in turn, is influenced by the biophysical nature of the landscape (Taylor et al. 1993), i.e. the composition and configuration of habitat patches within a given area, thereby – in combination with (e.g. trophic) interaction processes – generating patterns like the spatial distribution of a population at the patch- and landscape-scale (Bélisle 2005). The recognition of movement behaviour as a link between process and pattern in landscape ecology has led to the formulation of the concept of 'landscape connectivity' to capture the organismic response to physical landscape features as an explicit component of landscape structure (Bélisle 2005).

Landscape connectivity in its original meaning (Taylor et al. 1993) is described as a dynamic emergent property of species-landscape interactions (Taylor et al. 2006; Baguette et al. 2013), which implies two dimensions: the landscape and the organism (Kindlmann and Burel 2008). Consequently, different landscapes may have different degrees of connectivity for the same species and the same landscape may have different degrees for different species or even for the same species at different times (Tischendorf and Fahrig 2000; Calabrese and Fagan 2004; Kindlmann and Burel 2008). The functioning of an ecosystem is therefore not independent from its spatial context in the landscape, and connected systems may behave differently depending on the degree of isolation (Mumby and Hastings 2008). This implies that connectivity is specific for a given situation, and the transferability of results has to be tested against underlying causal factors.

A closer look at the connectivity definition reveals that, even though landscape patches can be connected to one another by a variety of physical, chemical, and biological processes, not all of them are inherent parts of the connectivity concept. Due to its intuitive nature and generality, however, many authors equate very different kinds of (patch-)connecting processes with connectivity (see text box 1 for an overview of common definitions). As a result, numerous conceptual and operational definitions exist with no unifying framework having emerged yet (Kool et al. 2013). Tischendorf and Fahrig (2000), for example, recommend using connectivity in its original meaning defined by Taylor et al. (1993), while Kindlmann and Burel (2008) suggest distinguishing between landscape connectivity (connectivity as a landscape-scale property) and patch connectivity (connectivity as a patch-scale property). Lindenmayer et al. (2008), on the other hand, propose a distinction between landscape connectivity (i.e. physical connectedness of patches of a particular land cover type as perceived by humans), habitat connectivity (i.e. connectedness of habitat patches for a given taxon) and ecological connectivity (i.e. connectedness of ecological processes at multiple spatial scales).

Deviating from its original meaning in the terrestrial context, connectivity in marine studies is often related to the dispersal of organisms and their propagules and commonly defined as the extent to which populations are linked by exchange of larvae, recruits, juveniles or adults (e.g. Palumbi 2003; Sale et al. 2005; Grober-Dunsmore et al. 2009). The different components of connectivity discussed in these studies are very diverse, relate to different integration levels, and their meanings may vary from one author to the other.

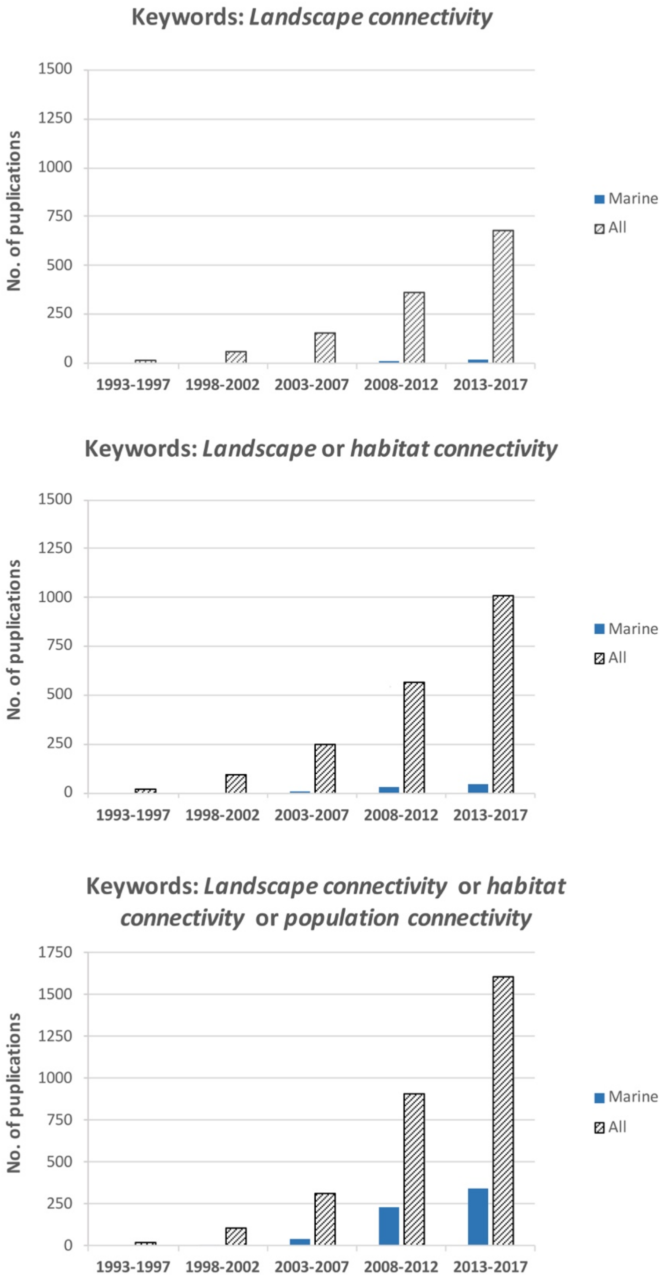
Furthermore, ‘connectivity’ is not only used as a functional concept, but also in a structural way (see text box 2). In contrast to ‘functional’ connectivity, ‘structural’ connectivity is denoted as being independent of any behavioural attributes of the organisms considered (Taylor et al. 2006). Instead, it is based entirely on the landscape structure and often equated with spatial contagion or contiguity of the habitat (Tischendorf and Fahrig 2000; Kindlmann and Burel 2008). Hence, if the physical ‘connectedness’ between habitat patches increases so does the ‘structural’ connectivity, whereas ‘functional’ connectivity increases when changes in the landscape structure enhance the movement of organisms through that landscape (Taylor et al. 2006). Habitat patches therefore do not need to be structurally connected to provide functional connectivity and vice versa (Taylor et al. 2006).

Due to the diverging definitions (text box 1) measuring connectivity is not straightforward, and one can find at least as many metrics as there are definitions in the literature (Calabrese and Fagan 2004; Kindlmann and Burel 2008). The original measure for a given organism is based on the probability of movement between all points or resource patches in a landscape (Taylor et al. 1993). Beyond this, there are many more metrics available ranging from simple measures such as nearest-neighbour-distances to more complex ones based on genetic analyses (see Kool et al. 2013 for a comprehensive metrics summary). These measures all vary in the type of data they require and the level of detail they provide (Calabrese and Fagan 2004). Hence, the same landscape may have different connectivity values when different metrics are applied (Kindlmann and Burel 2008).

3 Deficiencies of the current use of landscape connectivity

The concept of landscape connectivity has been largely defined from a landscape point of view focusing on the terrestrial domain with the perspective of individual organisms moving between an assemblage of suitable habitat patches with definable neighbourhood properties. The low number of publications, that could initially be found for marine applications clearly denotes the terrestrial origin (Fig. 1). The concept emerged and thrived in the context of an increasing understanding of the importance of spatial processes for population development and conservation. It thus has become an essential requisite to understand the spatial heterogeneity and temporal variability of populations, and the concept of landscape connectivity can well be used to foster specific conservation measures (Lindenmayer et al. 2008; Haddad et al. 2015; Worboys et al. 2016).

From this starting point, the concept has been applied to many different situations, with an increasing ambiguity in its use (see part 2), but without being adequately adapted to incorporate its application to other than terrestrial systems. Consequently, a variety of processes are missing in the current concept such as passive transportation or different life-history situations including temporal aspects of connectivity. Despite a high number of studies in the marine realm having a ‘connectivity’ label, the marine realm has only been marginally touched (e.g. Grober-Dunsmore et al. 2009; Turgeon et al. 2010; Baguette et al. 2013). In marine systems, the concept of ‘population connectivity’ plays a more prominent role (e.g. Kool et al. 2013; Treml et al. 2015, Fig. 1). Therefore, we deem a conceptual extension including the mentioned processes to be highly desirable. In the following we explicate these neglected processes and argue why they should be incorporated in a general concept of (landscape) connectivity.


Keywords: *Landscape connectivity*

Keywords: *Landscape* or *habitat connectivity*

Keywords: *Landscape connectivity* or *habitat connectivity* or *population connectivity*

Fig. 1 Use of different connectivity concepts in the terrestrial and marine realm. The search was conducted on *Web of Science* with keywords '"landscape connectivity"', '("landscape connectivity") or ("habitat connectivity")', and '("landscape connectivity") or ("habitat connectivity") or ("population connectivity")' and respectively with the supplement 'and marine' for the given periods.

3.1 Neglected processes: Passive transport and different life stages

Most definitions of connectivity focus either exclusively on actively moving animals, ignoring passive movement of early life- or otherwise dispersal stages, or emphasise the so-called structural connectivity, which solely relies on the physical landscape structure neglecting the organismic component (Tischendorf and Fahrig 2000; Kindlmann and Burel 2008). This considerably limits the scope of the concept as these definitions exclude relevant processes and organism groups. Passive transportation as opposed to active movement is equally relevant for connecting different land- or seascape elements. For a wide range of taxa propagules or organisms in larval stages are transported passively, contributing significantly to colonisation processes or interconnections of dispersed populations (Jones et al. 2009).

In aquatic systems, passive dispersal triggered by water currents or streams is essential for exchange processes between habitats. Very many life forms, even if sessile in the adult stage such as corals, have planktonic propagules which are initially highly dependent on water currents for dispersal. With increasing age and size, a gradual change from passive transport to more active dispersal movements may take place, but the extent to which active movement potentially influences dispersal or selection of settling grounds is debated for the different species (Rocha et al. 2002; Bird et al. 2007; Almany et al. 2007). In this context, the pelagic larval duration (PLD) plays an important role in the discussion on the dispersal abilities as it potentially determines the distance a larva can cover (Duda and Palumbi 1999; Faurby and Barber 2012). The complex interactions between variable water currents and life-history patterns determining larval dispersal and subsequent settlement on one hand and species migrations on the other hand play a central role in the analyses of the interconnectedness of marine populations and are being discussed as fundamental for the design of effective marine protected areas (MPAs) or protected area-networks (PAN) and the successful management of marine resources (Worboys et al. 2016; Williamson et al. 2016).

The dispersal of plant seeds is another distinctive example, where passive transport plays a prominent role. In order to assess plant connectivity, it is important to consider which parts of a given land-/seascape are reachable for plants, i.e. their seeds, and we see no valid reason to exclude this big group of organisms or mode of dispersal. Initially, plants may have been disregarded due to their partial subordination of physical landscape structures to form ‘habitat patches’ for which faunal dispersal is defined. However, in the context of recolonization processes and conservation planning plant dispersal needs to be considered (Kirchner et al. 2003; Minor and Gardner 2011). Auffret et al. (2017) strongly advocate the concept of plant functional connectivity thereby considering propagules as well as pollen and with the addition that the dispersed unit must contribute actively (effectively) to the target population by reproducing. In contrast to faunal dispersal, plant settlement depends more on physical and pedological environmental factors and their analysis becomes more important than biotic landscape features when investigating plant connectivity.

Furthermore, an inclusion of passive dispersal facilitates the integration with other concepts in ecology such as succession or recolonization processes after disturbances. Succession (primary as well as secondary) relies on the availability of propagules as well as the surrounding species pool, and their dispersal properties determine the succession processes and community assembly. For example, the destruction of mangroves due to the Tsunami on the Nicobar Island in 2004 has led to a new species composition determined by transport processes (Nehru and Balasubramanian 2011).

Passive movement requires a vector, which in the marine realm is mostly present as water currents, whereas in the terrestrial environment it includes multiple vectors such as wind- (anemochory) or animal- (zoochory) mediated (seed) dispersal. For example, aquatic plants are frequently transported by waterfowl, burs cling to the fur of an animal, or seeds only germinate after an intestinal transit (Robledo-Arnuncio et al. 2014) which may also imply a considerable transport distance. Interestingly, zoochory touches a further dimension of connectivity: Apart from the target organism, the availability and dispersal of the organisms needed for the transport processes may have to be considered as well as the extent to which they connect habitats suitable for the target species. Additional processes exist, for which it is difficult to decide to what extent they are driven by active movement or passive transport, e.g. the ballooning of spiders (Bonte et al. 2004).

When analysing how land- or seascapes contribute to the connectedness of populations we also need to consider varying dispersal abilities, which may change with different life stages (ontogenetic movements) – a process that has often been neglected in the context of landscape connectivity. In the marine realm, for instance, early life stages of many organisms are dispersed by passive current-mediated drift, thus being highly mobile with the larvae contributing substantially to the gene flow between local populations and the colonisation of suitable environments (see part 3.2). In later stages, the movement range may considerably change and movements between adjacent habitats might become more important when (sub-)adults utilise resources of different habitat types. A common example for exchange processes linking neighbouring but distinct habitats are the nursery grounds for many coral reef fishes within mangrove forests (Nagelkerken et al. 2001; Olds et al. 2012). Adult fish are also known to leave their relatively narrow home ranges for reproduction and migrate to distant spawning grounds (Dingle 1996). The same applies to marine invertebrates like mud crabs (*Scylla* spp.) which migrate offshore for spawning (Alberts-Hubatsch et al. 2016), while the larvae return to coastal areas (nursery grounds) within mangroves and seagrass beds. Worboys et al. (2016) demonstrated the importance of life-history dependent migration for marine connectivity processes with the example of the Red Emperor (*Lutjanus sebae*) which subsequently uses a wide range of habitats including inshore estuaries, coral reefs and deep-water seagrass communities. Ontogenetic movements can therefore constitute a significant part of the exchange processes in marine environments. Generally, in the marine realm, early life stages contribute substantially to the gene flow between local populations and the colonisation of suitable environments due to the high mobility of the larvae (see part 3.2), whereas in terrestrial environments other mechanisms like wind- or animal-mediated dispersal may become more relevant.

3.2 The marine environment, a neglected realm

Another essential aspect not included in the original connectivity concept is the marine realm, despite recent years having seen an increasing number of studies with the keyword ‘connectivity’, especially for coastal and marine habitats (Fig. 1). In marine studies, connectivity often focuses on the dispersal of organisms which leads to larvae-linked populations (e.g. Jones et al. 2009). The typical fields of application in both coastal marine habitats and the open ocean encompass, for instance, the exchange processes between coral reefs via planktonic larval dispersal (Galindo et al. 2006), between fish populations either by active movement (Turgeon et al. 2010) or passive transport of larvae (Cowen et al. 2006).

Strikingly, while in terrestrial studies the organismic component is more likely to be neglected (see text box 1, structural connectivity), it is the landscape dimension that is often not explicitly addressed in marine studies (see text box 2) or limited to the consideration of water currents (Sale et al. 2010; Kininmonth et al. 2011; Kool et al. 2013; Manel and Holderegger 2013). Moreover, it still remains unresolved how meaningfully terrestrial landscape metrics and statistical techniques can be applied to marine species and seascapes (Wedding et al. 2011), although most of the here reviewed studies assumed that the approaches are equally applicable to marine ecosystems.

Nonetheless, when discussing concepts of connectivity, we have to bear in mind, that terrestrial and marine habitats are fundamentally different, mainly as a result of the disparate characteristics of their basal medium, air and water, respectively. As organisms adapted to the medium's physical and chemical properties in the course of evolution, pronounced differences in life-forms, life history, community composition and trophic structure have emerged (May and Godfrey 1994). In contrast to terrestrial environments, where long distance dispersal is often mediated by network elements such as corridors and stepping stone habitats (Saura et al. 2014), in marine systems water currents facilitate or determine the direction and extent of displacement of passively drifting organisms with several important consequences. Current-based dispersal is asymmetric (Dibacco et al. 2006) favouring the current’s downstream direction. Movement against the predominant water current would have to be achieved by active movement of (adult) organisms, other transport processes or by potential short term (seasonal) changes of current directions. The extent of displacement due to this passive current-mediated dispersal is assumed to be at least a factor 10 higher than in terrestrial systems (Lett and Kaplan 2010), and marine populations are thus supposed to be more open than terrestrial ones (Cowen et al. 2006). These divergences from terrestrial habitats are particularly relevant for the successful planning and management of marine reserves and thus, characteristic life-history development, predominant passive dispersal, and its extent as well as divergent human impacts should be taken into account (Carr et al. 2003).

Furthermore, for the analysis of habitat boundaries as preferred locations for many marine organisms such as fish, a further dimension has to be added when investigating connectivity in marine environments. In terrestrial areas, different habitats are often easy to identify based on simple observations, aerial photography or satellite images because habitats are related to basic plant communities or easily detectable physical landscape features. For shallow coastal waters, where benthos processes are dominant, the situation is very similar, and e.g. reefs, sea grass beds, salt marshes or mangrove forests can be distinguished analogously to terrestrial habitats up to certain water depths (Kabiri et al. 2013). However, in deeper waters the distinction gets more ambiguous due to the general difficulties in observing marine systems. Additionally, in deeper areas and pelagic waters areas of species occurrence are mainly determined by the physical and/or chemical properties of the water body which vary depending on water movement (currents, upwelling) as well as biological and chemical processes. Here, stratification becomes decisive for defining clear boundaries between water masses that have distinct properties with respect to physical (temperature, light) and chemical (e.g. O_2-saturation, pH, ammonium, CO_2) characteristics relevant for organismic occurrence.

A definition of connectivity which encompasses both the marine and the terrestrial realm has to take the above-mentioned differences into account and has to include active as well as passive movement of organisms, changes during ontogenetic development and a broader definition of the term habitat.

4 Delimiting a new concept of land-/seascape connectivity

To develop an overarching approach and thus improve comparability of connectivity studies, it is compelling to define, and measure connectivity based on the original definition by Taylor et al. (1993) but also to encompass the specifications of marine and terrestrial ecosystems as well as the new developments in its usage. This approach should be clearly organism-centred as the concept is inherently premised on the interactions between an organism and the landscape it inhabits. Within this framework land- or seascape connectivity cannot exist independent of any behavioural attributes of the target organisms. In nature, the same environment is used differently by organisms with different traits, e.g. with respect to size, motility, potential to survive in hostile environments, sensoric capabilities, or larval survival times in marine environments, which inevitably results in different connectivity values. Thus, land-/seascapes have to be viewed through the eyes of the respective species, i.e. independent from a standardized anthropogenic consideration of the correct scale or patch size to measure ‘connectivity’ as a landscape feature.

Connectivity as a function of the organism-landscape interaction manifests itself on different spatial and temporal scales, depending on organism size (Gaillard et al. 2010) but also on different life-histories (Worboys et al. 2016) and movement behaviours (Börger et al. 2008). Connectivity is an inherently spatial concept with the spatial scale at least implicitly considered via the organismic activity range and movement between habitats. Also, these exchange processes have a relevant temporal dimension, when measuring e.g. exchange rates between habitats or gene flows between populations. We believe the temporal dimension, frequently neglected so far, has to be explicitly defined whenever using any measurements or indices related to connectivity in order to obtain unambiguous results. Similar to the spatial scale, also the temporal range depends on the organism of interest (Tischendorf and Fahrig 2000; Grober-Dunsmore et al. 2009): smaller organism, e.g. small rodents, can reach fecundity within several weeks and may reproduce several times a year, whereas large vertebrates, such as deer, have much longer generation times and may only reach physical (temperature, light) and chemical (e.g. O_2-saturation, pH, ammonium, CO_2) characteristics relevant for organismic occurrence.

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Central questions that should always be answered in a study investigating connectivity is: What exactly does it mean when stating high or low connectivity between areas, which metrics are most informative and what are the implications? Does high connectivity, for example, imply that there is a high potential for an organism to get from habitat A to habitat B and/or vice versa or are there continuously high exchange rates of individuals between landscapes patches? Or should high (low) connectivity refer to high (low) genetic similarity between two populations? It thus deems necessary to not only distinguish between different forms of connectivity but also to explicitly state the underlying criteria. To allow for a comparison between studies it is important to know (i) to what the measured connectivity relates, e.g. to individuals or genes, (ii) whether it is a function of populations or habitat characteristics, and (iii) at what spatial and temporal scale it is defined. Only if we explicitly state this information when investigating and measuring connectivity, it will become possible to compare its values across species and landscapes. Based on the outlined criteria, we propose to subdivide connectivity into three categories: ‘potential connectivity’, ‘area connectivity’, and ‘effective connectivity’ (Fig. 2, Table 1) each related to different spatial and temporal scales.

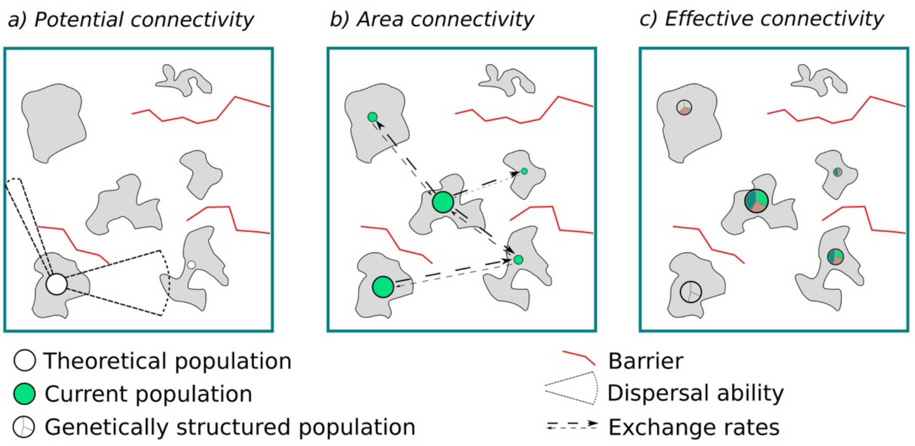

Fig 2: Connectivity categories with different relevant times scales: a) less than one generation (level of the individual), b) ~ 1 generation (level of the individual) c) > 1 generation (population level).

Tab. 1 Overview of suggested categories of land-/seascape connectivity and their main characteristics.

Term	Main characteristics	Temporal range (generations)	Focus of indices	Measurements, methods and models (examples)
Potential connectivity	Theoretical consideration of potential movement of a given organism in a specific landscape. Requires knowledge on the movement ability of the target organism, e.g. scale of movement, implications of different landscape elements to facilitate or inhibit dispersal as well as information on the land-/seascape at a relevant scale.	0 – < 1	Distance calculations in relation to organismic dispersal properties and landscape features.	• Expert knowledge on connectivity estimates • Simple dispersal models and dispersal kernels including reactions to landscape • Individual-based models addressing species behaviour to landscape elements and movement abilities • Lagrangian approaches considering organismic properties and land-/seascape structure
Area connectivity	Focuses on the actual exchange of organisms between suitable habitat patches. A priori information on organismic reactions to landscape at a relevant scale necessary.	~ 1	Exchange rates (of individuals) between habitats (ideally as part of population to estimate relevance for connectivity)	• Different forms of telemetry and tagging (acoustic telemetry, satellite tags, mark-recapture studies) to track individuals • Gut content analysis to investigate feeding migrations • Isotope analysis of growth structures (e.g. otoliths, statoliths) to determine ontogenetic movements
Effective connectivity	Summarizes cumulative long-term effects of organismic exchange between populations at different locations and its contribution to genetic population structure. However, does not give information population still exchange	>> 1	Genetic similarity/distance of populations	Molecular and genetic analysis of population structure and gene flow using e.g. mitochondrial DNA or microsatellite analyses.

4.1 Potential connectivity

This type of connectivity focuses on the land-/seascape structure in relation to the movement ability and movement behaviour of a species. It considers which habitats could theoretically be reached by organisms if they were placed at any location in the land- or seascape investigated. This category is closest to the former structural connectivity (Tischendorf and Fahrig 2000; Kindlmann and Burel 2008) but explicitly refers to the motility of the target organism. It incorporates knowledge on the relevant scale of organismic movement which may range from a few centimetres to many kilometres. Thus, analysing ‘potential connectivity’ requires information on how far the organism can move depending on its life stage as well as on how it would react to different land-

/seascape elements (stepping stones, barriers, currents). The timescale may not be explicitly considered but will typically range within one generation as longer time frames would require including colonisation success and population processes. Relevant metrics will refer to landscape properties (habitat patch distances, barriers effects, stepping stones, dispersal corridors) and relate them to the potential dispersal of the target organism, making the resulting values comparable between different species in the same landscape.

Studies, that investigate ‘potential connectivity’ are, for example, those using dispersal models like Lagrangian approaches (Smouse et al. 2010). In marine systems these approaches are mainly used to analyse larval drift (related to currents, larval development time) and may include behavioural properties of the larva such as selecting currents (via vertical movement) or settlement areas (based on the sensoric perception of environmental cues, Cowen and Sponaugle 2009). To investigate the (larval) exchange of corals between Hawaiian reefs, Wren et al. (2016), for instance, applied a Lagrangian particle transport model coupled with information on water currents. In the terrestrial realm, example studies of ‘potential connectivity’ are those of Jopp and Reuter (2005) who applied an individual-based model to Carabid data to analyse different dispersal kernels for long-distance dispersal and functioning of corridors and stepping stones, or Katul et al. (2005) who used 3-D dispersal kernels to describe seed dispersal of forest trees. Saura and Pascual-Hortal (2007) used graph theory to explicitly estimate the movement probability of organisms to integrate connectivity in landscape (conservation) planning. Furthermore, least-cost path including the length cost as well as potential ecological cost of connectivity are frequently applied methods to analyze potential connectivity between different landscape elements (e.g. Etherington and Holland 2013).

4.2 Area connectivity

‘Area connectivity’ addresses the actual exchange of organisms between suitable habitat patches, i.e. the realised transport or movement of individuals between different resource or habitat patches or the arrival of an individual in a new habitat patch (following (Auffret et al. 2017), which could (i) either potentially sustain a population or (ii) parts of it to facilitate reproduction, or (iii) which are regularly frequented by the target organism (feeding or reproductive migrations). Thus, ‘area connectivity’ depends on the measurement of species-specific empirical data regarding movements of individuals between different landscape elements in relation to the (physical) arrangement of these elements. Individual movement data can be collected using a variety of approaches including telemetry and tagging devices to follow individual movements (Heupel et al.

2006; Hübner et al. 2015; Hooten et al. 2017), marking individuals to re-capture them later at different locations (Marques et al. 2013) or presence-absence studies (Royle and Nichols 2003). Previously utilized habitats may be identified via isotope studies through their chemical signatures allowing for reconstruction of life-history-related movements (Rubenstein and Hobson 2004; Thorrold et al. 2007).

'Area connectivity' is thus based on the level of the individual organism with the distance a single individual can cover in its lifetime as the appropriate spatial scale and a temporal scale of one generation time. The measured exchange rates for a given landscape will depend on several factors such as population size and density whereas the importance of this exchange will be determined by the fraction of a population which is moving, the frequency of movement events and the traits influencing potential colonisation processes. Interesting examples for this category of connectivity are the studies by Turgeon et al. (2010) who recorded and analysed fish movements to retrieve behavioural responses to different habitats and their barrier function, or by Espinoza et al. (2015) who investigated the efficacy of a marine reserve for reef sharks, using acoustic telemetry.

4.3 Effective connectivity

'Effective connectivity' summarises the cumulative results of exchange processes between populations at different locations. It therefore comprises what is often termed 'population connectivity' in marine studies, and to our understanding it encompasses all processes which contribute to a population exchange on a time scale longer than that of a single generation. For large time scales, this will be identical to 'population connectivity' (Cowen et al. 2002; Saenz-Agudelo et al. 2011). To analyse and understand how barriers or other landscape variables affect gene flow between populations, different methodologies exist with the most commonly used being molecular markers such as microsatellites (Storfer et al. 2010; Manel and Holderegger 2013) or next generation sequencing technologies (Schwartz et al. 2010). These methodologies allow for parentage analysis (one generation) or analysis of genetic similarity (multiple generations, Kool et al. 2013) and can be a powerful tool, e.g. for measuring larval connections between marine populations (Galindo et al. 2006).

Connectivity studies using microsatellites are common in both the marine and the terrestrial realm, e.g. for DNA parentage analysis to estimate the connectivity of clownfish populations within a network of MPAs (Planes et al. 2009), for the analysis of population structure and connectivity of an African surgeon fish (Otwoma et al. 2017), or to investigate how biological corridors determine gene flow and population structure of bat populations (Cleary et al. 2017). Different model application can contribute to the analysis of dispersal across generations. Saura et al. (2014), for example, describe the large-scale range expansion of a forest bird species under consideration of stepping stones using a network dispersal model.

However, while having the ability to reveal connectivity patterns over long time periods on a population level, genetic data do not provide information whether populations are still connected at the time of investigation. For conservation management, it might thus become necessary to additionally consider e.g. ‘area connectivity’ to enable managers to assess the current status of a system and make informed management decision. Yet, genetic data allow for analysing large scale patterns of population structure, and a reliable estimate of (past) gene flow can provide the ultimate measurement of landscape connectivity (Baguette et al. 2013).

5 Conclusions

As an ecological concept, land-/seascape connectivity is inherently organism-centred, and it cannot exist independently of any behavioural attributes of the studied organisms. However, to become a unifying framework for terrestrial and marine ecology, the definition of connectivity has to be extended to include passive movement and transport mechanisms which constitute a large part of 'connectivity' in the marine realm and often involves early life stages. Furthermore, we encourage using connectivity solely according to its strict definition to achieve unambiguous and comparable results and make it a meaningful concept for ecological theory as well as for applied sciences like conservation planning and reserve management. To derive common indices applicable to different situations we further deem it necessary to state all relevant criteria used in any connectivity study. Here, we distinguish three main categories of connectivity: ‘potential connectivity’, ‘area connectivity', and ‘effective connectivity’, which relate to different spatio-temporal scales and integration levels. We propose to apply these categories depending on the temporal scale of the investigation (in relation to generation time), and whether it is intended to assess individual movement or population structure. Following these categories facilitates that both aspects, the landscape and the organismic response, are integrated and related to relevant spatial and temporal scales, enabling both comparison among studies and an informed decision-making for managers considering connectivity in conservation.

Text box 1 Partially overlapping and/or conflicting definitions of ‘connectivity’

- **Ecological connectivity:** Interactions among ecosystems by movement of animals, and by exchange of nutrients and organic matter or as ‘ecosystem connectivity’ with regard to ontogenetic or larvae dispersal (Mumby and Hastings 2008).
- **Functional connectivity**: The degree to which the landscape facilitates or impedes movement among patches (Taylor et al. 1993) considering the organisms’ behavioural responses to individual landscape elements (Tischendorf and Fahrig 2000; Taylor et al. 2006), the spatial configuration of the entire landscape (Kindlmann and Burel 2008), and the landscape matrix (Baguette et al. 2013). It additionally may involve benefits associated with habitat features (Turgeon et al. 2010) while ‘plant functional connectivity’ relates to the effective dispersal of propagules or pollen among habitat patches in a landscape (Auffret et al. 2017) based on the successful establishment of individuals.
- **Genetic or evolutionary connectivity:** The exchange of organisms and genes (Grober-Dunsmore and Keller 2008) or the degree to which gene flow affects evolutionary processes within populations (Saenz-Agudelo et al. 2011) or the amount of gene flow occurring among populations over a timescale of several generations determining the extend of genetic differences (Sale et al. 2010).
- **Habitat connectivity:** Focuses on the habitat structure in landscapes and describes the extent of the exchange of individuals between habitat types (Dorenbosch et al. 2005) or ‘connectedness’ of habitat patches for a given taxon (Lindenmayer et al. 2008) or as ‘(biological) inter-habitat connectivity’ related to the migration of fauna between habitats, at different stages of their life cycle and/or following diel and tidal cycles (Unsworth et al. 2008).
- **(Landscape) connectivity:** This often refers to the original definition by (Taylor et al. 1993) specified as ‘the degree to which the landscape facilitates or impedes movement among resource patches’; partially supplemented with more elements referring to genes, species or other ecological flows among habitats (Blazquez-Cabrera et al. 2014), highlighting specific processes such as spread of plant diseases amongst host patches (Papaïx et al. 2014) or the extent to which populations in different parts of a species’ range are linked by exchange of larvae, recruits, juveniles, or adults ((Palumbi 2003) in the context of marine reserves). It can encapsulate the combined effects of landscape structure and the species’ use (Tischendorf and

Fahrig 2000; Cowen et al. 2002) or the flux of items between location types including nutrients, sediments, pollutants and individual dispersing organisms (Sale et al. 2010)**.**

- **Larval connectivity**: Linkages of populations via larval dispersal (Botsford et al. 2009) or between a reproductive source and recruitment of larvae (Steneck et al. 2009). Often based on ‘oceanographic connectivity’, which encompasses the general flow of materials (Grober-Dunsmore and Keller 2008).

- **Population connectivity:** Mostly used in the marine context and denoting the exchange of individuals among geographically separated sub-populations that comprise a metapopulation (Cowen et al. 2002) or the exchange between local groups (Grober-Dunsmore and Keller 2008) and with evolutionary (genetic) consequences ((Sale et al. 2010) as ‘demographic connectivity’).

- **Structural connectivity**: Based entirely on landscape structure with no direct link to any behavioural attributes of organisms (Kindlmann and Burel 2008), the ‘physical relationships’ between habitat patches, i.e. physical distances (Unsworth et al. 2008; Baguette et al. 2013).

Text box 2 Common (overarching) classifications of (landscape) connectivity

Initially, **(landscape) connectivity** was formulated as a (single) species-centred approach and defined as an emergent property of species-landscape interaction (Taylor et al. 1993, 2006) without being divided into subcategories. Over time, however, different classifications were proposed in the literature to make the approach more applicable for a wide range of situations):

- **Structural vs functional connectivity:** Here, structural connectivity solely considers the physical relationship (e.g. distance) among habitat patches independent of organismal attributes (contiguity of habitat), while functional connectivity encompasses the organismic response to individual landscape elements as intended by the original concept, (e.g. Tischendorf and Fahrig 2000; Taylor et al. 2006; Kindlmann and Burel 2008; Kadoya 2009).

- **Structural vs potential vs actual connectivity**: Structural connectivity (as above) relates to the physical structure of the environment, whereas potential connectivity considers indirect information on movement/dispersal of the target species) and actual connectivity quantifies the movement of individuals through the land-/seascape (Calabrese and Fagan 2004; Grober-Dunsmore et al. 2009).

- **Habitat vs landscape vs ecological connectivity**: (Lindenmayer and Fischer 2007) made a distinction between a) habitat connectivity as the connectedness of habitat patches for a given taxon, b) landscape connectivity as the physical connectedness of patches of a particular land cover type as perceived by humans (because landscape is seen as a human concept), and c) ecological connectivity as the connectedness of ecological processes at multiple spatial scales.
- **Biological vs geo-physical connectivity**: Linkage of different realms allowing for movement of species vs for transfer of energy and matter (Beger et al. 2010). In the context of conservation and exchange processes between the terrestrial, marine, and freshwater realms these were categorised as narrow (e.g. riparian strips), broad (e.g. estuaries) interfaces or constraint (limited by corridors) or diffuse relating to e.g. feeding or reproductive migrations.
- **Genetic vs demographic vs oceanographic connectivity**: Following (Grober-Dunsmore and Keller 2008) connectivity encompasses the exchange of materials and can be subdivided into genetic connectivity as the exchange of organisms and genes, demographic connectivity as the exchange of individuals among local groups, and oceanographic connectivity as the flow of materials and circulation patterns and variability that underpin all these exchanges.

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5 Synopsis

Nowadays it is common knowledge that coral reef systems are precious and unique ecosystems characterized by a spectacular biodiversity. They also provide many different ecosystem services including protection against waves and coastal erosion, tourism, and fisheries which provide food and livelihoods for millions of people (see (Harvey et al. 2018) for review). At the same time coral reefs have proven to be particularly vulnerable to the adverse effects attributed to climate change like increasing ocean warming and acidification (e.g. (Bellwood et al. 2004; Hughes et al. 2007; Harvey et al. 2018)). They are further endangered by anthropogenic activities such as coastal development, pollution, and overexploitation leading to estimates that the world's coral reefs will not survive the century and by 2050 more than 90 % may have died (Harvey et al. 2018; Hoegh-Guldberg et al. 2018).

To maximize coral reef resilience under climate change and counteract its ongoing degradation, marine spatial planning and the implementation of marine protected areas (MPAs) are increasingly gaining importance (Grober-Dunsmore et al. 2007; Sale and Kritzer 2008; Botsford et al. 2009; Harvey et al. 2018). In this context reef fish and herbivorous species in particular, are often a target group for conservation because of their economic and ecological relevance (Davis et al. 2017b). Moreover, stocks of herbivore fishes are already critically depleted by anthropogenic activities which may result in major disruptions of reef ecosystem processes in the future (Bellwood et al. 2004).

Diurnal herbivores like parrotfishes generally constitute a large part of tropical reef fish populations regarding abundance as well as biomass and are thus important for biomass turnover and energy transfer between trophic levels (Nagelkerken et al. 2000, 2008; Clark et al. 2009; Hitt et al. 2011). Furthermore, they are important bioeroders and producers of sand in coral reef systems (Bellwood 1995) and keep algal turf and macroalgae at a low cropped state by scrapping them off rock and dead coral. Herbivorous fish can thereby improve coral growth and reef resilience and are hence considered to play a key role in controlling coral-algae phase shifts (Lokrantz et al. 2008; Mumby 2009; Olds et al. 2012a).

Parrotfishes like many coral reef fishes undertake diel migrations to utilize resources from different habitats (e.g. (Meyer et al. 2010)). These mostly take place at small scales (Helfman 1993; Green et al. 2015) and have the potential to influence ecological interactions like predation (Lima and Dill 1990) or nutrient transfer between different habitats (Nagelkerken et al. 2000, 2008; Clark et al. 2009; Hitt et al. 2011). To provide effective protection it is therefore critical to consider diel movement patterns of the target species and to enclose habitats that are consistently used both during day and night by individual fish when designing an MPA (Chapman and Kramer 1999; Eristhee and Oxenford 2001; Beets et al. 2003; Meyer et al. 2007; Afonso et al. 2008; Grüss et al. 2011; Semeniuk et al. 2011; Davis et al. 2017b).

Currently, however, only about one third of MPAs meet their management goals due to significant gaps in the ecological science of marine reserves (Sale et al. 2005), particularly in terms of how habitats are ecologically connected by animal movements. Thus, it remains essential to quantify space use patterns of mobile (juvenile and adult) fishes and to understand how they may be affected by changing environmental conditions.

Animal movement behaviour is notoriously complex due to the potential involvement of many different factors and the individual ability to evaluate rewards and risks, weigh this information and process it to a movement decision (Manassa et al. 2013; DeAngelis and Diaz 2019). As numerous studies have shown space utilization patterns of reef fish, for instance, are driven by the underlying seascape and its three-dimensional structure and that greater complexity correlates with higher fish abundances and species richness (Pratchett et al. 2008). The influencing mechanism is attributed to the fact that an increased structural complexity can moderate competitive interactions and predation intensity, e.g. by providing more or less suitable refuges (Lima and Dill 1990; Christensen and Persson 1993; Jones and Syms 1998; Overholtzer-McLeod 2006; Pratchett et al. 2008; McCormick and Lönnstedt 2013; Catano et al. 2016; Roff et al. 2019).

Foraging patterns of prey organisms like herbivorous fishes are thus shaped and constrained by the habitat configuration and the perceived 'landscape of fear' (Laundré et al. 2010; Catano et al. 2016; Madin et al. 2019), which is a species-specific landscape characteristic. Nowadays unique organism-habitat relationships have been observed across a wide range of taxa and spatial scales (Chittaro 2004; He et al. 2019) and are often discussed in the context of 'landscape connectivity' (Taylor et al. 1993, 2006). In heterogenous environments fish populations are therefore not evenly distributed across habitats (He et al. 2019), which – depending on the ecological role of the species – can have important impacts on community structure and ecosystem function.

Another group of potential key determinants in shaping the spatial distribution of fishes and which are often neglected in empirical studies (see Bijoux et al. (2013) for review) are natural cycles like lunar, diel or tidal phases. These cycles induce different behavioural patterns in the fishes' diel activities, e.g. foraging movements (Hobson 1973; Ogden and Quinn 1984; Robblee and Zieman 1984; Helfman 1986), causing predictable fluctuations over short timescales in fish communities and their composition. To correctly evaluate how environmental change affects population distributions across space and successfully design conservation and management strategies it thus seems essential to be able to distinguish the different causes of their behavioural variation.

5.1 Major findings and advancements for coral reef science

Motivated by this need to better understand drivers behind movement patterns of herbivorous reef fishes and disentangle which are critical properties of their environment we dare a modelling attempt of small-scale fish movement behaviour incorporating dynamic decision making by using potential field methods. We thereby provide an application that incorporates a new way of representing how real individuals may decide on actions as well as current knowledge on the ecology of parrotfishes.

Our own assessment of the natural variation in reef fish assemblages caused by the lunar, tidal and/or diel cycle at Chumbe Island, Tanzania (Chapter 2)

(i) confirmed and emphasized the importance of incorporating natural cycles when studying fish movement behaviour in coral reef systems to correctly evaluate changes in behaviour and the relevance of habitats,

(ii) identified *C. sordidus* as a mobile link between different habitat types over short time periods,

(iii) indicating this parrotfish species as a suitable model organism for the study of habitat-related movement behaviour.

To realistically represent individual fishes and their behavioural mechanisms in a model system it is however further compulsory to have detailed information on a species' life history and related parameters such as growth rates or energy consumption (Bartholomew et al. 2008; Grüss et al. 2011). Fortunately, C. sordidus is a ubiquitous parrotfish species and both of ecological importance and well-described in the literature making the relevant information and comprehensive data readily available.

As one of the main purposes of our modelling study is to simulate realistic spatial distributions, that emerge from individual movement behaviour we have chosen to use an individual-based model as it can readily be linked with observations (Breckling 2002; DeAngelis and Mooij 2003; Reuter et al. 2005; Breckling et al. 2006; Kubicek et al. 2015). This approach also allows for the simulation of a large number of individuals over long time periods in realistic environments (DeAngelis and Diaz 2019), which we deem essential to investigate how the increasing change of environmental conditions and habitat discontinuity may affect fish mobility and population persistence. Moreover, it enables us to link the energetic state of each individual with its movement decision-making process (Nathan et al. 2008; DeAngelis and Diaz 2019) and thereby explicitly integrates one of the (arguably) most neglected factors in conservation management: a more mechanistic understanding of the energetic requirements of an organism and how they influence population dynamics (Tomlinson et al. 2014). The actual decision-making process is further embedded in a system of potential fields representing food availability as an attractive force and/or predation risk as a repellent force to integrate the motivational basis for a fish to move. To our knowledge, our IBM is the first ecological model, that makes use of potential field methods in a new and innovative approach to represent movement behaviour in animals.

The results of our simulation experiments (Chapter 3) suggest that

(i) individual movement decisions over small spatio-temporal scales have the potential to affect individual energy budgets with reproduction being the most susceptible key life history trait,

(ii) these individual decisions further shape the distribution of the population across space, which becomes increasingly irregular with a growing fragmentation of the habitat structure,

(iii) the spatial configuration of the underlying seascape thus influences the spatial exploitation of microhabitats by a dilution of the foraging effort in some reef patches which at the same time leads to a concentration in others.

(iv) by guiding individual movement decisions, the physical features of the environment may also impact encounter rates between individuals and in the long-term the overall social structure of a population.

Our findings hence agree with the notion that animals move through a landscape driven by trade-offs between risk taking and the need to gain energy and make movements across or around physiologically challenging environmental barriers (see e.g. (Tomlinson et al. 2014). Which habitat features or configurations act as barriers or corridors, however, may largely be species-specific as different species are likely to vary in their life history characteristics, foraging strategies and/or habitat requirements

(Meyer et al. 2010). To save as many species as possible from extinction the preservation of enough habitat that is accessible for the organism in question, may play a particular role. In this context it appears valuable to improve our general understanding of how land- or seascapes are ecologically connected, a landscape property also referred to as 'landscape connectivity' and often mentioned as a key component for the overall effectiveness of MPAs. However, even though it is frequently used this concept remains ambiguous both in its definition and its usage. To make it a more quantifiable and comparable framework we suggest (Chapter 4) that the concept has to be

(i) extended to include passive movement and transport mechanisms and thereby allow for an application to a broad range of organisms and life stages in terrestrial as well as marine ecosystems

(ii) used solely according to its strict and organism-centred definition, and

(iii) divided into three main categories ('potential connectivity', 'area connectivity', 'effective connectivity') referring to different spatio-temporal scales and integration levels.

5.2 Future developments and outlook

Due to its structure and modular composition our model offers several interesting perspectives for further developments. We believe the following to be of primary interest:

- **Density dependence**. Field studies of parrotfish populations (Gust et al. 2002; Nash et al. 2012; Tootell and Steele 2016; Davis et al. 2017a) indicate that short-term mobility, individual growth patterns as well as fish biomass and energy reserves are density dependent and that reduced resource levels and/or greater scarid densities lead to a reduced growth. Although our model indirectly accounts for density-dependent processes via changing levels of food availability, it seems desirable to extend the abilities of a model fish to be able to explicitly evaluate densities of conspecifics or competitors when moving across habitat patches.
- **Extension of the movement decision-making system (potential fields)**. Individual differences in size, sex, body condition, and hunger levels have been hypothesized to influence the individual perception of risk (Milinski 1993; Manassa et al. 2013). Hunger levels, for instance, can change the compromise between feeding and antipredator behaviour and a starving fish might take greater risks (Lima and Dill 1990; Hart 1993; Milinski 1993; Bélisle 2005). By implementing a weighing factor for each external factor considered in an individual movement decision our model explicitly allows for the reflection of these trade-offs: Given sufficient computational capacity an individual fish can be enabled to dynamically adjusting the weighing factor for predation risk depending on its energetic state rather than using a static value.
- **Learning and memory**. Studies of prey organisms have demonstrated that prey animals have the ability to learn and can e.g. respond to differing levels of predation risk by adjusting their behaviour even at a loss of feeding opportunities (Laundré et al. 2010). Learning, which is a product of individual experience involving memory of past events (DeAngelis and Mooij 2005), may alter e.g. feeding strategies by learning good food items and good how-to feed, assessing changing quality of food patches or remembering topographic features to be able to return to suitable food patches. The integration of learning and memory into our model may potentially

be facilitated by the recent advancements made in the field of neural networks and machine learning and seems an exciting extension of our model.

Also, the inclusion of other abiotic components such as depth or tidal cycles, which can exert strong influences on the movement behaviour of mobile fishes (Helfman 1993), may be of interest depending on the research question and the system under study.

The possibilities to extend our model are hence manifold and we hope that by being adaptable to a wide range of reef fish species (via the life-history related parameters) and habitat configurations (via custom habitat maps) our model will be useful to analyse and evaluate various local settings and scenarios. By publishing it free and open source our application will further be available for everyone to use. We also believe that the integration of potential field methods into IBMs is a promising strategy to represent the complexity of dynamic decision-making of animals in applied models. Its great potential lies in its straight-forward adjustment to include different behaviours including more complex ones like topographic memory, which however constitutes a new field of application.

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7 Publications

7.1 Peer-reviewed publications

Kruse M, Schneekloth F, Meyer C, Reuter H (in preparation) Best places to go in a heterogenous seascape: How potential field methods can help to simulate trade-offs in fish movement behaviour.

Kruse M, Reuter H (in submission) Landscape connectivity revisited – A unifying conceptual framework for the marine and terrestrial realm. Landscape Ecology.

Kruse M, Taylor M, Muhando CA, Reuter H (2016). Lunar, diel, and tidal changes in fish assemblages in an East African marine reserve. Regional Studies in Marine Science 3: 49-57.

Reuter H, **Kruse M**, Rovellini A, Breckling B (2016). Evolutionary trends in fish schools in heterogeneous environments. Ecological Modelling 326: 23-35.

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7.2 Presentations

Kruse M, Reuter H. How do fragmented seascapes influence individual movement behaviour of reef fishes? Talk at the 8th European Conference on Ecological Modelling, October 27-30, 2014, Marrakesh, Morocco.

Kruse M, Reuter H. Small-scale movement patterns of fishes in tropical coastal habitats. Poster at the Evaluation Committee Meeting, October 04-05, 2012, Leibniz-Centre for Marine Tropical Research, Bremen, Germany.

Kruse M, Reuter H Small-scale movement patterns of fishes in tropical coastal habitats. Poster at the Advisory Board Meeting, June 2012, Leibniz-Centre for Marine Tropical Research, Bremen, Germany.

Kruse M, Reuter H. Inter-habitat connectivity for fishes in tropical coastal habitats – an individual-based model approach. Poster at the 42th Annual Meeting of the Ecological Society of Germany, September 10-14, 2012, Lüneburg, Germany.

Kruse M. Inter-habitat connectivity for fishes in tropical coastal habitats – an individual-based model (IBM) approach. Talk at the PhD colloquium, July 11, 2012, Leibniz-Centre for Marine Tropical Research, Bremen, Germany.

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9 Eidesstattliche Erklärung

(Gem. § 6(5) Nr. 1-3 PromO)

Hiermit versichere ich, dass ich die vorliegende Arbeit:

1. ohne unerlaubte Hilfe angefertigt habe,
2. keine anderen, als die von mir im Text angegebenen Quellen und Hilfsmittel benutzt habe,
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Bremen, 19. December 2019

Maren Kruse

Declaration on the contribution of the candidate to a multi-author article/manuscript which is included as a chapter in the submitted doctoral thesis

Chapter: 2

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design: ca. 70 %

Experimental work and/or acquisition of (experimental) data: ca. 50 %

Data analysis and interpretation: ca. 80 %

Preparation of Figures and Tables: ca. 90 %

Drafting of the manuscript: ca. 90 %

Chapter: 3 Best places to go

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design: ca. 90 %

Experimental work and/or acquisition of (experimental) data: ca. 80 %

Data analysis and interpretation: ca. 90 %

Preparation of Figures and Tables: ca. 90 %

Drafting of the manuscript: ca. 90 %

Chapter: 4 Landscape Connectivity

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design: – ~~ca. __%~~

Experimental work and/or acquisition of (experimental) data: – ~~ca. __%~~

Data analysis and interpretation: ca. 70 %

Preparation of Figures and Tables: ca. 70 %

Drafting of the manuscript: ca. 70 %

Date: 25.10.19

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