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**A dynamic model of parrotfish (family: *Scaridae*) populations for the management of herbivory on Caribbean coral reefs**

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*Sparisoma viride*

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## Résumé

Les herbivores ont un rôle central pour la santé et la résilience des récifs coralliens. Aujourd'hui, le poisson perroquet est l'herbivore le plus important des Caraïbes et celui qui contribue le plus à maintenir des niveaux d'herbivorie fonctionnels sur les récifs coralliens en limitant la croissance et la colonisation des algues compétitrices des coraux (Hughes *et al.*, 2007). *Sparisoma viride* est l'une des espèces de poisson perroquet contribuant le plus au maintien de cette herbivorie fonctionnelle sur les récifs coralliens des Caraïbes (Mumby, 2006). Ces dernières années, la santé des récifs coralliens des Caraïbes s'est sévèrement dégradée suite à une combinaison de perturbations d'origines naturelles et anthropiques, entraînant un changement de régime sur de nombreux récifs autrefois dominés par du corail vivant mais aujourd'hui dominés par les algues (Hughes 1994; Hughes *et al.*, 2003). *S. viride* est la plus pêchée des espèces de poissons perroquets dans les Caraïbes (Mumby *et al.*, 2006). En perspective des changements globaux et de l'augmentation des perturbations, le besoin est urgent de développer des outils de gestion à échelles locales pour la protection des poissons perroquet qui permettra le maintien de niveaux d'herbivorie fonctionnels. Pour implémenter des mesures de gestion efficaces, il est nécessaire d'avoir des connaissances sur la dynamique des poissons perroquets. Cependant, ces connaissances sont insuffisantes. La création d'un modèle de dynamique des populations de *S. viride* peut permettre d'améliorer ces connaissances en vue d'une mise en place de mesures de gestion telles que des quotas de pêche. Nous avons développé un modèle de dynamique des populations de *S. viride* structuré en tailles et catégories d'habitat. Ce modèle simule l'abondance de *S. viride* en fonction de la mortalité naturelle, de la croissance individuelle et du recrutement. Les catégories d'habitat des plus grands poissons sont basées sur la densité dépendance dans l'habitat profond du récif, inférée par un nombre limité de mâles matures dans cet habitat profond lié à la territorialité. Le modèle a été calibré avec une série temporelle d'abondance de *S. viride* collectée à Bonaire (Antilles Hollandaises). La population de *S. viride* de Bonaire possède une pression de pêche très faible et considérée comme étant à l'équilibre écologique. Le pas de temps choisi pour le modèle est de 3 mois pour concorder avec la fréquence de collecte des données à Bonaire. Avec ce modèle calibré, une pression de pêche a été simulée pour étudier la capacité du modèle à reproduire le rétablissement de la population de poissons perroquet observé aux Bermudes suite à la mise en place d'un moratoire sur l'utilisation des pièges à poissons.

Trois phases sont distinguables chez *S. viride* : la phase juvénile (J), la phase initiale (PI), individus femelles, et la phase terminale (PT), individus mâles. Les poissons perroquets sont des hermaphrodites et les femelles (PI) peuvent changer de sexe au cours de leur vie. La population de *S. viride* de l'île de Bonaire est organisée socialement et spatialement. Une zone de territoires est distinguable dans l'habitat profond du récif (>4m). Chaque territoire est mené par un mâle dominant (PT) et regroupe un harem de femelles. Dans l'habitat peu profond (<4m), les individus sont organisés sans structure particulière et constituent un simple groupe d'individus (J+PI+PT). Des individus mâles peuvent migrer de l'habitat peu profond vers un territoire pour prendre la place d'un mâle dominant lorsque celui-ci meurt ou émigre. Les femelles de l'habitat peu profond peuvent migrer également vers l'habitat profond pour devenir part du harem d'un TP mâle.

Nous disposons de plusieurs jeux de données pour cette étude. Nous avons calibré le modèle avec la série temporelle d'abondance de *S. viride* collectée à Bonaire par van Rooij *et al.* (1996b) entre 1989 et 1992. Ces données ont été récoltées par comptage visuels et organisées par phases et taille des individus. Ces données ont permis de calibrer le modèle et d'estimer la valeur des paramètres à l'équilibre. Pour l'implémentation de la mortalité naturelle dans le modèle, nous avons testé 3 fonctions de mortalité: une mortalité constante selon la taille, une mortalité linéairement décroissante avec la taille et une mortalité exponentiellement décroissante avec la taille. Ces deux dernières fonctions supportent

l'hypothèse que les poissons de plus petite taille sont plus vulnérables à la prédation et donc possèdent une mortalité supérieure à celle des poissons de plus grande taille. L'étape d'optimisation avec le solveur *Global Search* de Matlab a été conduite en choisissant de minimiser la somme des carrés des écarts entre les densités de classes de tailles observées à Bonaire et celles estimées par le modèle. L'optimisation n'a pas permis d'obtenir un meilleur fit aux données de Bonaire avec une fonction de mortalité dépendant de la taille. C'est donc la mortalité constante par classe de taille qui a été retenue pour étudier le modèle à l'équilibre. La croissance a été implémentée par une matrice de transition car le modèle est structuré en taille. Les entrées de cette matrice ont en particulier été calculées grâce aux données de correspondance taille-âge d'individus de *S. viride* communiquées par le Prof. John Howard Choat (School of Marine Biology and Aquaculture, James Cook University, Townsville, Australie) qui nous ont permis d'estimer les paramètres  $L_{inf}$  et  $K$  de von Bertalanffy. Ces données ont été complétées par des données obtenues dans la base de données Fishbase. Le recrutement a été implémenté comme une addition constante de poissons de 5cm à chaque pas de temps. La valeur de recrutement estimée à l'étape d'optimisation a montré une valeur proche des valeurs de densités de poissons de même taille dans des sites du Belize et des Bahamas. Enfin, la densité dépendance a été implémentée pour recréer la limitation du nombre de territoires de l'habitat profond à Bonaire. Les migrations de poissons de l'habitat peu profond vers l'habitat profond ont été simulées par une simple limitation de la transition en fonction de la capacité limite de cet habitat profond.

Après un certain nombre de pas de temps, le modèle se stabilise à un état d'équilibre : les densités des classes de taille ne varient plus au cours du temps. La distribution de taille estimée par le modèle à l'équilibre a montré de fortes similitudes avec celle observée à Bonaire bien que les densités par classes de tailles soient globalement sous estimées. Le modèle calibré et à l'équilibre a permis de tester différentes hypothèses. (1) Les conditions initiales n'influent pas sur l'état d'équilibre. (2) L'utilisation d'un pas de temps plus important (12 mois) engendre un déplacement vers les classes de tailles les plus grandes car les plus petits poissons du modèle grandissent directement vers des classes de tailles plus grandes. (3) La densité des poissons de l'habitat profond n'atteint pas sa capacité limite avec les valeurs de paramètres du modèle calibré, si la mortalité diminue, cette capacité limite peut être atteinte.

Enfin, des données des Bermudes montrant le recouvrement de la population de *S. viride* nous ont permis de simuler une pression de pêche sur la population de *S. viride* à l'équilibre pour exploiter la capacité du modèle à reproduire ce recouvrement observé aux Bermudes. Le recouvrement estimé par le modèle est 3 fois plus lent que celui des Bermudes. Le très rapide recouvrement de la population de *S. viride* aux Bermudes a pour première hypothèse un faible taux de prédateurs. En effet, aux Bermudes seuls les pièges à poissons ont été interdits alors que la pêche à la ligne ciblant en grande majorité les gros poissons prédateurs des poissons perroquets, était encore autorisée. Résulte de ceci, un faible taux de mortalité des poissons perroquet par l'absence de pièges à poissons d'une part, et le faible taux de prédateurs d'autre part. Cependant, d'autres hypothèses telles que des différences géographiques et écologiques entre le nord (Bermudes) et le sud de la Mer des Caraïbes (Bonaire) pourraient expliquer ces différences de vitesses de rétablissement.

L'originalité de ce modèle réside dans sa structure en taille mais également dans sa flexibilité. En effet, cette étude a pour but d'être généralisée à d'autres sites de Caraïbes et d'autres espèces de poissons perroquet. Ainsi, les paramètres du modèle peuvent être aisément changés et remplacés pour d'autres études et seule la matrice de croissance aurait besoin d'être recalculée lors de l'utilisation d'un autre pas de temps ou d'autres paramètres de croissance. Cette étude bien que préliminaire a montré une reproduction satisfaisante de la distribution de taille observée à Bonaire et les valeurs des paramètres estimés concordent avec les données de la littérature. Une étude plus approfondie,

notamment pour l'implémentation de la mortalité et du recrutement seraient nécessaire pour généraliser ce modèle à d'autres espèces de poissons perroquets.

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## Introduction

Coral reefs are well known for being very important marine sources of biodiversity and for supplying many nations with goods and services such as fishing and tourism activities (Hughes, 1994; Hughes *et al.*, 2003). However, in the past decades, the health of coral reefs has been severely degraded, due to a combination of natural events (hurricanes, coral bleaching) and anthropogenic disturbance such as pollution and overfishing (Hughes *et al.*, 2003; Hoegh-Guldberg *et al.*, 2007). It is estimated that nowadays 30% of coral reefs in the world are heavily damaged (Hughes *et al.*, 2003). Coral reefs in the Caribbean have been severely impacted and the situation is critical (Mumby *et al.*, 2006). Because of the multiplying source of disturbances, in many places the reef community structure has shifted from a coral-dominated to a macroalgal-dominated state (Hughes 1994; Hughes *et al.* 2003). In regards of climate change and ocean acidification, disturbances are expected to rise and worsen the health of Caribbean coral reefs. There is an urgent need to develop local strategies for managing coral reef resilience and biodiversity in the Caribbean.

Herbivory is one of the most important ecological functions driving the resilience of Caribbean reefs. Indeed, herbivores organisms (mostly sea urchins and fish) graze algae growing on the dead coral substrate (Burkpile and Hey, 2008; Mumby and Steneck, 2008) thus liberating space for coral recruits and growth. Without this grazing activity by herbivores, coral life cycle is negatively affected by overgrowing algae and the maintenance a coral-dominated state is impaired (Hughes *et al.*, 2007; Mumby and Steneck, 2008). The sea urchin *Diadema antillarum* was the main grazer in the Caribbean in the past but between 1983 and 1984, due to a disease, it experienced high death levels (Mumby, 2006; Carpenter, 1990; Lessios, 1988) depriving the Caribbean reefs from its main algal grazer. Since then, *Scaridae* (parrotfish) became the most important grazer in the Caribbean (Mumby, 2006), representing over 80% of the biomass of herbivorous fishes in the Caribbean (Mumby, 2009).

In the past decades, the number of top-carnivore species, such as snappers and groupers, has dropped to very low levels (Mumby *et al.*, 2007). As a result, parrotfish have become a target species with interesting commercial value for many countries of the Caribbean such as Saba, Puerto Rico, St Lucia, Jamaica and Dominica (Hawkins and Roberts, 2003). However, little is documented on parrotfish landings every year in the Caribbean and no possible stock assessment has been conducted so far (FAO, 2011). The abundance and the biomass of parrotfish are clearly higher in the areas where the fishing pressure is the lowest (Bonaire) compared to high fishing pressure areas (Dominica, Jamaica) (Hawkins and Roberts, 2003; Tuya *et al.*, 2007). In highly fished areas, the size-distribution of exploited parrotfish populations is affected with a decrease of the largest individuals and a global decrease of the average size (Hawkins and Roberts, 2003). Some parrotfish species are hermaphrodite and can change sex during their life, and fishing seems to affect sex-changing: females tend to transform into males at smaller sizes in heavily fished islands (Hawkins and Roberts, 2003).

In many areas parrotfish populations have been depleted due to intense trap fishing (Hawkins and Roberts, 2004). Traps are well known to have very high depletory effects on fish populations (Wolff *et al.*, 1999; Hawkins and Roberts, 2007) but traps are unfortunately one of the most used fishing gear on Caribbean coral reefs (Gobert, 1988). As a consequence, fishing affects the levels of fish herbivory, thus compromising the ability of corals to recover from disturbances (Mumby *et al.*, 2007; Mumby and Steneck, 2008). Therefore, the maintenance of serviceable levels of fish herbivory is now a major concern for the conservation of Caribbean coral reefs. Restoring and protecting parrotfish populations are expected to moderate the future effects of bleaching events rising in frequency and severity with climate change (Mumby *et al.*, 2006; Edwards *et al.*, 2011).

Face to global warming and ocean acidification, it is necessary to protect parrotfish species by acting locally with management actions. Protecting parrotfish is sought to delay the negative effects of climate change by maintaining a serviceable level of herbivory for coral reef resilience (Mumby *et al.*, 2013). Yet, implementing efficient management action requires sufficient knowledge on parrotfish population dynamics. But while the importance of parrotfish ecological role is well appreciated, little is known on parrotfish natural mortality, fishing mortality, biomass production, and responses to various fishing pressures. The knowledge on dynamics of the parrotfish is essential to understand the ability to recover from depleted stocks.

*Sparisoma viride* was chosen for this study for 3 reasons: (1) it is the fish contributing the most to grazing on many Caribbean reefs (Mumby, 2006); (2) *S. viride* is the most known parrotfish species with available data on it; (3) it is the parrotfish species the most targeted by fishing (Mumby *et al.*, 2006). *S. viride* is found on the tropical part of Western Atlantic, from Florida to Brazil, including the Gulf of Mexico. The model created in this study is a discrete-time model structured by size and habitat categories (shallow/deep reefs) with the implementation of four ecological processes: natural mortality, growth, recruitment, density dependence in habitat occupation. The model was first calibrated to a time series of fish abundance collected at Bonaire Island, a marine reserve where parrotfish populations are expected to be at equilibrium. In a second step, fishing pressure was added to explore the ability of the model to reproduce the recovery of the parrotfish population. This recovery was compared to the one observed in Bermuda where a fishing ban was implemented.

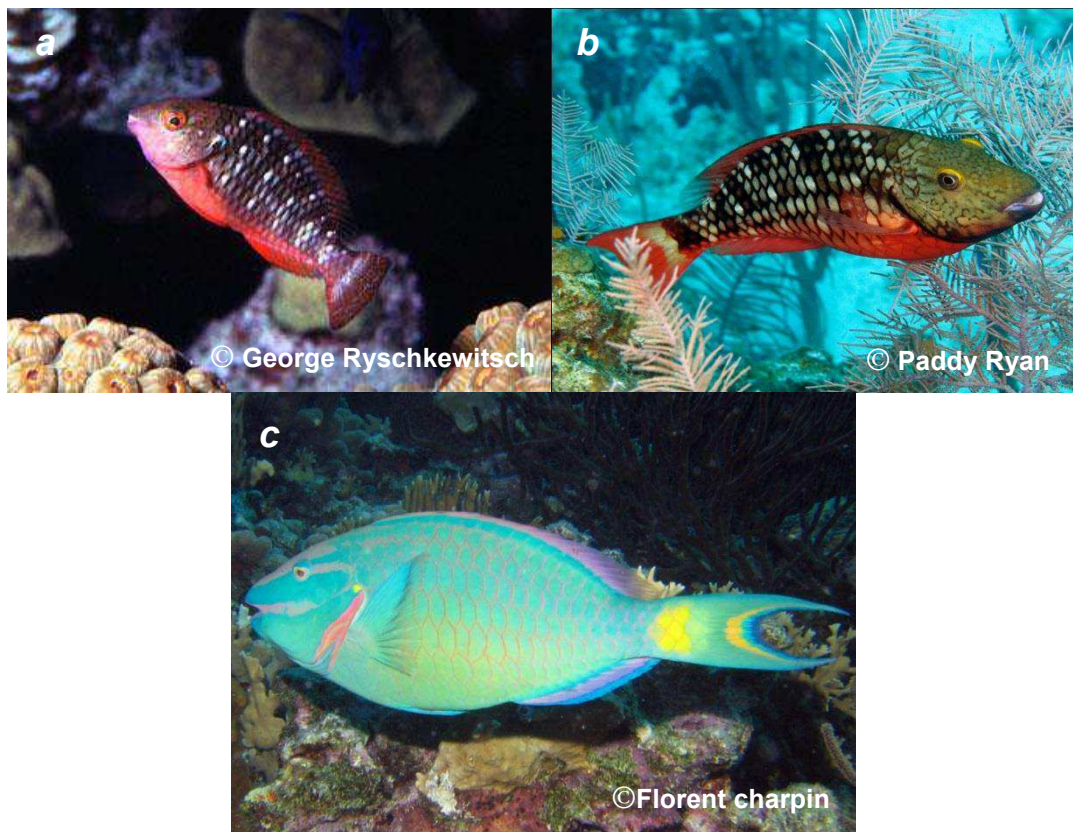
## 1. Material and Methods

### 1.1. Animal study: *Sparisoma viride* (*S. viride*) biology

Parrotfish (family *Scaridae*, order Perciformes) were named after physical similarities with parrot birds. Indeed, the assembling of their teeth creates a structure very similar to a parrot's beak (van Rooij, 1996b) and their feeding mode called "pharyngeal mill". Parrotfish is a protogynous hermaphrodite; some individuals during their life will experiment sex-changing from female to male to improve their lifetime or increase their reproductive success (Warner, 1987). For parrotfish, sex-changing occurs only one way from female to male, and can be followed by a change in body colour (van Rooij *et al.*, 1996b). Sex-changing is a process requiring a lot of energy but increases the reproductive capacity. Therefore, this is a trade-off between high energetic costs and the number of off-springs potentially produced in the future (Warner, 1987).

Three different phases can be distinguished in the life cycle of the parrotfish *Sparisoma viride* (van Rooij *et al.*, 1996b): the juvenile phase (J), the initial phase (IP) and the terminal phase (TP). Juveniles set up on the reef at a length of about 1cm, after a pelagic larval stage (van Rooij and Videler, 1997). After growth and having acquired sexual maturity they become an IP fish. The colour patterns of IP (**Figure 1b**) fish are close to those of juvenile fish (**Figure 1a**) (van Rooij *et al.*, 1996b), with a mottled brown colour, white scales and a white vertical band on their tail. TPs colour pattern is significantly different: they are characterized by a blue emerald body and yellow spots on the opercula and at the base of the tail (**Figure 1c**). IP females can either remain a female for the rest of their life or change sex and colours to become a TP male. However, IP fish can be either male or female (Robertson and Warner 1978; Cardwell 1989). In Bonaire, over 90% of the IP fish are females (van Rooij *et al.*, 1996). Therefore, they were restricted to females in this study. TP fish are always mature males

The particularity of parrotfish population in Bonaire is the spatial and social structure in two different habitats (van Rooij *et al.*, 1996b): a shallow one (<4m) and a deep one (>4m). The deep habitat is divided into social and spatial territories. Each territory is lead by a dominating male the Territorial Terminal Phase male (TTP) and group a harem of 10 to 14 female Territorial Initial Phase (TIP). The number of territories in Bonaire was estimated to 17 with a size range of 240 to 820m<sup>2</sup>. TTPs seemed to show a defending behaviour towards conspecifics with males that do not belong to their territories. This support the assumption that territories are set up mating purposes (van Rooij *et al.*, 1996a). Territorial fish (TTP+TIP) represent less than 20% of the whole population but control up to 77% of the reef (van Rooij *et al.*, 1996b). Every TTP reproduces with its harem every day but also occasionally with non-territorial/group females from the shallow habitat that invade the deep habitat. The shallow habitat has no particular social structure and it groups non-territorial fish, briefly called group fish or shallow fish. This shallow habitat groups females, Group Initial Phase (GIP) and males, Group Terminal Phase (GTP). The Shallow habitat can group up to 14 males and 28 females (van Rooij *et al.*, 1996b). It was observed that GTPs hardly ever reproduce. Their reproducing rate was considered null. The territorial fish are globally bigger than the non-territorial fish: TTPs measure 30-37 cm fork length (FL) and TIP 20-35cm whereas GTP measure 21-39cm FL and GIPs 17-29cm FL. Morphologically, GTPs and TTPs just as GIP and TIPs cannot be distinguished by their colour pattern as it is the same (described above). Unlike mature males and females, juveniles do not belong to a territory or not even to the shallow group. They are equality distributed on the reef.



**Figure 1:** *Sparisoma viride* phases: (a) Juvenile phase (flower Garden Banks, Texas, USA), (b) Initial phase (Glover's reef, Belize), (c) Terminal phase (Bonaire, Netherlands)

## 1.2. Available data on *Sparisoma viride*

### 1.2.1. Bonaire time series of abundance data

Bonaire was set up as an entire marine reserve in 1979, well before van Rooij (1996) parrotfish surveys. The total densities of *S. viride* as well as the size distribution of the population are considered constant over the period 1989-1992 (van Rooij and Videler, 1997), suggesting a population at ecological equilibrium. Therefore we used this time series to calibrate the model at equilibrium.

van Rooij (1996b) has collected abundance data of *S. viride* between 1989 and 1992 in Bonaire (Netherlands Antilles). Stationary visual censuses (Bohnsack and Bannerot 1986) were performed on quadrats to record fish densities of different phases (J, IP and TP) per 5cm (FL) size class. A number of five permanent quadrats were used to record these densities. Fish quadrats were positioned at increasing depth strata: 0-2m, 2-4m, 4-6m, (10x15m quadrats for the 0-2m, 2-4m, 4-6m ranges and 15x15m for the range quadrats 6-12m and >12m). Although no distinction was made between group and territorial TP fish during the survey, this can be inferred by the depth of the quadrates. We classified quadrats as “shallow” (<4m) or “deep” (>4m) habitats according to van Rooij (1996b). The shallow habitat gathers group TPs exclusively, whereas the deep habitat is characterised by the presence of group and territorial TPs, the former making brief incursions into the deep territories. van Rooij (1996b) thus estimated that approximately 50% of the TP fish surveyed were actually transient group TPs coming from the shallow reef. A number of twenty-six field surveys were performed between 1989 and 1992 and grouped per trimesters. As a result, seven density estimates of *S. viride* are available in Bonaire for this study.

### 1.2.2. Growth data

#### *Size-at-age data*

We used size (in fork length, FL) at age measurements performed on *S. viride* individuals by Choat *et al.* (2003) in Los Roques Archipelago (Venezuela). Those data, communicated by Prof. John Howard Choat (School of Marine Biology and Aquaculture, James Cook University, Townsville, Australia), were estimated after otolith processing (Choat *et al.*, 2003). They were used to estimate growth parameters of *S. viride* population from Los Roques which are assumed to be similar to Bonaire parrotfish populations, since the two reef areas are characterised by a very low fishing pressure and are only distant from 150 km within the same latitudinal range (12° 20' N).

Information about the growth of *S. viride* populations in the Caribbean was completed with Fishbase data that was used to calculate growth. Five couples of von Bertalanffy parameters, Linf and K, for *S. viride* are available on fishbase, mostly from Choat *et al.*, (2003) estimations.

#### *Conversion between parrotfish recorded lengths*

Fish sizes having been measured as fork length (FL) in Los Roques, we used available coefficients of conversion between the standard length (SL), fork length (FL) and total length (TL) of *S. viride*. These conversions are the following:

$$SL = 0.83FL \text{ (Choat et al., 2003)}$$

$$FL = 0.90TL \text{ (Fishbase, 2011)}$$

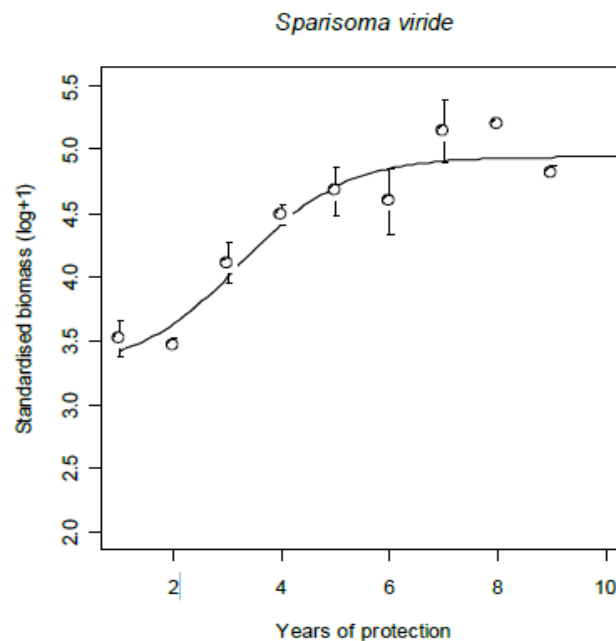
### 1.2.3. Additional data

#### ***Bahamas and Belize abundance data***

The data recorded in the Bahamas and in Belize were used to compare recruitment and the size distribution of parrotfish population estimated by the model. These data were communicated by Dr. Alastair Harborne (Marine Spatial Ecology Lab, University of Queensland, Australia). The dataset contains the abundance of individuals of *S. viride* recorded by visual censuses along transects. The abundances are given in densities per 120m<sup>2</sup> and per 1cm size (TL). The surveys were performed on four different sites of the Bahamas (Andros, Exuma Cays Land and Sea Park and San Salvador), in Turk and Caicos island and Glover's atoll in Belize.

#### ***Bermuda abundance data***

Abundance data of *S. Viride* recorded in Bermuda were used to simulate a recovery of the parrotfish population in Bonaire after a virtual fishing disturbance. In Bermuda, a fishing ban was decided in April 1990 (Luckhurst, 1999) due to a high decrease of many reef fish (Butler *et al.*, 1993). However, only trap fishing was completely banned and hook-a-line fishing targeting top predators essentially was still authorized. After the implementation of the fishing ban, *S. viride* populations were monitored at regular time intervals using stationary visual censuses (Luckhurst 1999). A first analysis of this dataset (O'Farrell, 2011) has shown that parrotfish populations recovered and reached a maximum in only 8 years (Figure 2). The abundance of parrotfish population was multiplied by 2-3 during this 8 years period (O'Farrell, 2011).



**Figure 2:** Changes in biomass of *Sparisoma viride* between 1990 and 1998 (from O'Farrell, 2011) biomass is given is relative abundance to the first observation

## 1.3. Model development

### 1.3.1. Choice of the type of model

Previously, a life phase-structured model was designed at the Marine Spatial Ecology Lab

to reproduce observations of parrotfish recovery in Bermuda after the ban on fish traps in April 1990. This model was empirical and its ability to describe population size structure was limited to 3 broad size classes. Moreover, transitions between classes incorporated mortality but without being clearly explicit. Therefore, a more mechanistic model, structured by size with the incorporation of an explicit natural mortality and growth was developed in this study. The present model also includes recruitment and density dependence. The density dependence is assumed to be reflecting the saturation of TP territories in the deep habitat, which limits the emigration of new fish from shallow reefs.

The model was developed using Matlab for several practical reasons: 1) Matlab is an appropriate modelling software for matrix calculation; 2) Matlab has a very performing optimisation program (Optimisation Toolbox) to estimate the parameters of the model; 3) the model will be integrated *in fine* in a model of coral reef ecosystem, ReefMod (Mumby *et al.*, 2006; Edwards *et al.*, 2011), which describes the competition between corals and algae under the influence of herbivory, and which is currently developed in MatLab language.

### 1.3.2. Model structure

The model is structured by size and habitat categories. It recreates the evolution through time of the parrotfish densities.

#### ***Time step of the model***

A time step of 3 months was chosen for the model regarding the observations in time of Bonaire data. However, this time step is easily adaptable to other datasets studies and only needs to be changed only once in the script.

#### ***Structure by Size classes***

The model was designed in size classes because it aims at becoming a useful tool for fisheries management. With a structure in size classes, there is the possibility to predict the effect of fishing on parrotfish size distribution when simulating different fishing scenarios. Size classes were designed from Smin TL to Lmax TL in centimeters with an increment of 1 cm. Smin is the minimum size of fish considered in the model and Lmax is the maximum one. The model is designed in TL unlike Bonaire data recorded in FL because this study aims at becoming a useful tool for fisheries management. We defined Smin=5cm and Lmax=Linf. The recorded densities of fish below 5cm are usually underestimated when surveyed (Bozec *et al.*, 2011), we ignore the early stage processes occurring for the smallest fish. Therefore, sizes below 5cm TL were ignored in the model. Linf is the maximum hypothetical size of *S. viride* from von Bertalanffy equation. The calculation method of Linf is explained in 1.3.3.

#### ***Structure by habitat categories***

The purpose of a division of fish into two habitats categories (shallow and deep reef) is to reproduce the particular spatial and social structure of the parrotfish population observed in Bonaire. The model reproduces the migration of shallow fish to the deep habitat. Indeed, in Bonaire, males can migrate when taking over a territory and female when becoming part of a TTP harem in a territory. We defined 3 habitat categories for *S. viride*: (1) shallow+deep for small (J+IP+TP) fish (<30 cm FL), (2) shallow for large (adult IP+TP) fish (>=30cm FL), (3) deep for large (adult IP+TP) fish (>=30cm FL). Only TPs above 30 cm FL were observed in the territories (van Rooij *et al.*, 1996b). The small fish do not belong to a particular habitat and are assumed to be equally distributed on the reef. The migrations are implemented in the model by a transition of large shallow fish to large deep category. As their name indicates, the large shallow fish are constrained to the shallow habitat and the large deep fish to the deep habitat. The small fish bounds are Smin and Smax where Smax is the

maximum size of the small fish. The large shallow and large deep bounds are  $L_{min}$  and  $L_{max}$  where  $L_{min}$  is the minimum size of large fish.  $S_{min}$  and  $L_{max}$  are defined as above. The Large fish category bounds were defined regarding the size distribution of the TTPs in Bonaire: 62% of the TTPs belong to the 30-35 cm FL class and 38% to the >40 cm FL class. Therefore in the case of this study,  $L_{min}=30$ cm FL.  $S_{max}$  is an increment lower than  $L_{min}$  therefore,  $S_{max}=29$ cm FL. However, IP of the deep habitat in Bonaire measure 20-35cm FL and IP of the shallow measure 17-29cm FL. The number of IPs in the large deep category is then slightly underestimated and overestimated in the large shallow category, but the correct number of TTPs is properly estimated. If  $L_{min}$  was equal to 20cm FL like TIP size range suggested, the density of TTP fish and more generally the density of fish in the deep habitat, would have been overestimated. The large deep fish would have represented over the 20% of the population they actually represent in Bonaire.

A representation of the model structure for one time step is given in **Table 1**. There is no overlap between Small and Large fish: Small fish are strictly restricted to the size range  $S_{min}$  to  $S_{max}$ . Therefore, the densities of the small fish from  $L_{min}$  to  $L_{max}$  are always equal to zero. Large shallow and Large deep fish are restricted to the same size range  $L_{min}$  to  $L_{max}$ . Therefore the densities from  $S_{min}$  to  $S_{max}$  of both large shallow and large deep are always null (**Table 1**).

**Table 1:** Matrix of parrotfish densities for one time step per category (columns) and per size class (rows) at a time step  $t$ ; the densities  $S_i$ ,  $L_{s_i}$ ,  $L_{d_i}$  correspond to the size class  $i$ ,  $r$  is the recruitment

Sizes(in cm, TL)	Habitat Categories		
	SMALL	LARGE SHALLOW	LARGE DEEP
$S_{min}=5$	$r$	0	0
6	0	0	0
7	0	0	0
...	$S_6$	0	0
31	...	...	...
$S_{max}=32$	$S_{32}$	0	0
$L_{min}=33$	0	$L_{s_{33}}$	$L_{d_{33}}$
...	...	...	...
$L_{max}=L_{inf}$	0	$L_{s_{Linf}}$	$L_{d_{Linf}}$

### 1.3.3. Model parameterisation

In the model, within a time step of 3 months the parrotfish population experiences 4 ecological processes: natural mortality, growth, recruitment and density dependence.

#### **Natural mortality**

Only natural mortality was implemented in the model. No fishing mortality was considered in the first part of the study. To implement natural mortality in the model, two options were possible: implementing a constant mortality rate per size or implementing a size dependant mortality function. The mortality parameter stands for all the different types of natural mortality: mortality per predation, per senescence, per sickness and any factor inducing natural mortality other than by fishing.

#### *Constant instantaneous rate of natural mortality per size*

We tested the application of a constant mortality rate calculated by Choat *et al.* (2003) from



data collected at *Los Roques* Archipelago in Venezuela. To calculate this instantaneous mortality rate, *Choat et al. (2003)* used a linear regression of the logarithm of the age-frequency and the age at size. The regression slope gives the mortality per year (more details in *Choat et al., 2003*). At *Los Roques*, the mortality was estimated to be:  $m = 0.24$ . The associated survivorship per year using the exponential conversion is  $s = e^{-m} = 0.79$ . In the model, the survivorship was used instead of the mortality for more convenience. This survivorship  $s$  was converted for a time step of 3 months by the following operation:

$$s = 0.79^{t\_step/12}, \text{ for } t\_step = 3, \quad s = 0.94$$

At each time step of 3 months, this constant rate of survivorship per size was multiplied by the density of each size class which means that 94% of the population survives at each time step.

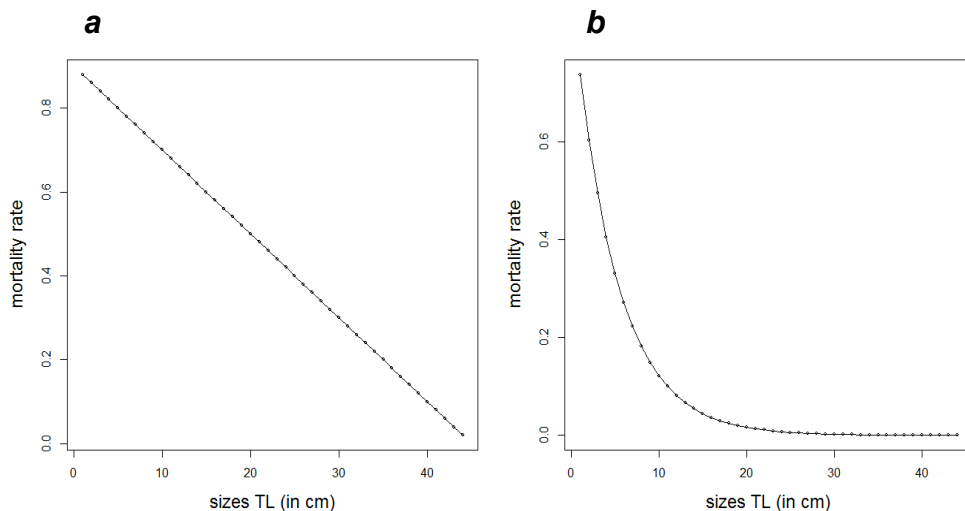
### Size dependent mortality

#### → Linear size dependent mortality

Because smaller sizes are more vulnerable to predation and then assumed to have a higher mortality compared to larger fish, we tested a size dependant mortality relation. First by implementing a simple linear relation:  $m_l = a * l + b$ , where  $m_l$  is the mortality,  $l$  is the length in TL of the fish,  $a$  and  $b$  are respectively the slope and the intercept of the mortality line. This mortality relation is based on the assumption that mortality is decreasing ( $a < 0$ ) linearly with the size of the fish (**Figure 3a**).  $b$  is the hypothetical mortality rate that would have a fish of size 0cm. The associated survivorship  $s_l$  is  $s_l = 1 - m_l$ .

#### → Exponential size dependent mortality

A more complex size-dependent mortality function was:  $m_l = b * \exp(a * l)$ , where  $m_l$  is the mortality,  $l$  is the TL of the fish,  $a$  and  $b$  are respectively the slope and the intercept of the mortality curve. As previously, this mortality function is based on the assumption that mortality decreases when the size of the fish increases. In this case, compared to a linear mortality, there is the existence of a threshold: from a certain size, 25cm (**Figure 3b**), and a fish can escape mortality per predation which appears more realistic. The associated survivorship  $s_l$  is  $s_l = 1 - m_l$ .



**Figure 3:** Size ( $l$ ) dependent mortality ( $m_l$ ) functions:  
 (a) linear:  $m_l = a * l + b$ ,  $a = -0.02$  and  $b = 0.9$  (arbitrary) ;  
 (b) exponential:  $m_l = b * \exp(a * l)$ ,  $a = -0.2$ ,  $b = 0.9$  (arbitrary);

In our study, we used the survivorship  $s$  instead of the mortality for practical reasons in the implementation. However, we named  $a$  and  $b$  the respective slope and intercept of the size-dependant mortality functions.

## Growth

To implement growth in the model, we used a growth transition matrix because the model is structured by size. Therefore, this matrix was necessary to implement growth transitions between size classes. Growth transition matrices give the probabilities of growing from one size class into others within a given time step. An example of growth transition matrix is given in Haddon (2011) (Figure 4). In Haddon (2011) the growth matrix is calculated using a probability density function. However, the growth matrix of Haddon required parameters we were unable to obtain with our data. We decided to use the growth transition matrix developed by Chen *et al.* (2003). The construction of this matrix is based on the same assumptions than Haddon (2011). However, Chen *et al.* (2003) growth matrix is more precise because its calculation takes in consideration the difference of growth rates between smaller fish and larger fish. Smaller fish grow faster than larger fish during the same period of time. Moreover, Chen *et al.* (2003) growth matrix required inputs that could be calculated with data we obtained from Pr. J. Choat. This growth transition matrix is generated by the function *growtrans* from the R package *Fishmethods* created by Chen *et al.* (2003). For each size class, *growtrans* calculates the probabilities to grow from a size to others within a year using the von Bertalanffy equation. Eight inputs are needed for the calculation of this matrix: TLmin, TLmax, Linc, Linf and K (parameters of the von Bertalanffy equation) and their associated standard errors SELinf and SEK, and finally the coefficient of determination between Linf and K, rhoLinfK, obtained from a regression between ln(K) and ln(Linf). Using these 8 inputs and von Bertalanffy equation, the *growtrans* function realises Monte Carlo simulations to generate probabilities for a fish of a particular size to grow to another length within a time step. In our model, this matrix is constant through time and is calculated before model simulations. Any change in the time step requires a recalculation of this growth matrix with the appropriate time step.

$$\begin{bmatrix} G_{1,1} & 0 & \cdot & \cdot & 0 \\ G_{1,2} & G_{2,2} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & 0 \\ G_{1,44} & \cdot & \cdot & G_{44,43} & G_{44,44} \end{bmatrix}$$

**Figure 4:** The growth transition matrix:  $G_{ij}$  are the probability that one fish of size class  $j$  will grow in size classes  $i$  at the considered time step (from Haddon, 2011, chapter 13, Figure 13.2)

### → Defining TLmin, TLmax, Linc

TLmin, TLmax and Linc are defined in millimeter. TLmin was set up at 50 mm like the starting length of the model, Lmax=Linf+1 as Lmax must be an increment higher than Linf (Chen *et al.* , 2003). Like in the model, the increment was chosen equal to 1cm, Linc=10mm.

### → Calculation of Linf and K and their associated standard error

To calculate Linf and K and their associated standard errors Choat *et al.* (2003) data of size-at-age were used. These size-at-age data were fitted the von Bertalanffy equation:

$$L_t = Linf (1 - e^{-K(t-t_0)})$$

Where  $L_t$  is the estimated size of a fish at age  $t$ , Linf and K are the parameters of the equation of von Bertalanffy, and  $t_0$  is the estimated age at the hypothetical size 0. We used in our study the  $t_0=0.06$  estimated by Choat *et al.* (2003) for the *S. viride* population of Los Roques. This regression was executed by doing a non-linear regression with the function *nls* in R

(Ritz and Streibig, 2009). This regression was processed after conversion of FL data in TL as the model is structured in TL. We also performed this regression in SL to compare our results with the results obtained in SL by Choat, *et al.* (2003).

→ Calculation of rhoLinFK

To calculate the coefficient of determination between Linf and K, we used the 5 couples of Linf and K of *S. Viride* available in fishbase data. We applied the method developed in Chen *et al.* (2003). This method is based on the assumption that Linf and K are negatively correlated: populations or species whose Linf is high, tend to have a lower K, and vice versa (Chen *et al.*, 2003). This calculation method consists in doing a linear regression between ln(K) and ln(Linf). The coefficient of determination of this regression is the input of the growth transition matrix.

**Recruitment**

In this study, we defined recruitment as a constant addition of 5cm fish in the population at each time step. In the model, a recruit is a juvenile fish of 5 cm settled on the reef that already experienced mortalities due to the early stages. This size threshold (5 cm) in the definition of recruits was chosen since no information is available these early stages. In addition, no abundance data of fish less than 5cm can be reliably used due to biases in surveys (Bozec *et al.*, 2011). The model also ignores any stock-recruitment relationship.

**Density dependence in the deep habitat**

As observed by van Rooij and Videler (1997), the number of territories in the deep habitat is limited. Consequently, the density of fish in the deep habitat is limited. The maximum density of the deep habitat is the carrying-capacity ( $K_{Ld}$ ). When a TTP leaves its territory (through migration or mortality), a GTP replaces it. IP females can also migrate from the shallows to become part of one TTP's harem. These migrations of the fish from the shallow to the deep were reproduced in the model by implementing a transition rate. The transition matrix  $T_{Ls \rightarrow Ld}$  from Ls to Ld gives the proportion of Ls transiting to Ld, this proportion is weighted by the density of each size class in the Ls category by  $\frac{Ls_{i,t}}{\sum Ls_{i,t}}$ , where  $\sum Ls_{i,t}$  is the total density of Ls of all sizes at time step  $t$ . The transition proportion of Ls transiting varies at every time step and is estimated based on the carrying capacity  $K_{Ld}$  of large deep population by  $\frac{\sum Ld_{i,t}}{K_{Ld}}$ , where  $\sum Ld_{i,t}$  is the sum of the Ld of all sizes.

The transition matrix from Ls to Ld is given by:

$$T_{Ls \rightarrow Ld} = \left(1 - \frac{\sum Ld_{i,t}}{K_{Ld}}\right) \frac{Ls_{i,t}}{\sum Ls_{i,t}}$$

**1.3.4. Model implementation and outputs**

**Model implementation**

→ Habitat categories

There is no overlap between categories S, Ls and Ld. If after experiencing growth, a small fish becomes larger than Smax, it automatically transits to the Ls category. Small and large shallow categories could have been grouped together in one single category from Smin to Lmax. However, they were distinguished in 2 categories. First because large shallow fish represent fish constrained to the shallow habitat whereas small fish are equally distributed on the entire reef with no habitat distinction. Secondly, separating small and large shallow allowed us to implement and represent density dependence in the deep habitat more easily.

→ Recruitment

The addition of 5cm fish is made after all other processes described above.

→ Density dependence

Only large shallow fish are given the possibility to transit to the large deep category if the carrying capacity of the deep fish was not reached at the previous time step. Small fish cannot transit directly to the large deep fish (van Rooij *et al.*, 1996c). However, if after growth, a small fish transited to the large shallow category, it is then eligible to transit to the large deep category within the same time step.

→ A flexible model

The model was created to be first calibrated with Bonaire data. Consequently, the categories, size classes, and the parameters were implemented following Bonaire observations. However, the model is very flexible and adaptable and the time step can be easily changed, as well as the size limits  $S_{min}/S_{max}$  and  $L_{min}/L_{max}$ . In addition, the model is designed in TL but the model outputs can be converted in FL or SL given the empirical relationships presented above. The recruitment and the carrying capacity of large deep fish can also be changed in the model. The structure in habitat categories can also be removed to keep a structure in size classes only. Only the growth transition matrix would need to be recalculated if using another  $L_{inf}$  and  $K$ , and time step. The structure of this model was then made to be as general and flexible as possible because this study aims at being generalized at other parrotfish species and other sites of the Caribbean.

## The model

$$\begin{aligned} S_{l,t+1} &= (s_l g_l S_{l,t}) (1 - T_{S \rightarrow L_S}) + r \\ L S_{l,t+1} &= (s_l g_l L S_{l,t} + s_l g_l S_{l,t} T_{S \rightarrow L_S}) (1 - T_{L_S \rightarrow L_d}) \\ L d_{l,t+1} &= s_l g_l L d_{l,t} + (s_l g_l L S_{l,t} + s_l g_l S_{l,t} T_{S \rightarrow L_S}) (T_{L_S \rightarrow L_d}) \end{aligned}$$

$S_{l,t+1}, L S_{l,t+1}, L d_{l,t+1}$  are respectively the densities of the small, large shallow and large deep categories at time  $t+1$  and size  $l$

$S_{l,t}, L S_{l,t}, L d_{l,t}$  are respectively the densities of the small, large shallow and large deep categories at time  $t$  and size  $l$

$s_l$  is the size-dependent survivorship

$g_l$  is the growth probabilities for a fish of size  $l$

$r$  is the recruitment

$T_{S \rightarrow L_S}$  the transition matrix from S to  $L_S$ . It includes the matrix of 0 and 1 values to control the transition of S fish of appropriate size (every fish larger than  $S_{max}$  automatically switches from S to  $L_S$ )

$T_{L_S \rightarrow L_d}$  is the transition matrix from  $L_S$  to  $L_d$ . It gives the proportion of  $L_S$  transiting to  $L_d$ , those proportions varies at every time step and are estimated based on the carrying capacity of  $L_d$  population

### Outputs of the model

As the purpose of the study is recreating the size distribution observed in Bonaire with the model, we represented the densities per size classes as outputs of the model. These size classes are the following (in FL): 5-9cm, 10-14cm, 15-19cm, 20-24cm, 25-29cm, shallow 30-34cm ( $s_{30-34cm}$ ), shallow >35cm ( $s_{>35cm}$ ), deep 30-34cm ( $d_{30-34cm}$ ), deep >35cm

( $d > 35\text{cm}$ ). We summed the densities of the size classes of the model having an increment of 1cm to obtain these output size classes. We grouped together for each habitat the size classes 35-39cm and  $>40\text{cm}$ . First, because the density of fish over 40cm is very low therefore the  $>40\text{cm}$  fish did not need a particular size class. Secondly, with a time step of 3 months, fish from 35cm and above remain at each time step at their current length and do not grow enough. Therefore, in terms of growth, there is no possibility to distinguish a fish from the size class 35-39cm and the size class  $>40\text{cm}$ .

## 1.4. Model calibration: population at equilibrium

### 1.4.1. Re-organisation of Bonaire data

#### **Re-organisation of the categories and size classes**

The model was first calibrated with Bonaire data as the population of *S. viride* is considered at equilibrium. For this purpose, Bonaire data were reorganised because the model is not structured life phases (does not involve sex change transition) like these data. In addition, this new organisation was necessary in order to implement density dependence occurring in the deep reef of Bonaire. These size classes are the same described in the output of the model. We also reorganised the data in habitat categories like in the model: in the data, the small fish category was created by summing the J, IPs and TPs of size range 5-29cm FL. Large shallow and large deep categories were created by summing the IPs and TPs from 30-34cm to  $>40\text{cm}$  of the corresponding habitat (shallow or deep).

→ Re-organisation in categories: Small, Large shallow and Large deep fish

**Large shallow fish** groups together all the fish of size range 30cm-40cm FL, of the shallow quadrats ( $<4\text{m}$ ), independently from their life phase (IP+TPs).

**Large deep fish** groups together all the fish of size range 30cm-40cm FL, of the deep quadrats ( $>4\text{m}$ ), independently from their life phase (IP+TPs).

**Small fish** are the fish covering the size range 1-29cm FL independently from their life phase (J+IP+TPs). Small fish are assumed to be equally distributed on the reef (van Rooij and Videler, 1997). Therefore, we organized the Small fish independently from the depth they have been recorded. The densities of TTPs and GTPs had to be adjusted in the data. Indeed, the invasion by GTP of TTPs territories conducted to overestimate the number of TTPs (van Rooij and Videler, 1997). Therefore, the density of TPs in the deep quadrats (standing for TTPs) was halved and the other half was added to TPs of the shallow quadrats standing for GTPs (van Rooij and Videler, 1997). To estimate the mean density per category, we aggregated the data per observation and per type of habitat and proceeded to the adjustment of TPs following van Rooij procedure. We then calculated the mean density for each category (S, Ls, Ld) on Bonaire times series and associated standar errors.

→ Re-organisation in size-classes

The re-organisation of Bonaire data follows the same scheme as the output of the model to ease comparison. To create the small fish size classes (from 5-9cm to 25-29cm FL) from Bonaire, we summed for each observation, the fish (J+IP+TP) densities corresponding to the range of the size class. Then, we calculated the mean and associated standard error of these size classes over the time series of Bonaire. For the Large fish size classes (30-34cm and  $>35\text{cm}$  FL), we summed the fish (IPs+TPs) densities of the shallow quadrats for the large shallow fish and of the deep quadrats for the large deep fish. We calculated the mean and associated standard error for each habitat category.

#### **Implementing initial conditions in the model**

Densities per size classes in Bonaire were used as initial conditions for the model. However, Bonaire size classes have an increment of 5cm and the model have an increment of 1cm

for the size classes. Therefore, the density of each observed size class converted in TL was divided by five in order to determine the initial density of the 1-cm size classes of the model.

#### 1.4.2. Optimisation of model parameters

We optimised two parameters of the model: natural mortality and level of recruitment (density of fish entering the model at 5cm). Using optimisation we also tested the 3 different formulations of natural mortality on model fits to Bonaire data.

##### ***Optimisation method with the Global Search solver***

The *Global Search* solver from Matlab optimisation toolbox was used to optimise the parameters of this study. *Global Search* is designed to find one global minimum and other local minima of an objective function, using a constrained nonlinear optimisation solver. We used *fmincon* as the constrained nonlinear solver. The solver *fmincon* is designed to find a local minimum around a starting point. *Global Search* set up multiple starting points using a scatter-search algorithm (Mathworks, *Global Optimisation Toolbox*, 2013). Then, it filters non-promising starting points based upon objective and constraint function values and local minima already found. Finally, *Global Search* runs *fmincon* from the remaining starting points to find minima around these starting points. Among all the local minima found, the one considered as the global minimum of the objective function is the one having the lowest value of this objective function (Mathworks, *Global Optimisation Toolbox*, 2013).

##### ***Application of the optimisation method***

In this study, the objective function to minimise with the *Global Search* solver is the sum of squared differences between the model estimations and Bonaire observations for of the 9 size classes described previously. The optimisation aims at reproducing the size distribution observed in Bonaire with the model by minimising the sum of squared differences. The optimisation is based on a confrontation between densities per size classes estimated by the model and mean densities per size classes observed in Bonaire. We chose not to optimise using the habitat categories as they have only been designed to implement the density dependence parameter. With this method, we tested the 3 functions of survivorship described previously: (1) we tested the constant rate of survivorship and the associated value of recruitment  $r$  by optimising these 2 values, (2) we tested each of the 2 size dependant survivorship functions by optimising the slope  $a$  and the intercept  $b$  of the mortality functions, and the associated value of recruitment  $r$ .

##### ***Starting points and bounds***

For each of the value to optimise,  $s$ ,  $a$ ,  $b$  and  $r$ , initial values and bounds are required for *Global Search* to work. In addition, they must have ecologically meaningful values. As  $r$  is a totally arbitrary value, a wide range of values was given (**Table 2**).  $s$  is a survival rate, therefore  $s$  can only vary between 0 and 1. For the parameters  $a$  and  $b$  of the size dependent mortality functions, we chose the same values:  $a$  (slope) must be negative as we assume that mortality decreases with the size and  $b$  (intercept) is assumed to be constrained between 0 and 1 as it represents the mortality of a fish of hypothetical size 0. For starting points, after adjusting the model by hand, we chose the values that seemed to provide the best fit to the data.

**Table 2:** Starting points of the values to optimise and their constrained bounds

parameters	Starting value	Lower bound	Upper bound
<b>r (individuals per 3 months)</b>	0.3	0	100
<b>s (constant survivorship rate)</b>	0.94	0	1
<b>a (slope of the linear mortality function)</b>	-0.02	-200	0
<b>b (intercept of the linear mortality function)</b>	0.9	0	1
<b>a (slope of the exponential mortality function)</b>	-0.2	-200	0
<b>b (intercept of exponential function)</b>	0.9	0	1

### 1.4.3. Exploration of the optimised model

The model behaviour was explored with the optimised parameters. This step is required to understand the impact of these parameters on the model at equilibrium.

#### ***Influence of the initial conditions***

We tested the evolution of the densities of the 3 habitat categories when implementing different initial conditions. Three sets of initial conditions were tested are: (1) the initial conditions of Bonaire, where the 9 initial densities correspond to the average densities observed in Bonaire between 1989 and 1992, (2) initial conditions set arbitrary to lower densities than Bonaire from 1989 to 1992 (all densities equal to 0); (3) initial conditions set arbitrary to higher densities than Bonaire from 1989 to 1992 (all densities equal to 1).

#### ***Influence of the time step***

We tested the influence of a different time step (12 months) on the size distribution estimated by the model at equilibrium. A new growth transition matrix was calculated accordingly, and model parameters were optimised in a similar manner to the 3-month time step model. Size distributions of both models were assessed visually.

#### ***Influence of the survivorship $s$ on the density dependence***

We tested the influence of different values of the survivorship on the large deep category density and its ability to reach its carrying capacity.

### 1.4.4. Sensitivity analysis of the model to the parameters

We tested the sensitivity of the model to survivorship  $s$  and recruitment  $r$ . We used a method consisting in fixing one of these two parameters at the optimised value and making the other parameter vary within a defined range of values. The effects of these variations were observed on the variations of a fit. For this fit, we used the objective function described in the optimisation method.

$r$  (recruitment) was made to vary between + and – 30% of its optimised value with a 10% increment

$s$  (survivorship) was made to vary down to -30% of its optimised value with a 10% increment. For higher values, only two values 0.94 (Choat *et al.* (2003) survivorship) and 0.98 were chosen. Indeed,  $s$  cannot exceed 1.

## 1.5. Model application: recovery after applying fishing pressure

The model was used for a preliminary approach of calibration to the data collected in Bermuda. In Bermuda, after the implementation of a fishing ban (on traps only), the *S. viride* population recovered in 8 years only. A plateau was reached after 8 years and the recovery factor was 2-3. With the model calibrated on Bonaire data, we simulated fishing disturbance equivalent to the one in Bermuda before the fishing ban: we divided the densities of the size

classes by the recovery factor in Bermuda. Then, we ran the model to test if the speed of recovery was similar to the one observed in Bermuda.

## 2. Results

### 2.1. Model construction: the Growth Transition Matrix

#### ***Non-linear regression of size-at-age data***

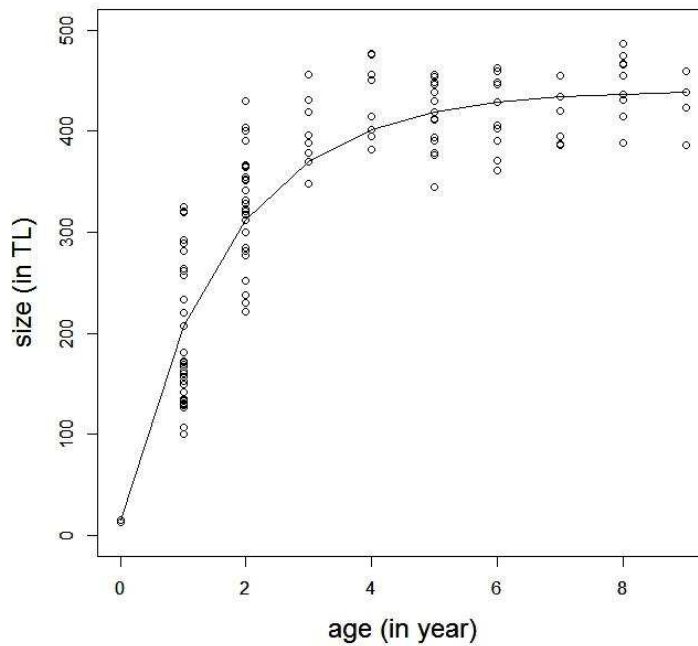
Choat *et al.* (2003) data were used to estimate Linf and K and their associated standard errors that are necessary inputs for the estimation of the growth transition matrix (Chen *et al.*, 2003). We re-estimated Linf, K by performing a non-linear regression between sizes and ages of *S. viride* individuals following the von Bertalanffy equation. The results are given for the regressions with body size expressed as TL and SL (**Table 3**).

**Table 3:** Results of the non-linear regression of size-at-age data, in SL and in TL

Modele	Parameters of Von Bertalanffy	Estimate	Standard error	Pr(> t )
<b>a) body size as TL</b>	Linf	44 cm	10.3	2.10 <sup>-16</sup>
	K	0.6 year <sup>-1</sup>	0.03	2.10 <sup>-16</sup>
<b>a) body size as SL</b>	Linf	28 cm	6.2	2.10 <sup>-16</sup>
	K	0.6 year <sup>-1</sup>	0.03	2.10 <sup>-16</sup>
Choat <i>et al.</i> (2003)	Parameter	Estimate	Standard error	Pr(> t )
<b>body size as SL</b>	Linf	28 cm	N/A	N/A
	K	0.6 year <sup>-1</sup>	N/A	N/A

Because sizes in our population model are expressed in TL, Linf in TL was used to estimate the growth transition matrix. **Figure 5** represent the sizes (TL) at age plots with the fit of the von Bertalanffy growth model.

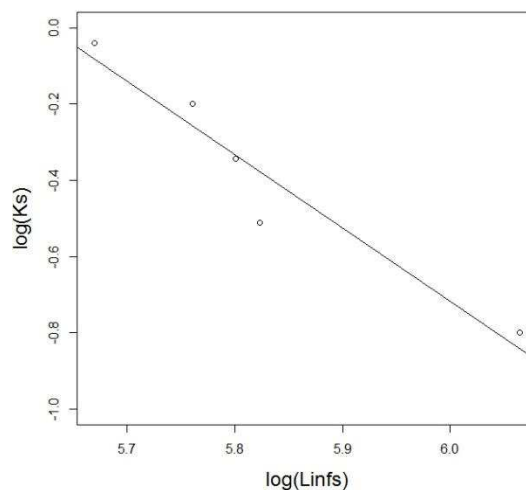




**Figure 5:** Size (TL) at age plots and fitted von Bertalanffy growth equation with estimated  $L_{inf}$  and  $K$  from non-linear regression of size-at-age data

#### **Correlation between logarithmic K and $L_{inf}$**

The linear regression between logarithmic  $K$  and  $L_{inf}$  values provided by Fishbase was performed with the R *lm* function. The adjusted coefficient of determination ( $R^2$ ) of this relationship is 0.90 (**Figure 6**). These estimates were subsequently used as an input for the calculation of the growth transition matrix (Chen *et al.*, 2003).



**Figure 6:** Logarithmic  $K$  and  $L_{inf}$  (TL) of *Sparisoma viride* plot and fitted regression line between logarithmic  $K$  and  $L_{inf}$  (TL),  $\ln(K) = 10.87 - 1.92\ln(L_{inf})$ ,  $Pr(t) = 0.008534$ ,  $adj. R^2 = 0.90$ ,

## Final inputs of the growth transition matrix

**Table 4** summaries all the necessary inputs values to calculate the growth transition matrix.  $K$  is estimated in year-1, therefore it was used in the model converted in 3months-1 by multiplying it by 3 and dividing it by 12. The same conversion was applied to the standard error of  $K$ .

**Table 4:** Values of input parameters used for the estimation of the growth transition matrix for a time step of 3 months, mm=millimeters

Parameter	Signification	Value
<b>TLmin as TL (mm)</b>	Minimum length considered in the study	50
<b>TLmax as TL (mm)</b>	Maximum length of the growth matrix (must an increment higher than Linf)	450
<b>Linc as TL (mm)</b>	Increment between Lmin and Lmax	10
<b>Linf (TL) (mm)</b>	Von Bertalanffy parameter estimated above	440
<b>SELinf (mm)</b>	Standard error associated to Linf	10.07
<b>K (year-1)</b>	Von Bertalanffy parameter estimated above	0.6
<b>SEK (year-1)</b>	Standard error associated to K	0.03785
<b>rhoLinfK</b>	Coefficient of determination of regression between logarithmic K an Linf	0.9

## 2.2. Optimisation results

We used the *Global Search* solver from Matlab to compare the 3 survivorship functions and then estimate the value of recruitment at equilibrium.

The 3 survivorship functions were tested and the values of objective function for these 3 survivorship functions are equivalent (**Table 5**). We obtained from the optimisation step the values of the constant survivorship and the values of the parameters  $a$  and  $b$  of the size dependent mortality functions and associated values of recruitment (**Table 6**).

**Table 5:** Values of the objective function (Fval) given by type of survivorship

survivorship	Constant rate per size	Linear	Exponential
<b>Fval</b>	0.44	0.47	0.46

**Table 6:** Estimation of the parameters (survivorship function and  $r$ ) of the model by the *Global Search* solver

Parameters	Estimated values
<b>1) Constant survivorship rate</b>	
<b>s (rate of survivorship for 3 months)</b>	0.92
<b>r (individuals per 3 months)</b>	0.28
<b>2) Linear survivorship function</b>	
<b>a (slope of the linear mortality function)</b>	-0.0065
<b>b (intercept of the linear mortality function)</b>	0.29
<b>r (individuals per 3 months)</b>	0.55
<b>3) Exponential survivorship function</b>	
<b>a (slope of the exponential mortality function)</b>	-0.0671
<b>b (intercept of exponential function)</b>	0.62
<b>r (individuals per 3 months)</b>	0.82

Using a more complex function does not provide a better fit (**Table 6**). At this stage, we considered that the constant survivorship was enough and acceptable. The exponential function did not improve much the fit. Moreover, there is no study in the literature about the use of an exponential mortality function. We then decided to keep the values of the constant survivorship  $s$  and associated recruitment  $r$  obtained from the optimisation step.

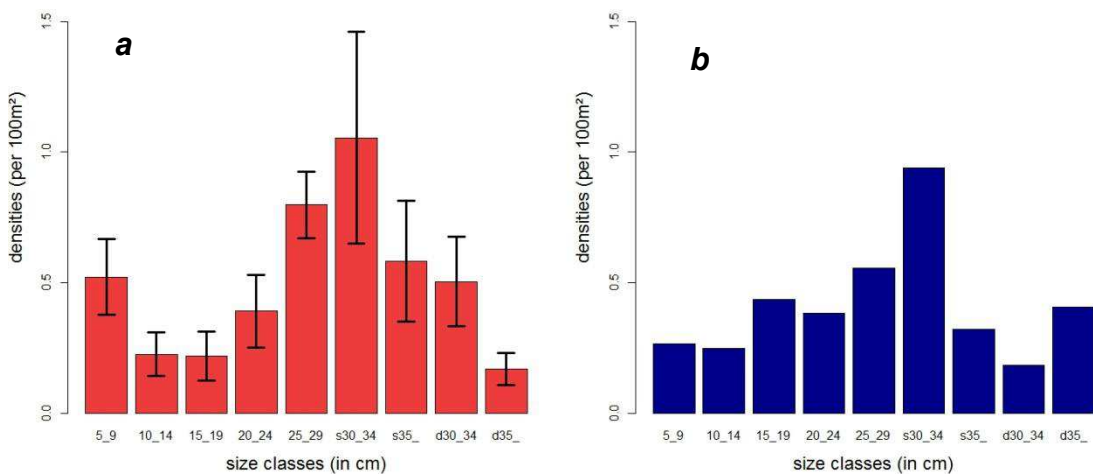
### 2.3. Exploration of the model with optimised parameters

After a number of time steps the model converges to equilibrium. This equilibrium is always the same for a given value of  $s$  and  $r$ .

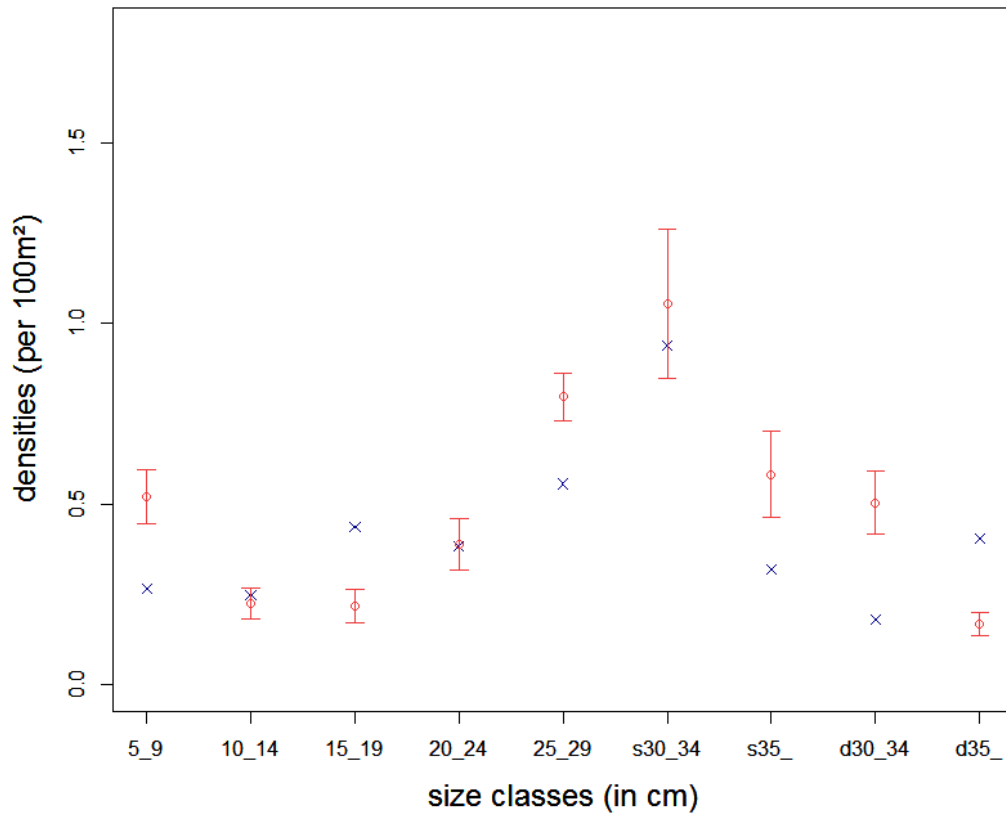
#### 2.3.1. Model at equilibrium

##### *Size distribution at equilibrium*

The size distribution of the population of *S. viride* estimated by the model at equilibrium (**Figure 7b**) fitted well with the average size distribution observed in Bonaire (**Figure 7a**). For some size classes (10-14cm, 20-24cm, s30-34cm), model estimates were within the 95% confidence limit of the observed density (**Figure 8**). For the other size classes (5-9cm, 15-19cm, 25-29cm, d30-34cm, s>35cm, d>35cm), the model often underestimated the densities which are out from the 95% confidence interval (95%CI) of the observed density.



**Figure 7:** Size distribution of Bonaire (a) and estimated by the model at equilibrium (b), the bars are the densities per size classes represented with the 95%CI for Bonaire observations



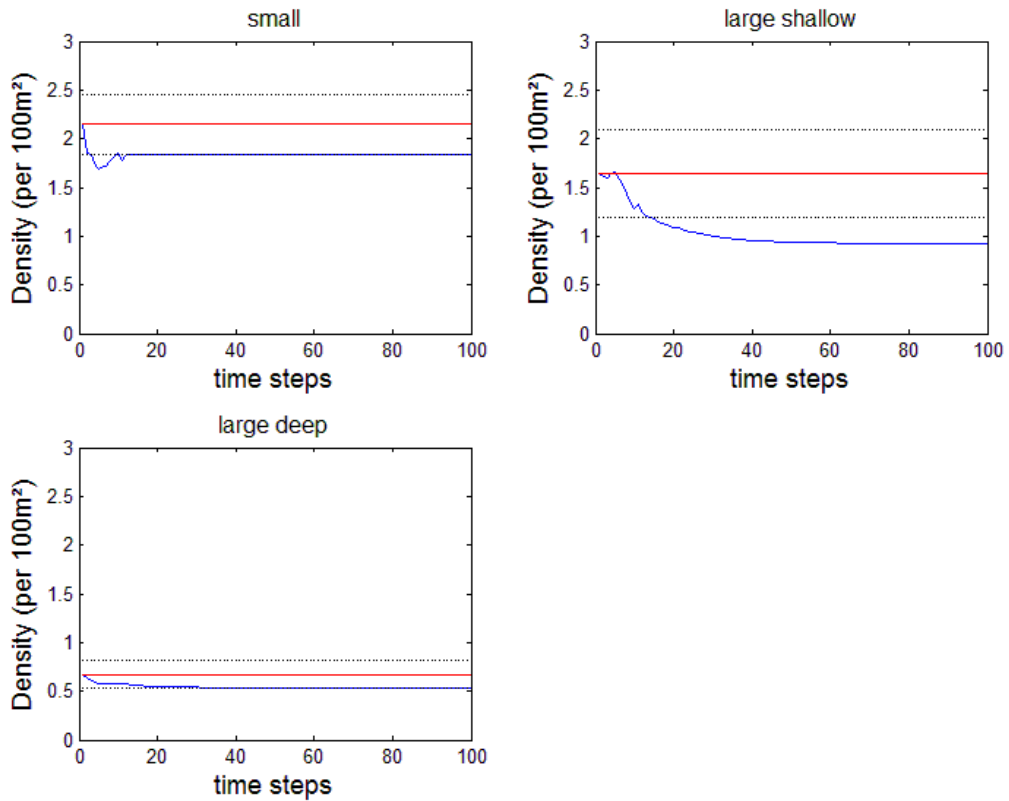
**Figure 8:** Mean densities observed in Bonaire per size class with error bars (95%CI) (red dots) and densities per size class estimated by the model (blue crosses)

### **Habitat categories at equilibrium**

Each of the 3 habitat categories reaches a value at equilibrium close to the corresponding average observed in Bonaire (**Figure 9**). However, the model underestimates the densities of the 3 habitat categories as these values are globally lower than the ones calculated in Bonaire (**Table 7**). The estimated density for the large shallow is below the lower bound of the 95% CI of the observed density. The small and large deep densities are close to the value of the lower bound of the 95% CI.

**Table 7:** Mean densities of Bonaire with associated standard errors (SE) and estimated densities by the model at equilibrium for the 3 habitat categories for total density of *S. viride*

Model populations	Bonaire (average 1989 - 1992)	SE of the mean densities in Bonaire	Model estimates (equilibrium)
<b>Small</b>	2.15	0.15	1.89
<b>Large shallow</b>	1.64	0.22	0.92
<b>Large deep</b>	0.67	0.07	0.53
<b>Total</b>	4.46	0.22	3.28



**Figure 9:** Evolution of the model densities (blue) of the 3 habitat categories through time until equilibrium, red lines are the mean densities of Bonaire for each habitat category, the black dot lines delimitate the 95% CI

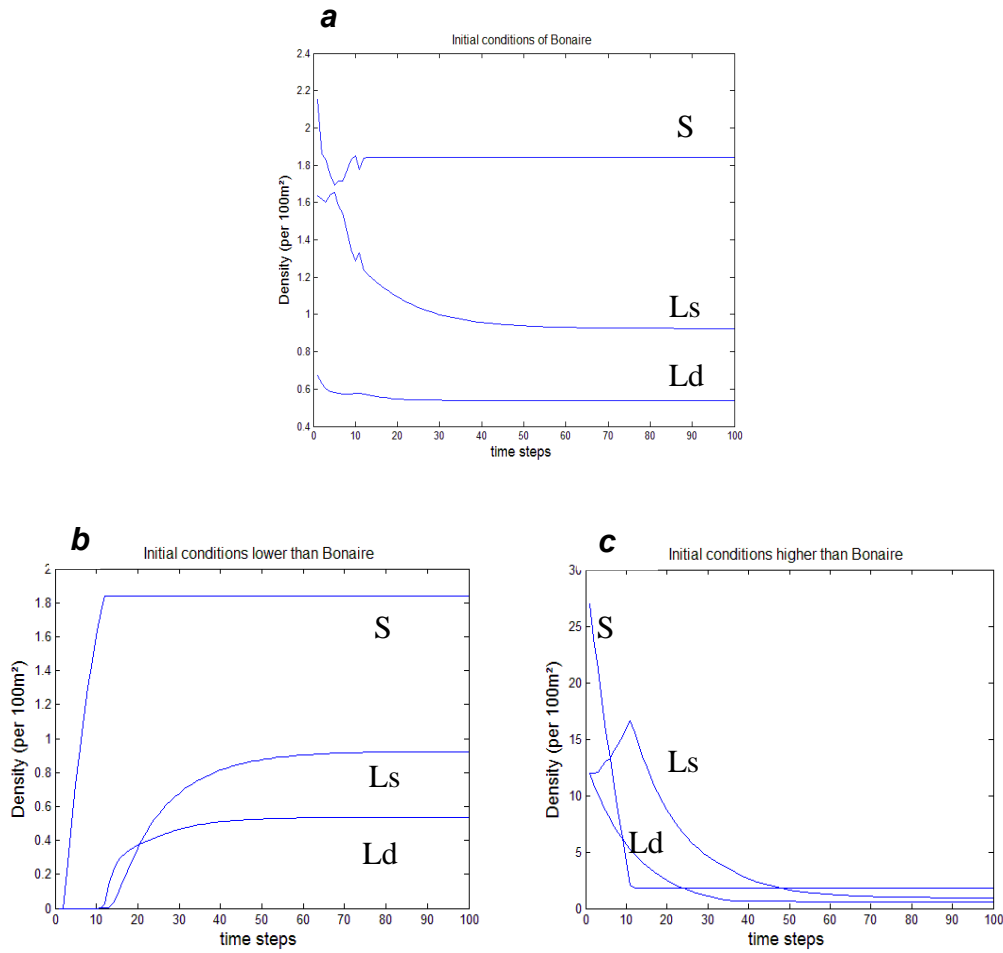
### **Density dependence in the deep habitat at equilibrium**

The large deep fish category does not reach its carrying capacity with the optimised parameters  $s$  and  $r$  (Table 4) and stabilises at an equilibrium value lower than its carrying capacity (Figure 9).

## **2.3.2. Exploration of the behaviour of the optimised model**

### **Influence of the initial conditions on the equilibrium**

For a given value of recruitment  $r$  and survivorship  $s$ , the values of densities estimated by the model at equilibrium are not influenced by the initial conditions: the densities for a given habitat category always reaches the same values at equilibrium (Figure 10). When initial conditions are lower than Bonaire densities (Figure 10b), the densities of the 3 habitat categories increase until it stabilises at equilibrium. The opposite occurs when the densities are higher than Bonaire densities: the densities of the 3 habitats categories decrease until they reach equilibrium (Figure 10c).



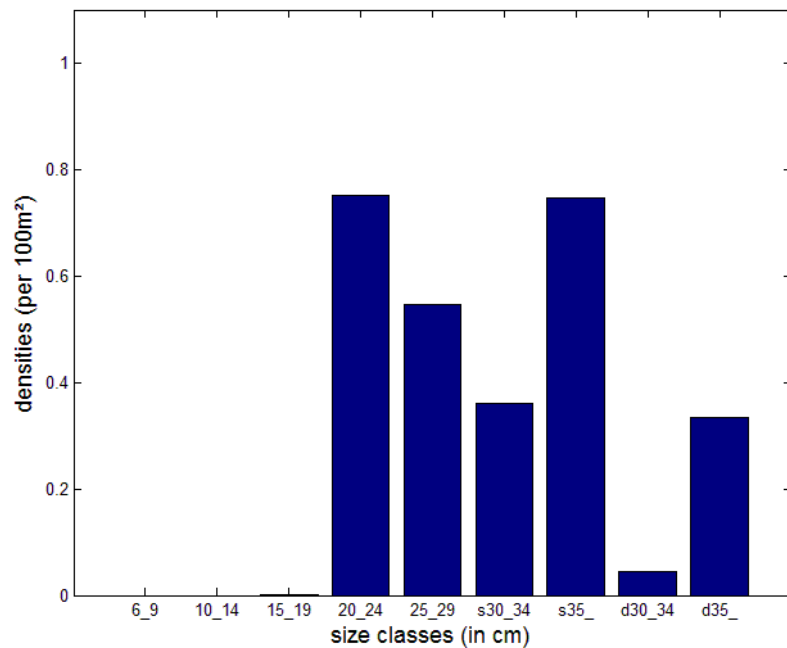
**Figure 10:** Evolution of the model densities of the 3 habitat categories small (S), large shallow (Ls), large deep (Ld), subject to 3 initial conditions (note the scales are different for the 3 plots)

### ***Influence of the time step***

We re-calibrated the model to Bonaire data with a 12-months time step to understand the influence of this time step of the size distribution. The values obtained previously for the survivorship  $s$  and the recruitment  $r$  for a time step of 3 months (**Table 8**) were standardised for a 12 month period and compared to the values obtained for a time step of 12 months. For a time step of 12 months, the recruitment is four times more important compared to a time step of 3 months. For a time step of 12 months, the survivorship is the 4<sup>th</sup> root of the survivorship for a time step of 3 months. The size distribution with a time step of 12 months show differences compared to the size distribution for a time step of 3 months (**Figure 11**): the density of smaller fish (size < 20cm FL) are nearly null and the densities of size classes >20cm are significantly higher.

**Table 8:** Optimised values of  $s$  and  $r$  a time step of 12 months and a time step of 3 months standardised to a time step of 12 months

parameters	Time step=12months	Time step=3months (standardised to 12 months)
<b>s (rate of survivorship per 3 months)</b>	0.73	0.72
<b>r (individuals per 3 months)</b>	1.03	1.12



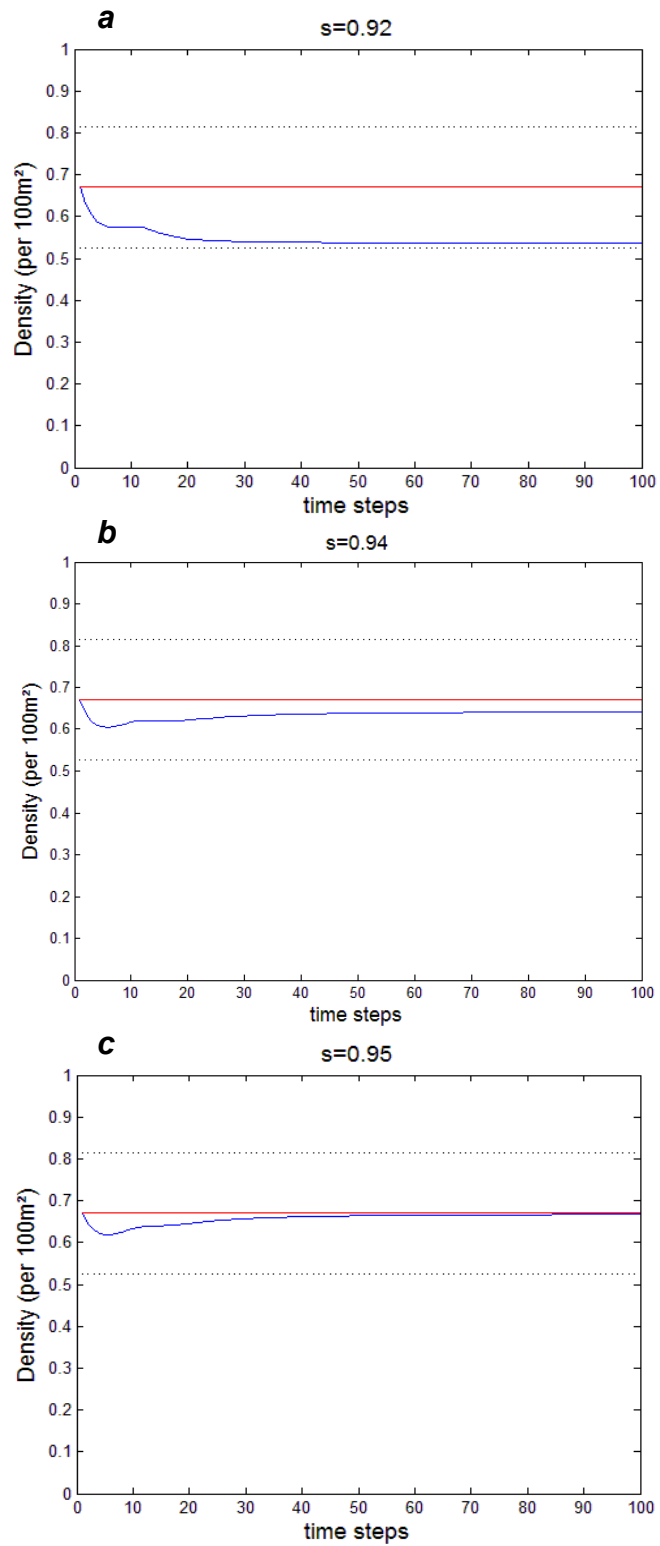
**Figure 11:** Size distribution of Bonaire at equilibrium with optimised parameters for a time step of 12 months

### ***Influence of the survivorship on the density dependence***

We tested 3 values of survivorship 0.92 (optimised value), 0.94 (estimated by Choat *et al.* (2003) for the site Los Roques) and 0.95. We followed the evolution of the large deep category density (**Figure 12**) to explore the impact of the survivorship on the ability of the large deep fish to reach their carrying capacity.

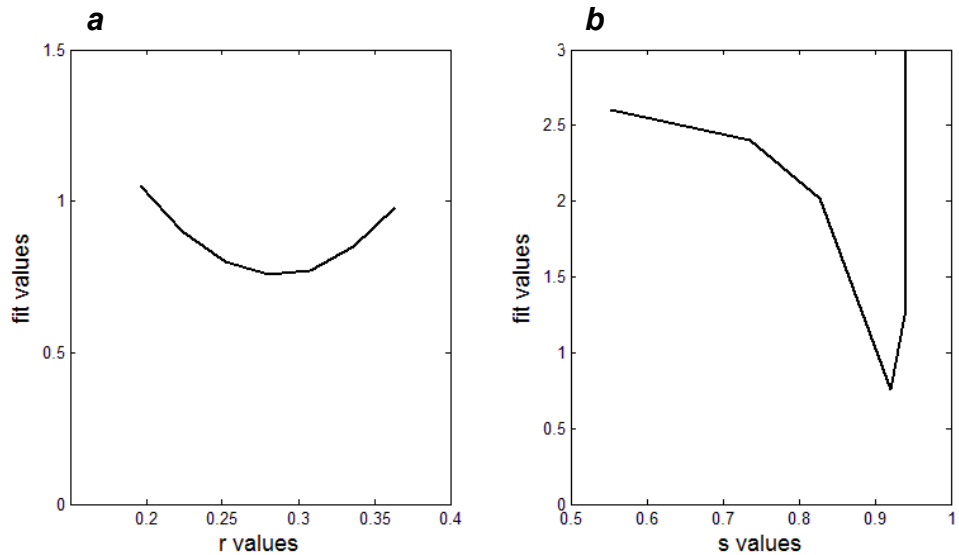
## **2.1. Sensitivity analysis: influence of the parameters on the size distribution**

We conducted a preliminary sensitivity analysis of the model by testing the sensitivity of the model to the parameters  $s$  and  $r$  by observing the evolution of a fit when changing the values of  $r$  (**Figure 13a**) and  $s$  (**Figure 13b**).



**Figure 12:** Evolution of the large deep category density (blue) through time for different values of survivorship ( $s$ ) red lines are the carrying-capacity (mean density of Bonaire for large deep fish), black dots lines are the bounds of the 95%CI

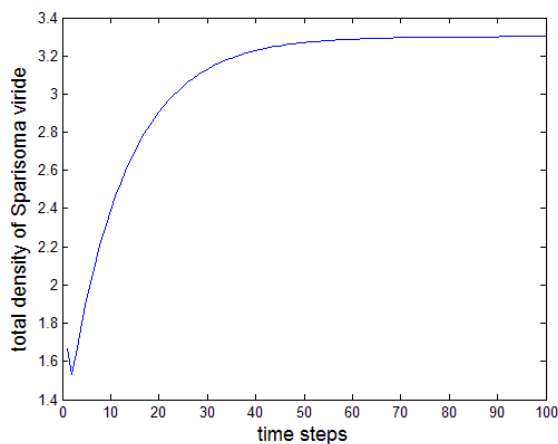




**Figure 13:** Evolution of fits ( $F_{val}$ ) for different values of  $r$  (a) and  $s$  (b)

## 2.2. Recovery of the population after fishing disturbance

We simulated a fishing disturbance on the model at equilibrium to test the ability of the model to reproduce the recovery observed in Bermuda after the fishing ban. After simulating the virtual fishing disturbance, the maximum of the total density of *S. viride* is reached after 80 time steps which represent 20 years (**Figure 14**). Note the decrease of the total density at the first time step due to the application of the natural mortality at the beginning of the time step.



**Figure 14:** Evolution of the total density of the parrotfish population after fishing disturbance

## 3. Discussion

This study aimed at developing a population model of *S. viride* to help understanding its dynamics and the influence of various demographic processes on its size distribution. The model presented here must be considered as a preliminary approach, and further exploration of model behaviour and sensitivity will be necessary for the development of a robust modelling tool for parrotfish management. However, at this stage, the ability of the model to reproduce population size structure as observed on different Caribbean reefs is

quite satisfying. In the following, we discuss the model structure and behaviour, the results of the model and we establish priorities for future work with the model.

### **3.1. Model structure and behaviour**

#### **3.1.1. Model structure**

Our model is structured by size classes which is an advantage in the context of fisheries. Indeed, the model recreates a size distribution. Therefore, the effect of different fishing scenarios on the size distribution of *S.viride* could be explored. The structure by habitat categories was introduced only to implement the density dependence in the deep habitat. There is, however, no current evidence in other populations of *S.viride* that such a spatial and social structure exist. Yet, applying the model to other parrotfish populations would just require the suppression of the large deep fish category. The model could also be used with its structure in size classes only. The originality of this model stands in its flexibility which is a high advantage for the generalisation of this model.

#### **3.1.2. Model processes**

Regarding our results, it appears that a constant survivorship rate per size class is satisfying to reproduce the size distribution observed in Bonaire. In addition, the optimised survivorship is very close to Choat *et al.* (2003) estimated survivorship. The size dependent mortality did not provide a better fit and we followed the parsimony principle and decided to build our model with the constant mortality per size. Moreover, the slope of both linear and exponential mortality functions was estimated close to 0. This means that the resulting shapes of the linear and negative exponential curves are very close to a constant mortality rate per size.

Recruitment was implemented as an addition of 5cm individuals at each time step, and a value of 0.28 fish per 3 month was satisfying to reproduce the size distribution of Bonaire with the model. However, 5cm is an arbitrary value and this implementation may need to be adapted when applying the model to other sites of the Caribbean, or to other parrotfish species. Indeed, some parrotfish species settle on the reef at a length of about 10cm. *S.viride* arrives on the reef at a length of 1cm which is very specific to this species of parrotfish.

Density dependence in the deep habitat was implemented as a simple logistic function. Our results, with optimised values of survivorship  $s$  and recruitment  $r$ , showed that the carrying capacity (KLd) is not reached by the large deep category. The ability for the large deep fish to reach their carrying capacity is dependent from the value of the mortality. If the survivorship is lower than 0.95, the carrying capacity of large deep fish is not reached and their density remains lower than  $KLd=0.67$ . When the survivorship is equal to 0.95 or higher, the large deep category is able to reach its carrying capacity. Indeed, with a higher survivorship, the large deep fish can regenerate more rapidly by transition from large shallow fish. Other formulations could be considered to accelerate the transition of large shallow fish to the large deep category in order for them to reach the carrying capacity at optimised values of  $s$  and  $r$ . Other ways to formulate could also improve the size distribution of the large deep classes (d30-34cm and >35cm FL) estimated by the model.

#### **3.1.3. Model optimisation**

We made the choice to optimise the model using the density of the 9 size classes instead of using the density of the 3 habitat categories. This could explain why the model densities of the habitat categories are relatively lower from the ones in Bonaire. Habitat categories were created only to implement the density dependence therefore optimising with them would not have been relevant of the purpose of this study which was reproducing the size distribution of Bonaire. Future work may include the development of a multi-objective optimisation, where the size classes and habitat categories constitute two separate

objectives. Finally, the method we used to optimise the model was looking for the minimum of the sum of squared differences between observations and model estimations. This method is based upon a strong assumption stating that the distribution of the residuals is a Normal distribution. Other criteria may be used in the future, such as the maximum likelihood.

## 3.2. Model results

### 3.2.1. Growth

We estimated Linf and K from size-at-age data. Our estimated values were identical to those obtained in Choat *et al.* (2003) using the same dataset. The influence on the model of other values of Linf and K could be tested to assess the ability of the model to reproduce the size distribution of other *S. viride* populations. The growth transition matrix from Chen *et al.* (2003) used in our model takes in consideration that the growth rate of smaller fish is higher than the growth rate of larger fish within the same time step. This could explain the ability of the model to reproduce well the size distribution although the densities of the size classes are globally underestimated.

### 3.2.2. Recruitment

The model estimated a constant recruitment at 5cm of 0.28 fish per 100m<sup>2</sup> every 3 months. This value was compared to abundance data of 5cm individuals of *S. viride* from previous surveys performed in Belize and Bahamas. We calculated a global mean density of fish of size range 4-6cm for four sites of Belize and Bahamas (Table 9). The reason of considering a range of sizes around 5cm is that the precision in the visual estimation of fish size varies with the observed and the survey method (Thompson and Mapstone 1997; Edgar *et al.*, 2004). Choosing 5cm as the size of recruitment in the model is arbitrary and choosing 4cm or 6cm would not have impacted significantly the estimations of the model. Therefore, calculating the mean density of fish of size range 4-6cm smoothed the errors due to observations. The value of recruitment estimated by the model is relatively close to the average densities of fish of the considered sizes (4-6cm) recorded in Belize and the Bahamas, although densities vary from place to place. Note that the value of 0.20 fish per 100m<sup>2</sup> recorded for ECLSP (Bahamas) marine reserve is very close to the value estimated by the model for Bonaire, a reef with a very low fishing pressure.

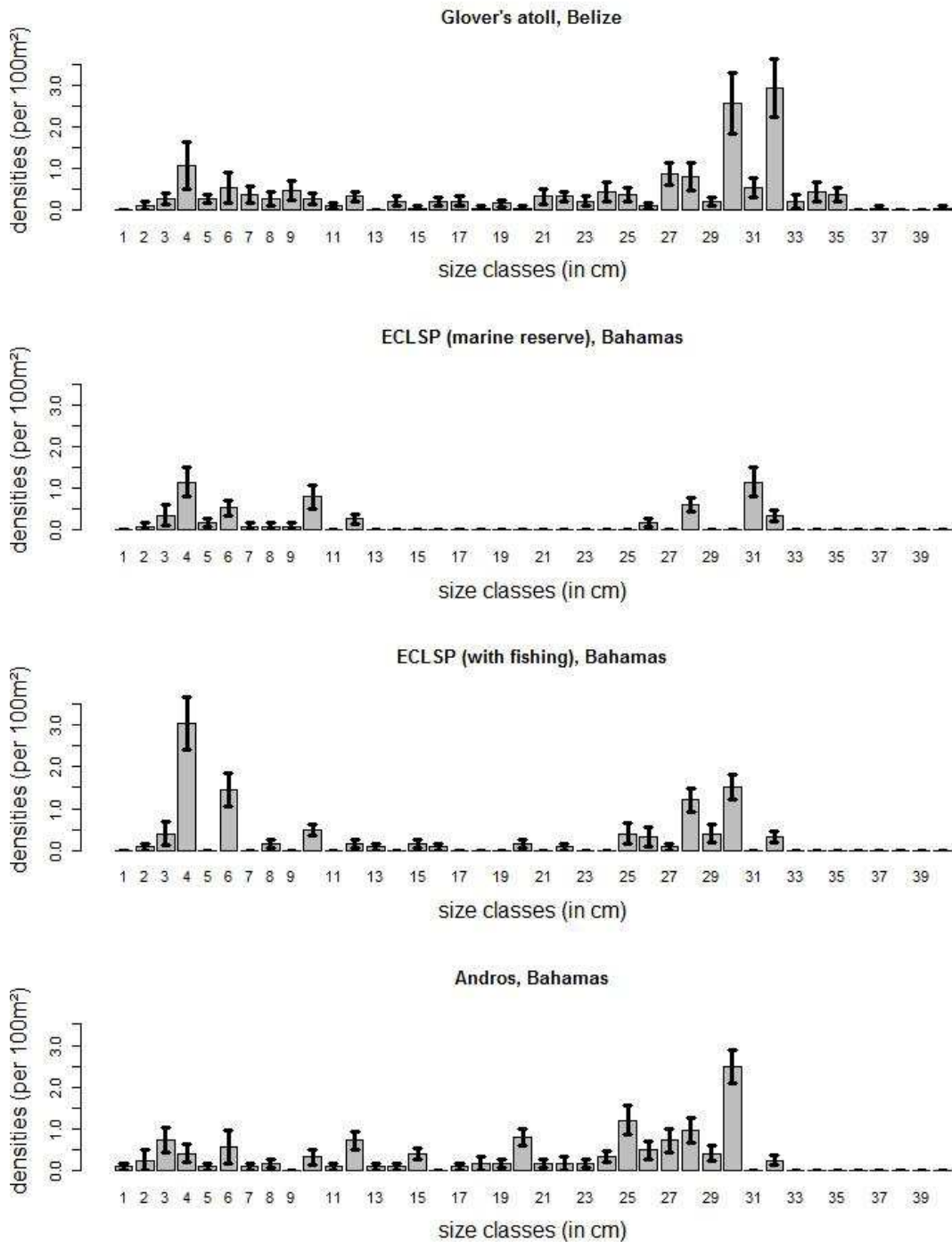
**Table 9:** Densities of mean densities of the 4, 5, 6 cm fish for Glover's reef and 3 sites of the Bahamas

r, model estimation	Glover's reef (Belize)	Andros (Bahamas)	ECLSP, with fishing (Bahamas)	ECLSP, marine reserve (Bahamas)
0.28	3.52	0.23	1.49	0.20

### 3.2.3. Size distribution at equilibrium

At equilibrium, the model represented the bimodality in the size distribution observed in Bonaire. This bimodality is also observed in other populations of *S. viride*, such as in Belize and in the 3 sites of the Bahamas (Figure 15). Two density peaks can be noticed: one for the classes of the smallest fish (<10cm FL) and another one for the largest fish (>30cm FL). If the density is well reproduced for the largest size classes, the model, however, seems to

underestimate the density of fish below 10cm FL. Unlike other species of parrotfish, *S. viride* has a short pelagic stage (van Rooij *et al.*, 1996b). Some parrotfish species settle on the reef at a length of about 10cm (van Rooij *et al.*, 1996b). This early settlement could explain the bimodality observed for *S. viride* whereas a single modality, higher number of big fish, is observed for other species of parrotfish.



**Figure 15:** Size distribution of *Sparisoma viride* in Belize and Bahamas, bars are the mean densities per size class with associated 95%CI

When using a different time step (12 months), the size distribution is different from the one with a time step of 3 months. The densities of size classes below 20cm FL are nearly null. Indeed, with a larger time step, all the recruits arriving in the model at 5cm grow straight to 20cm FL within 12 months which explains the null densities for the size classes below 20cm.

### 3.3. Sensitivity analysis of the model

Our sensitivity analysis of the model to the survivorship and the recruitment parameters is preliminary. The evolution of the fit when the value of one the parameter varies shows that the model seems to be more sensitive to a variation of the survivorship than a variation of the recruitment. However, both the survivorship and the recruitment were made to vary between + and – 30% of their optimised value with a 10% increment and variation of 10% does not have the same ecological meaning for the survivorship and the recruitment. Indeed, increasing or decreasing by 10% of the survivorship has an important impact on the population, whereas increasing or decreasing the recruitment by 10% has a limited impact on the population, especially considering the low number of recruits at each time step (0.28 per 3 months). This choice of making both parameters vary within the same range of values could explain the differences observed on the variation of the fit. These assumptions would need further exploration by assessing the impact on the size distribution at equilibrium and the habitat categories. Other methods could be developed to provide a better sensitivity analysis of the model.

### 3.4. Recovery after fishing disturbance

After simulating a virtual fishing disturbance on Bonaire parrotfish population, the time of full recovery estimated by the model (20 years) is 3 times more than the recovery time observed in Bermuda (8 years). Several reasons may explain such differences in the recovery rate: 1) a different mortality rate between Bonaire and Bermuda; 2) a different growth rate; 3) difference in the recruitment.

(1) In Bermuda the fishery ban only concerned the use of traps (which mainly catch parrotfish species), whereas other fishing gears, such as hook-and-lines, were still in use. Hook-and-line targets especially carnivorous fish such as groupers and snappers which are parrotfish main predators. Because the abundance of predators was still low after the ban of trap fishing (O'Farrell, 2011), a much lower mortality rate may explain a faster recovery in Bermuda than the one simulated for Bonaire.

(2) Von Bertalanffy parameters, Linf and K, are specific to each parrotfish population. As shown in Choat *et al.* (2003) the variability of Linf between 4 different parrotfish populations is important (Linf in SL from 263mm to 357mm). Bonaire and Bermuda are located geographically far from one another: Bonaire 12° 9' N, Bermuda 32° 19' 59" N. Therefore, the environmental conditions such as the water temperature and the ecological conditions are different between these two sites. As a consequence, the growth may be different between the populations in Bonaire and Bermuda and this may influence the speed recovery. However, such an assumption is unlikely to explain a faster recovery rate in Bermuda since we expect growth rate to be lower at higher latitudes.

(3) Recruitment could also be a factor influencing the speed recovery. Parrotfish populations with higher recruitment may show faster recovery. In Bermuda, fish smaller than 5cm did not show any increase after the fishing ban (O'Farrell, 2011), indicating the absence of a clear stock-recruitment relationship. *S. viride*, however, may recruit at a much higher rate in Bermuda compared to Bonaire. Future work will compare the abundance of small fish in the

two islands, which was not possible to assess for the present work due to incomplete data sets.

### 3.5. Future work with the model

In this study, we created a model that aims at becoming a useful tool for fisheries management to implement local actions to protect parrotfish and then maintain serviceable levels of fish herbivory on the Caribbean coral reefs. Indeed, this model will give the possibility to create different fishing scenarios by applying “Slot” fishing which consists in simulating fishing pressure on a particular size or on a group of sizes to predict the impacts on size distribution of the population. The purpose of such a model is to determine the threshold of fishing level where herbivory becomes too low for coral reef to maintain a coral-dominated state. This means determining the Maximum Sustainable Yield (MSY) of *Sparisoma viride*, and converts it in grazing rate. Indeed, a future extension of this work will be to associate this model to a model of coral reef ecosystem, ReefMod (Mumby *et al.*, 2006; Edwards *et al.*, 2011), which describes coral-algal dynamics controlled by herbivory. The purpose of coupling the two models is to explore the impact of fishing on coral-algal phase shifts, through the response of herbivory. However, reef supplies many nations in goods, and maintaining a certain level of fishing is vital. The model could be used to find a compromise between a functional grazing rate and the supply in marine resources for nations. Finally, this model may also be useful to explore the effect of an area closure on herbivory, and to predict the recovery rates of this crucial ecological function. However, fishermen need to be convinced of the benefits for themselves of an area closure. Therefore, the data and the predictions given by the model will help simulating the long term benefits of an area closure. The benefits will be ecological as an area closure is assumed to increase the levels of parrotfish biomass and also economical for the fishermen as the area closure will allow them to continue fishing in the long term.

## Conclusion

A population model of the Stoplight parrotfish (*Sparisoma viride*), an important herbivorous fish of Caribbean coral reefs, was developed to support the management and conservation of reef resilience. This study aimed at improving the knowledge of parrotfish dynamics to support the implementation of efficient management actions. The originality of the model created in this study is its structure in size and its flexibility for adaption to other populations of other sites of the Caribbean and other species in the future. Our calibrated model reproduced well the size distribution of the population of *S. viride* observed in Bonaire. When applying a virtual fishing disturbance, the calibrated model simulated a full recovery but at a much slower speed (3 times slower) than observed in Bermuda. Among other assumptions, the fast recovery observed in Bermuda could be due to a much lower mortality of *S. viride*. This preliminary model is a first step towards the development of a modelling tool in support of fisheries management and conservation in the Caribbean. Being the main herbivores on today Caribbean reefs, parrotfish are essential for the maintenance of corals face to global warming-induced disturbances. This model may thus become a useful tool for the exploration of fishing and conservation scenarios on herbivory and reef resilience in the Caribbean. Among others, future works based on our model could aim at (i) predicting herbivory levels after application of fishing scenarios, (ii) elaborating a trade-off between the protection of parrotfish and fishing activities (iii) providing a time frame for fishermen of the recovery of the population of *S. viride* after implementation of a marine reserve.

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Titre français: Un modèle de dynamique des populations de poissons perroquets (famille : *Scaridae*) pour la gestion de l'herbivorie des récifs coralliens des Caraïbes

Titre anglais : A dynamic model of parrotfish (family : *Scaridae*) populations for the management of herbivory on Caribbean coral reefs

**Abstract:** A population model of the stoplight parrotfish (*Sparisoma viride*), an important herbivorous fish of Caribbean coral reefs, was developed to support the management of reef resilience. The model is in discrete-time and structured by size and habitat occupation, and simulates the abundance of *S. viride* as a function of natural mortality, individual growth, and recruitment. Habitat occupation for large fish is driven by density-dependence in deep reef habitats, as suggested by observations of a limited number of mature adults on deep reefs due to territoriality. The model was developed and calibrated with a time series of *S. viride* abundance in Bonaire (Southern Caribbean), a marine reserve, where the population is assumed to be at equilibrium. With parameter values derived from the literature, the model was able to reproduce the size distribution of the parrotfish population. Different mortality functions were tested, and optimisation results showed that a size-dependent mortality did not improve much the model fit compared to a constant mortality per size. With the calibrated model, we then explored the ability of the parrotfish population to recover from a depleted stock by simulating a fishing disturbance similar in proportion to that experienced by *S. viride* in Bermuda (Northern Caribbean) before a fishery ban was implemented. The calibrated model simulated a full recovery at a much lower speed (3 times slower) than observed in Bermuda. Among other assumptions, a much lower mortality of *S. viride* in Bermuda is suggested to explain this difference. Being the main herbivores on today Caribbean reefs, parrotfish are essential for the maintenance of corals face to global warming-induced disturbances. Thus, this preliminary model may become a useful tool for the exploration of fishing and conservation scenarios on herbivory and reef resilience in the Caribbean.

**Résumé:** Un modèle des populations du poisson perroquet feu (*Sparisoma viride*), un poisson herbivore très important sur les récifs coralliens des Caraïbes, a été développé pour soutenir la gestion de la résilience des récifs. Ce modèle discret est structuré en tailles et par occupation d'habitat, et simule l'abondance de *S. viride* en tant que fonction de la mortalité naturelle, de la croissance individuelle et du recrutement. Les catégories d'habitat des plus grands poissons sont basées sur la densité dépendance dans l'habitat profond du récif, inférée par un nombre limités de mâles matures dans cet habitat profond lié à la territorialité. Le modèle a été développé et calibré avec une série temporelle d'abondance de *S. viride* à Bonaire (Caraïbes Sud), une réserve marine où la population est supposée être à l'équilibre. Avec des valeurs de paramètres dérivés de la littérature, le modèle a pu reproduire la distribution de taille de la population de poissons perroquet de Bonaire. Différentes fonctions de mortalités ont été testées, et les résultats de l'optimisation ont montré qu'une mortalité dépendante de la taille n'améliorait pas significativement le fit du modèle comparé à une mortalité constante par taille. Nous avons exploré l'habilité du modèle à reproduire le recouvrement d'une population de poissons perroquet en simulant une pression de pêche similaire en proportion à celle expérimentée par *S. viride* aux Bermudes (Caraïbes Nord) avant l'implémentation d'un moratoire de pêche. Le modèle calibré a simulé un recouvrement total mais 3 fois plus long qu'aux Bermudes. Parmi d'autres hypothèses, une mortalité bien plus faible de *S. viride* aux Bermudes expliquerait cette différence. Etant aujourd'hui les herbivores principaux sur les récifs des Caraïbes, les poissons perroquets sont essentiels pour le maintien des coraux face aux changements globaux. Ainsi, ce modèle préliminaire pourrait devenir un outil pour l'exploration de scénarios de pêches et de conservation sur l'herbivorie et la résilience des récifs.

**Mots-clés :** poissons perroquets des Caraïbes, dynamique des populations, modèle structuré en taille, densité à l'équilibre, rétablissement après moratoire de pêche

**Key words :** Caribbean parrotfish, population dynamics, size-structured model, equilibrium density, recovery after fishing

