# BIO-ÉCOLOGIE ET AQUACULTURE DU SIGAN CORDONNIER *Siganus sutor,* DANS UN CONTEXTE DE CONSERVATION ET DE SECURITE ALIMENTAIRE

**Thèse en cotutelle**

Université de Toliara, Madagascar

Et

Université de Liège, Belgique

**Présentée pour l'obtention de grade de Docteur :**

En Océanographie appliquée : E.D. Sciences Marines et Halieutiques (U. Toliara)

En Sciences : E.D. Océanographie (U. Liège)

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# Résumé

La forte pression de la pêche à Madagascar causée par la pratique de technique de pêche non réglementée combinée au manque de mesures de protections sur les poissons marins menace le stock de poisson marin. Cette thèse s'inscrit dans ce contexte de surexploitation des ressources halieutiques à Toliara, Madagascar, et explore les potentialités du poisson corallien, Sigan cordonnier ou *Siganus sutor* (*S. sutor*), comme espèce modèle pour des pratiques de pêche durable et d'aquaculture respectueuse de l'environnement. Le choix de cette espèce réside sur son abondance dans les captures dans les filets à moustiquaire (40% des captures). En plus de cela, c'est une espèce qui joue un rôle important dans la résilience des récifs coralliens en tant que poisson herbivore. Et sans oublier sa valeur commerciale (très apprécié par la communauté locale) et territoriale (endémique de la région Ouest de l'Océan Indien. Cette thèse s'intitule bio-écologie et aquaculture du Sigan cordonnier *Siganus sutor*, dans un contexte de conservation et de sécurité alimentaire. Elle a pour objectif de connaitre la biologie et l'écologie du *S. sutor* sur le Grand Récif de Toliara ainsi que de démontrer la faisabilité de son grossissement en milieu contrôlé.

La première partie de l'étude a porté sur la distribution spatiale et temporelle des juvéniles et des adultes de *S. sutor* dans la baie de Toliara. Les résultats ont montré que cette espèce effectue une migration ontogénétique entre les habitats côtiers et récifaux. En effet, les juvéniles sont principalement associés aux herbiers marins, en particulier dans les zones peu profondes protégées, tandis que les adultes sont plus abondants sur la grande barrière récifale et dans la pente externe. Les juvéniles colonisent la zone des herbiers, considéré dès lors comme leur zone de nourricerie et leur colonisation connait une variation saisonnière avec deux pics qui occurrent en janvier et en août.

Deuxièmement, l'analyse du régime alimentaire a été réalisée dans le but d'étudier des variation spatio-temporelle et aussi ontogénétique. Les résultats de l'analyse des contenus stomacaux combinés à ceux des analyses de l'isotope stable (C, N, S) ont révélé un régime à tendance omnivore chez les juvéniles avec prédominance de macroalgues, phanérogames marine et de proies benthiques mobiles. Les adultes consomment le même groupe de proies par contre la proportion de nourriture à base de plante prend de plus grande proportion. Une corrélation positive existe ainsi entre la taille des individus et l'abondance des proies végétales. Par contre, la corrélation est négative quand il s'agit des proies animales. Cette variation ontogénétique est reflétée sur une augmentation progressive de la longueur du tube digestive au cours de la croissance des individus. Cette croissance s’explique par la digestibilité du tube digestive dont la digestion dure beaucoup plus longtemps que pour les proies animales.

La troisième partie de cette thèse est consacré à l’étude du cycle de reproduction et la taille à la première maturité du *S. sutor.* La combinaison de l’étude de l’indice gonadosomatic avec l’étude histologique des gonades des poissons a permis d’étudier la biologie reproductive de cette espèce. Les résultats ont révélé que cette espèce présente une ponte biannuelle avec deux pics en saison fraiche (juillet) et en saison chaude (décembre à mars). La taille à la première maturité de cette espèce a aussi été déterminée à 20,84 cm et 21,38 cm (longueur totale) chez les femelles et les males respectivement.

Enfin, les trois expérimentations menées sur les post-larves et les juvéniles de *S. sutor* ont montré l’efficacité de l’élevage en captivité de cette espèce. Cette partie de la thèse servait à optimiser les paramètres d’élevage de cette espèce en se basant essentiellement sur les connaissances sur sa bio-écologie. Ainsi deux densités d’élevages et quatre différents types d’aliments ont été testé. Les résultats ont montré une différence significative de la croissance et la survie des *S. sutor* en fonction de la densité d’élevage et le type d’aliment. Parmi les aliments testés, la provende industrielle présentait de meilleur croissance alors que le riz cuit présentait le meilleur taux de survie. La provende formulée à base de laisse de marée, quand-à elle, représentait le prix le plus bas.

En conclusion, les résultats de cette étude ont permis de déterminer les habitats et moments clés à la survie des *S. sutor* aussi bien pour les juvéniles que les adultes. Cette étude a alors démontré le potentiel de *S. sutor* pour le développement d’une aquaculture durable à Madagascar, tout en renforçant les bases scientifiques pour une gestion écosystémique de la pêche artisanale.

# Abstract

Intensive fishing pressure in Madagascar, driven by unregulated fishing techniques and the lack of protective measures for marine fish, poses a serious threat to fish stocks. This thesis addresses the issue of overfishing in Toliara, Madagascar, by exploring the potential of the coral reef fish *Siganus sutor* (commonly known as the whitespotted rabbitfish) as a model species for sustainable fishing and environmentally friendly aquaculture. The choice of this species is based on its high abundance in mosquito net fisheries (accounting for 40% of catches), its ecological importance as an herbivore supporting coral reef resilience, its commercial value, and its endemic status in the Western Indian Ocean.

Entitled Bioecology and Aquaculture of the Whitespotted Rabbitfish (*S. sutor*) in a Context of Conservation and Food Security, this research aims to investigate the biology and ecology of *S. sutor* in the Grand Reef of Toliara and to assess the feasibility of rearing this species in controlled environments.

The first part of the study focused on the spatial and temporal distribution of juveniles and adults in Toliara Bay. Results showed an ontogenetic habitat migration, with juveniles primarily associated with shallow seagrass beds in sheltered areas, while adults were more abundant on the outer slope of the barrier reef. Juveniles colonize seagrass beds considered as nursery grounds, with two seasonal peaks in January and August.

The second part analyzed the species' diet to explore spatial, temporal, and ontogenetic variation. Stomach content and stable isotope analyses (C, N, S) revealed that juveniles have an omnivorous diet dominated by macroalgae, seagrasses, and mobile benthic prey. Adults consume similar groups, but with an increasing proportion of plant-based items. A positive correlation was observed between fish size and plant matter abundance, and a negative correlation with animal prey, reflecting a progressive increase in gut length as fish grow—an adaptation to the longer digestion time required for plant material.

The third section focused on the reproductive cycle and size at first maturity. Combined gonadosomatic index measurements and histological analysis of gonads showed that *S. sutor* spawns twice a year, with peaks in the cooler season (July) and the warm season (December to March). The size at first maturity was estimated at 20.84 cm for females and 21.38 cm for males (total length).

Finally, three aquaculture experiments on post-larvae and juveniles demonstrated the species' potential for captive rearing. Based on its bioecology, two stocking densities and four feed types were tested. Growth and survival varied significantly with density and diet. Industrial feed led to the best growth, while cooked rice gave the highest survival rate. Feed formulated from beach wrack proved to be the most cost-effective.

In conclusion, this study identified key habitats and periods critical to the survival of *S. sutor* at different life stages. It demonstrates the species' potential for the development of sustainable aquaculture in Madagascar, while contributing to ecosystem-based fisheries management for small-scale coastal communities.

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# Chapitre 1 : Introduction générale

## 1. Introduction aux pêches maritimes et aux défis mondiaux

Les ressources halieutiques contribuent considérablement à l'apport mondial en protéines. Le poisson représente notamment environ 16 % des apports protéiques d'origine animale (Sanchirico & Wilen, 2007). En 2018, la production mondiale de poissons a atteint 179 millions de tonnes dont 54% issues de la pêche. Un total de 156 millions de tonnes de cette production a été utilisé pour la consommation humaine, ce qui équivaut à un approvisionnement annuel estimé à 20,5 kg par habitant. Les 22 millions restant ont été destinés à une utilisation non alimentaire essentiellement pour la production de farine ou d'huile de poisson (FAO, 2020). De plus, la pêche constitue une source vitale de revenus et d'emplois pour de nombreuses personnes, en particulier dans les pays en voie de développement (Delgado et al., 2003).

Actuellement, les pêcheries du monde entier sont considérées comme étant en crise, entraînant une insécurité alimentaire et des menaces sur les moyens de subsistance dans les régions des pays en développement qui dépendent de la pêche (Allison, 2001). De plus, la pêche a un impact sur les ressources ciblées et peut également causer de graves dommages aux espèces, habitats, structures et fonctions non ciblés dans les écosystèmes marins (Hilborn, 2007). Il a été prouvé que la principale cause de dégradation mondiale des écosystèmes côtiers liée à l'action de l'homme est la surpêche (Jackson et al., 2001). En effet, la surpêche, se définissant par le prélèvement de biomasse sur une population marine supérieure à ce que celle-ci peut remplacer, a des conséquences irréversibles sur de nombreuses pêcheries dans le monde (Froese & Kesner-Reyes, 2002; Pauly et al., 1998; Srinivasan et al., 2010).

En plus du prélèvement de la biomasse, le déploiement d'engin de pêche destructeur est aussi un problème rencontré dans le secteur. Les engins de pêche actifs de contact avec le fond, comme les chaluts de fond, sont connus pour être un des engins de pêche les plus destructeurs en raclant le fond des habitats marins (Kaiser et al., 2002, 2003). De plus, la pêche industrielle aux chaluts de fond produit le plus grand rejet de « by-catch », c'est-à-dire la capture accidentelle d'espèces inutilisées ou non gérées (Kennelly & Broadhurst, 2002; Zeller et al., 2018). Ces pratiques ont des effets écologiques à la fois directs et indirects (Lewison et al., 2004), réduisant les populations (Heppell et al., 2000) et modifiant le système trophique dynamique des systèmes océaniques (Estes et al., 2011; McCauley et al., 2015).

La pêcherie récifale désigne l'ensemble des activités de capture ciblant les ressources biologiques associées aux écosystèmes récifaux, notamment les récifs coralliens. Ces écosystèmes, caractérisés par leur haute biodiversité et leur complexité écologique, fournissent des habitats essentiels pour de nombreuses espèces marines d'intérêt commercial ou de subsistance (Ferraris et al., 2004). La pêcherie récifale ne contribue que pour une petite fraction aux rendements halieutiques mondiaux (Pauly et al., 2003), représentant officiellement environ 10 % du total des débarquements mondiaux de la pêche maritime (FAO, 2020). Cependant, cette pêcherie est une source vitale de revenus et de protéines pour des millions de personnes, en particulier dans les pays en développement (Sadovy, 2005). Outre l'impact des grands chaluts déployés en haute mer, les petits chaluts de type senne, couramment utilisés par les pêcheurs artisanaux (ou « petits » pêcheurs), exercent également une pression considérable sur les écosystèmes marins (Tillin et al., 2006). Cet impact est particulièrement observable dans les pêcheries récifales, où ces engins peuvent altérer les habitats benthiques et affecter la dynamique des populations d'espèces ciblées et non ciblées (Newton et al., 2007).

L'Organisation des Nations Unies pour l'alimentation et l'agriculture (FAO) a tiré la sonnette d'alarme à plusieurs reprises face à des menaces sur le stock de poissons sauvages et a classé la plupart des poissons sauvages de soit pleinement exploitées, soit surexploitées (FAO, 2020). De plus l'étude de la FAO sur la production relative aux captures mondiales a révélé que les captures de la pêche à Madagascar sont en diminution (FAO, 2020). Les résultats de l'étude menée par Newton et al. (2007) sur la comparaison de l'état des pêcheries récifales sur plusieurs îles du monde ont classé les ressources des récifs coralliens de Madagascar comme étant surexploitées (Fig. 1.1). Dans le cadre des politiques de gestion et de développement des pêches, l'importance de la durabilité de la petite pêche est de plus en plus reconnue (Allison, 2001; Pauly & Chuenpagdee, 2003). Plus de 25 ans après l'adoption du Code de conduite des Pêches Responsables (FAO, 1995), l'importance de l'utilisation raisonnable des ressources de la pêche et de l'aquaculture est désormais largement reconnue et priorisée (FAO, 2020). Pour y parvenir, des politiques de gestion des pêches et de l'aquaculture fondées sur des données scientifiques, ainsi que des cadres prévisibles et transparents pour l'utilisation et le commerce international du poisson, sont largement reconnus comme des normes minimales essentielles pour une pêche et une aquaculture durables (FAO, 2020). Par exemple, en Afrique de l'Est, y compris Madagascar, la petite pêche a jusqu'à présent été gérée avec des restrictions sur les engins de pêche et la mise en place d'aires marines protégées (McClanahan & Mangi, 2004). Il existe généralement une taille minimale de capture et une taille minimale des mailles des filets mises en œuvre, mais l'application de ces restrictions est encore trop faible dans ces régions (Mangi & Roberts, 2006).

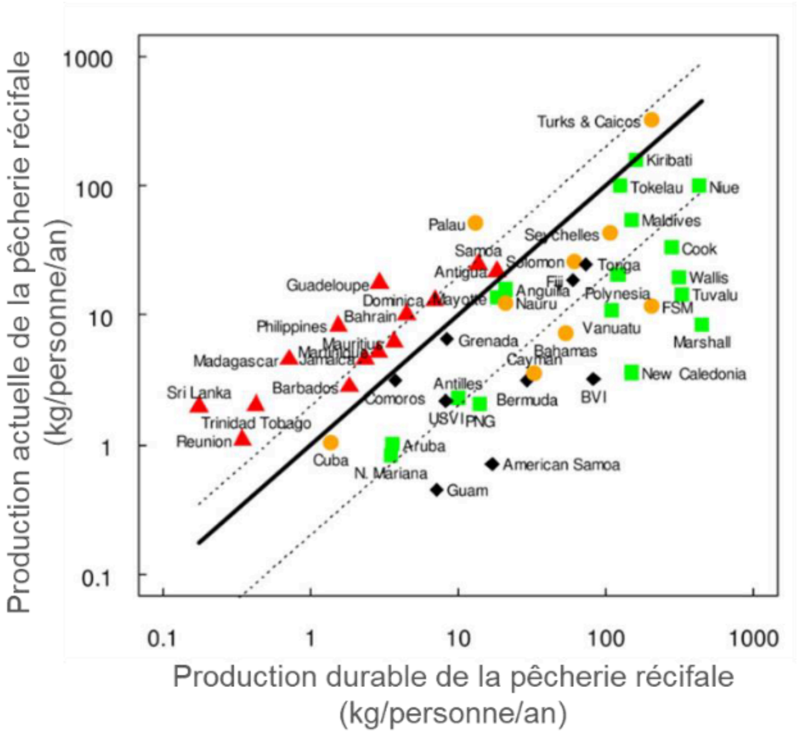

**Figure 1. 1.** Représentation de la production de la pêcherie récifale des îles. La ligne en gras représente une empreinte écologique de 1 (où la consommation de ressources équilibre la production durable de récifs, en supposant un rendement durable de 5 tonnes métriques (tm)/km$^2$/an). Les îles situées au-dessus et à gauche de la ligne grasse ont une empreinte non durable. L'état des pêcheries des récifs insulaires est représenté par quatre symboles : les carrés verts sont sous-exploités, les cercles orange sont pleinement exploités, les triangles rouges sont surexploités et les losanges noirs sont effondrés. Les lignes pointillées fines représentent les empreintes écologiques de 1 sous l'optimiste (ligne supérieure, 10 tm/km$^2$/an) et pessimiste (ligne inférieure, 1 tm/km$^2$/an). Scénarios MSY. Source : (Newton et al., 2007), modifié

## 2. Situation écologique et socio-économique de Toliara

Toliara est une ville portuaire clé du sud-ouest de Madagascar. Elle sert à la fois de centre régional de commerce et de centre administratif. Le littoral du sud-ouest de Madagascar est bordé par un des plus grands systèmes coralliens de la Terre, le Grand Récif de Toliara (GRT). Situé à moins de 2 km au large de la ville de Toliara, le GRT est un système de récif-barrière majeur de l'Ouest de l'Océan Indien. Il s'étend sur 19 km, entre le fleuve Fiherenana au nord et le fleuve Onilahy au sud. Ce récif représente environ 33 km² de zone récifale peu profonde à structure diversifiée (Andréfouët et al., 2013; Harmelin-Vivien, 1981; Harris et al., 2010; Pichon, 1978). Le GRT abrite la biodiversité marine la plus riche de l'ouest de l'Océan Indien avec 6 000 espèces répertoriées dont 700 de poissons de récif (Cooke et al., 2022). Le GRT a historiquement été l'écosystème le plus étudié de Madagascar et a fait l'objet d'efforts de recherche intensifs de la Station Marine de Toliara (devenue Institut Halieutique et des Sciences Marines) de 1961 à 1970 (Harris et al., 2010). Avec 62 genres de coraux répertoriés en 1978, le GRT avait à cette époque la diversité corallienne la plus élevée enregistrée dans l'ensemble de l'Indo-Pacifique (Pichon, 1978).

La population du Sud-Ouest de Madagascar est très dépendante des ressources marines pour leurs besoins alimentaires et monétaires (Chaboud, 2006). L'industrie de la pêche à Toliara soutient principalement les marchés locaux de subsistance. La petite pêche le long des côtes de Toliara a longtemps été pratiquée uniquement par le peuple « Vezo », le groupe ethnique le plus important de la région. Cependant, au cours des dernières décennies, d'autres groupes ethniques, notamment ceux impliqués dans l'agriculture et l'élevage, se sont également tournés vers l'exploitation des ressources côtières, entraînés par la baisse des rendements agricoles et de la productivité du bétail due à l'aggravation de l'aridité (Bruggemann et al., 2012; Chaboud, 2006). La pêche industrielle n'est pas pratiquée dans les eaux de Toliara (Chaboud, 2006; Laroche & Ramananarivo, 1995). Dans les années 1970, des bateaux à moteur étaient utilisés pour pêcher à l'intérieur et à l'extérieur du lagon. Ceux-ci ont disparu depuis 1984. De nos jours, la pêche se pratique à pied ou à partir de pirogues de 4 à 7 m de long, à voile ou à propulsion manuelle (Fig. 1.2) (Bruggemann et al., 2012).

**Figure 1. 2.** Petit pêcheurs à bord de leur pirogue à balancier remontant leur chalut à moustiquaire

Il est connu que la population malagasy ne cesse d'augmenter. Entre 1993 et 2018, la population de Madagascar a été estimée à 25 674 196 habitants, avec une densité moyenne de 43,3 habitants par kilomètre carré et un taux de croissance annuel de 3,01 % (Fig. 1.3) (Harivelo & Harifidy, 2022). Toliara n'échappe pas à cette croissance démographique. En effet, depuis les années 1960, la population de Toliara a augmenté rapidement, augmentant de 53 % entre 1993 et 2008 (INSTAT, 2017). La ville de Toliara comptait en 2018 près de 308 000 habitants (Ministère de l'économie et des finances, 2020).

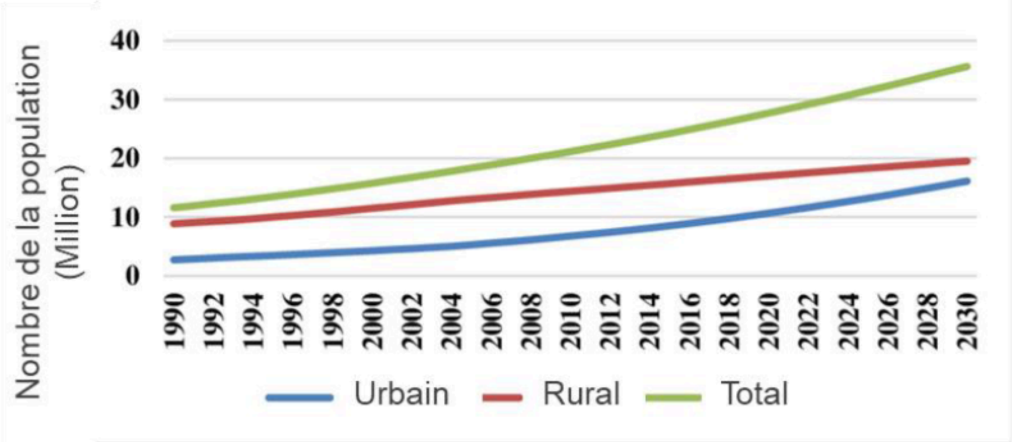

**Figure 1. 3.** Evolution de la croissance de la population de Madagascar avec une estimation jusqu'en 2023. Source : (Harivelo & Harifidy, 2022) modifié

## 3. La surpêche : une menace pour la durabilité des ressources marines à Toliara

La pression de pêche sur le GRT a augmenté avec la croissance démographique à Toliara générant une situation de surpêche et donc une dégradation l'état de santé du GRT. De plus, la forte sédimentation due au dépôt de limons et d'argiles des rivières voisines Onilahy et Fiherenana ont contribué à la baisse considérable de la couverture de coraux vivant sur le GRT (Harris et al., 2010). A cela s'ajoutent les conséquences du changement climatique et des phénomènes El Nino qui ont entrainés de sévères phénomènes de blanchissement des coraux sur le GRT en 1998 et entre 2015 et 2016 (Andréfouët et al., 2013; Obura, 2005; Obura et al., 2017). De récentes études ont démontré un retour récent vers des assemblages de coraux plus sains et plus diversifiés bien que la diversité enregistrée en 2021 restait encore inférieure à celle des années 1960 (Botosoamananto et al., 2021).

Le manque de réglementation en vigueur sur les engins de pêche fait en sorte que les pêcheurs utilisent des méthodes destructrices qui ont un impact considérable sur l'habitat marin et sur les ressources halieutiques. Il y a, par exemple, l'utilisation de barres et de coins en bois pour soulever et renverser les têtes de corail afin d'attraper les poulpes, les crustacés et les poissons cachés dans les crevasses (Langley, 2006; Raseta, 2020). Il est estimé que cette pratique détruit environ 1 km² d'habitat corallien chaque année sur les platiers récifaux du GRT (Salimo, 1997). Il y a aussi l'utilisation de chalut à moustiquaire à très petite maille (1mm) (Fig. 1.2) dont plus de la moitié de ses captures sont des poissons juvéniles (Jaonalison, 2019; Ranaivomanana et al., 2023). La dégradation des habitats marins associée à la forte pression de pêche a des impacts à la fois directs et indirects, affectant la communauté de poissons avec des réductions significatives de l'abondance des espèces (Bush et al., 2017; Russ & Alcala, 1989).

Les organisations œuvrant dans la conservation ont constaté une dégradation des milieux littoraux et de ses ressources à Madagascar depuis les années 1990 (Veriza & Couderchet, 2019). Avec la plus étendue zone côtière de la région est de l'Afrique, Madagascar a vu, au cours ces 30 dernières années, le développement d'une série d'activités importantes visant la conservation et la gestion de l'environnement côtier (Aricò & Rakotoary, 1997). Durant cette période, plusieurs ONG se sont implanté le long des côtes de Toliara avec la collaboration des autorités malagasy. Comme organisations de conservation de l'environnement pour le développement durable, il y a, du sud au nord : World Wildlife Fund (WWF), Wildlife Conservation Society (WCS), Reef Doctor (RD), Blue Ventures (BV) et Madagascar National Park (MNP) (Veriza & Couderchet, 2019). Ces ONG œuvrent dans la gestion et la conservation de différents types d'habitats marins (mangroves, herbiers, récifs, …) ainsi que les ressources dans leur zone d'intervention respective.

Toutefois, il manque toujours de règlementation sur les méthodes de pêche à Madagascar. Des périodes de fermetures temporaires des pêches aux poissons existent mais elles se limitent uniquement à la pêche continentale. Quant à la pêche en mer, les fermetures temporaires sont réservées uniquement à quelques produits tels que le poulpe, le crabe, la crevette et la langouste. Il n'existe pas jusqu'à présent de règlementation sur la fermeture temporaire de la pêche aux poissons marins dans des buts de conservation. Les autorités interdisent l'utilisation des engins destructeurs comme les chaluts à moustiquaire. Quand bien même, cela n'empêche pas les pêcheurs de certaines régions du pays de continuer à utiliser ces types d'engin, comme c'est le cas à Toliara.

Face à la diminution des stocks de poissons liée à la surpêche et à la dégradation des écosystèmes marins, il est essentiel de développer des solutions pour soutenir les communautés de pêcheurs tout en préservant les ressources marines. Parmi ces solutions, la promotion d'activités génératrices de revenus se distingue comme une approche durable et efficace. La pisciculture villageoise représente une solution prometteuse en permettant aux pêcheurs de diversifier leurs moyens de subsistance tout en participant à la conservation des écosystèmes marins. Une étude menée par Pomeroy et al. (2006) a mise en évidence la faisabilité financière et sociale de l'aquaculture comme alternative à la pêche sur les récifs coralliens dans la région Indo-pacifique. Les auteurs ont mis en avant plusieurs exemples concrets d'utilisation de l'aquaculture pour l'atténuation de la pression de pêche sur ces écosystèmes fragiles. Il y a l'exemple de l'aquaculture de poissons de récif destinés à la consommation humaine comme le mérou ayant pour but de répondre à la demande croissante tout en réduisant la surpêche des populations sauvages. En effet, l'élevage de ce poisson est largement développé en Asie comme le cas en Indonésie (Afero et al., 2010; Istiqomah et al., 2023) et dans le Pacifique, notamment en Australie (van Khoi et al., 2023). L'élevage se pratique principalement à partir de juvéniles issus du milieu naturel, pour répondre à une forte demande en mérous vivants à des prix élevés.

Cette pratique, axée sur l'élevage de poissons locaux peut être adaptée aux contextes communautaires à Madagascar grâce à des techniques simples, un faible investissement initial, et l'utilisation de ressources locales pour l'alimentation des poissons. En complément, des formations techniques et des initiatives de sensibilisation permettent d'autonomiser les pêcheurs dans la gestion de ces systèmes aquacoles, tout en renforçant leur engagement envers la protection des ressources naturelles. L'aquaculture villageoise n'est pas un sujet nouveau à Madagascar, car l'élevage de concombres de mer (Robinson & Benjamin, 2009; Vincent & Morrison-Saunders, 2013) et d'algues marines (Rodine et al., 2024) est déjà initié dans la région de Toliara pour soutenir la communauté locale de pêcheur. En offrant une alternative économiquement viable et écologiquement responsable, la pisciculture villageoise pourrait contribuer à réduire la dépendance à la pêche, à limiter la surpêche et à soutenir la résilience des stocks naturels de poissons marins.

Parmi les familles de poissons les plus exploités et prisés sur les marchés aux poissons de Toliara, il y a les : Lethrinidae, Siganidae, Lutjanidae, Gobiidae, Labridae, Blenniidae et Scaridae, (Ranaivomanana et al., 2023). Parmi ces familles, les Siganidae sont parmi les familles les plus fortement pêchées au stade de juvénile. En effet, dans les eaux du GRT, *Siganus sutor* représente près de la moitié des juvéniles pêchés par les chaluts à moustiquaire (Jaonalison, 2019). Or, l'écologie et la biologie de cette espèce endémique de la région Ouest de l'Océan Indien sont encore très méconnues (Woodland, 1990). Ces différentes raisons ont motivé le choix de cette espèce pour la présente étude. Il est important de mieux connaitre le mode de vie de cette espèce afin de mieux la conserver. Il est donc impératif d'identifier les habitats clés nécessaires à cette espèce, connaitre son cycle de vie et de comprendre les variations de sa biologie au cours de son ontogénie pour entreprendre des mesures adaptées et efficaces pour sa conservation. Ainsi, cette présente étude doctorale vise à approfondir les connaissances sur la biologie et l'écologie du *S. sutor* afin d'orienter la gestion durable de cette espèce, de soutenir sa conservation et de promouvoir des activités complémentaires à la pêche, telles que la pisciculture marine.

## 4. Biologie et rôles de *Siganus sutor*

Le sigan coordonnier, *S. sutor*, communément connu sous le nom de poisson-lapin, Margueritte ou « Amboramasaky » en malagasy, est un poisson téléostéen acanthomorphe (Grandcourt, 2002) appartenant à la famille des Siganidae (Fig. 1.4). Cette famille regroupant 32 espèces (Fricke et al., 2024) est connue comme étant largement répandue dans la région Indo-Pacifique (Froese et Pauly, 2024; IUCN, 2024), y compris la région orientale de la Méditerranée (Ben-Tuvia, 1966). *Siganus sutor* habite généralement les zones côtières peu profondes mais peut fréquenter des eaux jusqu'à 40m de profondeur (Woodland, 1983). Sa taille maximale avoisine les 45 cm (Woodland, 1990). Il se rencontre le plus souvent dans les herbiers à phanérogames marines en formant des bancs plus ou moins grands (Gilbert, 1993). Comme la plupart des poissons récifaux, *S. sutor* possède un cycle de vie complexe divisé en une phase larvaire océanique et pélagique et des stades juvénile et adulte démersaux associés à l'environnement côtier (Duray & Southeast Asian Fisheries Development Center, 1998a). À la fin du stade larvaire, les juvéniles migrent et colonisent généralement les habitats côtiers peu profonds tels les herbiers de phanérogames. Au stade adulte, ils se rencontrent dans les zones d'herbiers et les récifs coralliens (Ebrahim et al., 2020a; Maina et al., 2013).

**Figure 1. 4.** Aspect morphologique du Siganus sutor

*Siganus sutor* est un poisson herbivore (De la Torre-Castro et al., 2008; Harmelin-Vivien, 1981) et joue un rôle dans le maintien de l'état de santé des récif coralliens en contrôlant la prolifération des producteurs primaires benthiques, telles les macro- et microalgues (Burkepile & Hay, 2006; T. Hughes et al., 2007; Mumby, 2006). La présence de poissons herbivores a souvent été considérée comme un processus crucial façonnant les réponses des communautés benthiques face aux facteurs de stress associés à l'eutrophisation (Plass-Johnson et al., 2015). Au même titre que d'autres poissons herbivores, *S. sutor* joue des rôles cruciaux dans la dynamique des récifs tropicaux : (1) ils broutent des algues qui rivalisent en terme d'espace avec les coraux juvéniles ; (2) ils érodent les squelettes de coraux morts et contribuent ainsi à la production de sédiments récifaux ; et (3) ils constituent un lien trophique important entre leurs prédateurs et les producteurs primaires (Hughes et al., 2007). De plus, le broutage sur le socle corallien peut également pré-conditionner le substrat pour une meilleur fixation des larves de coraux, aidant ainsi à la résilience du récif (Bellwood et al., 2004).

En plus de ces valeurs écologiques, *S. sutor* possède aussi une valeur économique. En effet, c'est une espèce très appréciée en gastronomie en Afrique de l'Est, dans l'Océan Indien (Ebrahim, et al., 2020a; Mziray & Kimirei, 2016), en Asie du Sud-Est (Woodland, 1983) et au Moyen Orient (Shirinabadi et al., 2013). Avec une abondance stable toute l'année et une valeur économique variant de modérée à élevée, cela fait d'elle une espèce ciblée par la petite pêche (Visram et al., 2007). Ainsi, *S. sutor* participe au soutien de la petite pêche par un apport considérable aux revenus des petits pêcheurs locaux et contribue aux finances des familles œuvrant dans le secteur de la pêche.

Compte tenu de l'importance écologique et économique du *S. sutor*, très peu d'études ont été réalisées sur la biologie de cette espèce à Madagascar. Des recherches antérieures se sont principalement concentrés sur l'écologie de *S. sutor*, en particulier sur l'étude de son régime alimentaire. Ces recherches ont révélé la variation de l'écologie trophique de cette espèce, des connaissances essentielles dans le sauvegarde de cette espèce comme dans la promotion d'un aliment performant utilisé dans l'élevage de *S. sutor* à Madagascar.

## 5. Une connaissance parfaite de la biologie de *Siganus sutor* sur le GRT pour une politique de gestion efficace

Compte tenu de l'importance de *S. sutor* pour la petite pêche et la communauté qui en dépend, il est primordial de promouvoir une exploitation durable de cette espèce. Cependant, la forte dépendance de la population locale aux ressources marines (Gardner et al., 2016), associée à l'insuffisance des données sur les populations de poissons, entrave la mise en œuvre de mesures de conservation efficaces. Pourtant, une bonne gestion des ressources nécessite une grande connaissance de la biologie et de l'écologie de l'espèce. L'un des problèmes auquel il faut faire face est la surpêche. En effet, les communautés locales dépendent fortement de *S. sutor* pour leur nourriture et leur revenu. Des pratiques de pêche non durables, telles que la capture de juvéniles dans les zones de nourricerie (Jaonalison, 2019; Ranaivomanana et al., 2023) ou une pêche permanente y compris durant les saisons de reproduction, ont entraîné un déclin important des populations de poissons.

Les connaissances sur la biologie et l'écologie des poissons jouent un rôle crucial dans la conservation des espèces marines. La compréhension des cycles de vie et la connaissance des habitats clés pour la colonisation et la reproduction permet d'identifier des zones sensibles à la survie de cette espèce. Ces informations sont essentielles pour délimiter ces habitats et les protéger efficacement contre les pressions anthropiques. De plus, en analysant les périodes de reproduction des espèces, il est possible de mettre en place des fermetures temporaires de la pêche, permettant aux populations de se reproduire et de se renouveler sans perturbation. Ces mesures, basées sur des données scientifiques précises, contribuent à maintenir des stocks halieutiques durables tout en favorisant la résilience des écosystèmes marins face aux changements environnementaux et à la surpêche. De plus, étant donné l'importance du *S. sutor* pour la communauté côtière, la promotion de son élevage comme activité alternative est une solution efficace afin de réduire la pression de la pêche sur cette espèce.

## 6. L'aquaculture comme solution durable

En 2022, la production aquacole à Madagascar était de 30 000 tonnes/an. L'aquaculture de crevettes et d'algues marines produisent 23 130 tonnes/an, les 6 347 tonnes restantes sont issues de l'aquaculture continentale (Ministère de la pêche et de l'économie bleue malagasy, 2022). Ce rapport illustre le développement de l'élevage de poissons d'eau douce à Madagascar, faisant vivre plusieurs familles et entreprises à travers la grande île. Par contre, la production de poisson marin reste encore inexistante. Il faut admettre que la pisciculture de poissons marins est plus difficile que celle de poissons d'eau douce en raison de la nécessité d'une gestion précise de la qualité de l'eau, notamment du contrôle de la salinité, et d'un élevage de larves plus complexe, nécessitant souvent une alimentation vivante (Lindholm-Lehto, 2023; Melaku et al., 2024; Pan et al., 2022). Les poissons marins ont généralement des besoins alimentaires plus élevés en protéines, ce qui entraîne une augmentation des coûts, et sont plus sensibles aux maladies, ce qui nécessite des mesures de biosécurité avancées (Martinez-Porchas & Martinez-Cordova, 2012; Summerfelt & Vinci, 2008). De plus, les systèmes d'eau de mer nécessitent des infrastructures plus coûteuses et sont vulnérables aux fluctuations environnementales, ce qui les rend plus complexes à gérer que les systèmes d'eau douce relativement plus simples et plus abordables (Ifremer, 1987; Lazard, 2017).

En plus de l'exploitation du stock naturel, *S. sutor* a un potentiel en aquaculture. L'élevage des Siganidae a été initié durant les années 70 dans divers pays tels que l'Indonésie, les Philippines, le Kenya, le Tanzanie et l'Australie (Hasse et al., 1977). La combinaison de plusieurs facteurs comme la croissance rapide, la capacité de vivre en densité élevée, le régime alimentaire herbivore, … font des Siganidae une famille de poissons marins intéressante pour la pisciculture marine (Duray & Southeast Asian Fisheries Development Center, 1998a). Bien que l'élevage de Siganidae n'est pas encore développé à Madagascar, ce secteur peut être envisagé pour (1) l'aide au maintien des stocks naturels et pour (2) un apport supplémentaire en source de nourriture durable. Le développement de pratiques piscicoles durables pour le *S. sutor* serait intéressant. En effet, l'aquaculture offre une voie prometteuse pour garantir un approvisionnement stable en poisson sans surexploiter les populations sauvages (Naylor et al., 2000). Contrairement aux espèces comme les crevettes et le saumon qui nécessitent de grandes quantités de farine et d'huile de poissons (qui est une source d'épuisement des stocks de poissons sauvages), les espèces herbivores sont plus durables. Ils peuvent croître sans dépendre fortement de la pêche sauvage, ce qui en fait une option d'aquaculture plus respectueuse de l'environnement (Cao et al., 2015; Diana, 2009; Naylor et al., 2000).

En Afrique de l'Est, l'élevage de *S. sutor* a du potentiel mais reste encore à sa phase de développement avec l'application de l'aquaculture basée sur la capture et des essaies de fécondation en Tanzanie et au Kenya (Ateweberhan et al., 2018; Minyonga, 2022; Ntiba & Jaccarini, 1992). A Madagascar, la recherche sur l'aquaculture de *S. sutor* reste assez limitée, avec seulement un essai de grossissement en cage à Toliara mené par Rakotonirina et al. (2012). En plus de cela, un essai de grossissement de juvéniles de *S. sutor* en milieu fermé effectué durant mon mémoire de Licence en 2017 était très prometteur (Fig. 1.5). Ce travail démontrait la possibilité de l'élevage de cette espèce à Toliara, un potentiel qui reste encore non exploité malgré son importance pour la promotion de la pisciculture marine dans la grande île.

**Figure 1. 5.** Bac contenant des juvéniles de *Siganus sutor* pour un essai de grossissement à Toliara. Source : (Ravelohasina, 2017)**.**

## 7. Lacunes et apports de la thèse face à ces enjeux et problématiques

Malgré l'importance écologique et socio-économique de *S. sutor* à Toliara, de nombreuses lacunes subsistent quant à sa biologie et à son potentiel aquacole. Les données sur son cycle de vie, ses habitats critiques, et ses interactions trophiques restent limitées. Cela limite la compréhension de sa dynamique de populations, de son utilisation des habitats côtiers, de ses interactions écologiques au sein des récifs coralliens et des écosystèmes adjacents. Par conséquent, cet manque de connaissance entrave la mise en place de mesures efficaces pour sa gestion et sa conservation. Actuellement, les efforts de conservation locales (Province de Toliara) ciblent surtout les mollusques et crustacés, tandis que les politiques environnementales liées à la pêche demeurent peu développées.

Par ailleurs, bien que cette espèce soit prisée par les communautés locales, son élevage en captivité reste peu exploré, notamment en termes de grossissement, de production de nutrition adaptée et de prévention des maladies. Les lacunes scientifiques et techniques freinent le développement d'une pisciculture alternative et durable susceptible de réduire la pression de pêche sur les populations sauvages. Une étude approfondie sur la biologie et l'aquaculture de *S. sutor* est donc essentielle pour combler ces manques, favoriser la gestion durable des ressources marines et offrir des alternatives viables aux communautés de pêcheurs.

## 8. Objectifs de la thèse

Cette présente étude a pour objectif général de connaitre la biologie et l'écologie du *S. sutor* sur le Grand Récif de Toliara ainsi que de démontrer la faisabilité de son grossissement en milieu contrôlé. Plus précisément, cette étude vise à :

a) Connaitre la distribution des individus de *S. sutor* dans le système du Grand Récif de Toliara, en identifiant les changements d'habitats au cours de l'ontogénie de *S. sutor* et en déterminant les zones cruciales à sa survie comme les zones de nourricerie, zone d'alimentation et zone de reproduction ;
b) Déterminer le régime alimentaire de *S. sutor* et sa variabilité spatio-temporelle et ontogénétique ;
c) Déterminer le cycle de reproduction et la taille à la première maturité sexuelle de *S. sutor* ;
d) Évaluer et optimiser les méthodes de grossissement de *S. sutor* en utilisant les ressources et les moyens disponibles localement à Toliara.

## 9. Structure du manuscrit

Pour répondre à ces objectifs spécifiques, le manuscrit sera subdivisé en quatre chapitres :

Tout d'abord, le premier chapitre sera consacré à l'étude de la distribution des individus de *S. sutor* dans la baie de Toliara. Dans ce chapitre, les zones colonisées par cette espèce dès la colonisation seront identifiées. Les facteurs influençant le choix de ces zones d'installation seront déterminés. Et les zones de regroupement des sub-adultes et des adultes seront aussi étudiés afin de mettre en évidence l'existence ou non de ségrégation des habitats durant la croissance.

Le deuxième chapitre se concentre sur l'écologie trophique de *S. sutor.* Dans cette partie sera évaluer le type de régime alimentaire de cette espèce à Toliara en analysant les contenus stomacaux et en faisant des analyses des isotopes stables du carbone, de l'azote et du soufre. La combinaison de ces deux méthodes est en effet un outil très efficace pour étudier l'alimentation d'une espèce et pour mieux comprendre le réseau trophique (Hyslop, 1980; Mantel et al., 2004; Parkyn et al., 2001).

Ensuite, le chapitre trois sera dédié à l'étude de la reproduction de cette espèce. Deux points seront abordés dans cette partie via l'étude histologique des gonades (Kamukuru, 2009; Ntiba & Jaccarini, 1988). Le premier est l'identification du cycle de reproduction de cette espèce via l'étude du cycle de la maturation des gonades mâle et femelle au cours de l'année et en déterminant les périodes de reproduction de cette espèce à Toliara. Le deuxième point consiste à déterminer la taille à la première maturité sexuelle de cette espèce.

Enfin, le quatrième chapitre de résultats sera consacré aux essais d'élevage de *S. sutor* réalisés à la station Marine de Belaza. Deux essais distincts dans le temps seront faits. Le premier sera une étude sur le pré-grossissement et le grossissement de cette espèce. Le deuxième essai sera consacré uniquement au grossissement avec des méthodes améliorées par rapport au premier essai pour reproduire des conditions optimales à l'élevage de cette espèce. A la fin de ces essais le poissons seront relâchés pour reconstruire le stock naturel de cette espèce.

A la fin de ces quatre chapitres sera rédigé une discussion générale qui résumera les principaux résultats obtenus sur la bio-écologie et l'aquaculture de *S. sutor*, en les mettant en lien avec les objectifs initiaux de conservation et de sécurité alimentaire. L'ensemble de ces résultats sera discuté par rapport à la littérature scientifique et leur pertinence pour la gestion des ressources marines, tout en soulignant les implications pratiques pour la pêche durable et les communautés locales. Dans cette partie sera aussi abordé les limites de cette étude et par la suite, des perspectives pour des recherches futures seront proposées.

# Chapitre 2 : Matériel et méthodes générales

Cette partie se consacre à la description de la zone d’étude et de l’espèce cible de cette étude. Puis, les méthodes communes à plusieurs volets de cette étude sont décrites ci-dessous. Les approches spécifiques à chaque analyse sont présentées dans les sections 'Matériel et méthodes' propres à chaque chapitre concerné.

## 1. Zone d’étude

Cette étude a été réalisé à Toliara, au Sud-Ouest de Madagascar (région Ouest de l’Océan Indien). Madagascar est séparé de l’Afrique par le canal de Mozambique offrant à la côte Est une mer calme et peu profonde contrairement à la côte Ouest qui est bordée par l’Océan Indien. Deux principales saisons se succèdent à Madagascar : une saison pluvieuse et chaude, de novembre à avril et une saison sèche et fraîche, de mai à octobre. Le climat à Toliara est de type aride avec une précipitation moyenne annuelle de 500 mm et la température moyenne annuelle est d'environ 24 °C. Avec ce climat plus chaud, la saison fraiche n’y dure que de mai à août. Le climat y est fortement influencé par le vent dominant du Sud-Est, l’Alizé (Randriamarolaza et al., 2021).

Toliara est bordée par un récif corallien de type barrière : le Grand Récif de Toliara (GRT). Le GRT longe sur 19 km représentant sue superficie de 33 km$^2$ (Clausade, 1970; Pichon, 1978). Entre la côte de Toliara et le GRT se trouve un vaste lagon d’eau calme qui s’étend sur près de 20 km de long et entre 2 et 4 km de large avec une profondeur ne dépassant pas les 5 m. Le lagon abrite une variété d’habitats composé d’herbiers marins, de mangroves, de zones sableuses et vaseuses et des patates coralliens (Chevalier et al., 2015; Moustapha et al., 2021).

L’échantillonnage des *Siganus sutor* (*S. sutor*) a été réalisé dans la baie de Toliara entre la ville de Toliara et le village de Sarodrano (Fig. 2.1). La dissection et fixation des échantillons a été faite à l’Institut Halieutique et des Sciences Marines, Université de Toliara. L’élevage de S. sutor a été réalisé à la station de recherche aquacole de Belaza, située à 22 km au Sud de la ville de Toliara. Cette station est sous la co-direction de l’Université de Toliara via l’IH.SM, de l’Université de Liège et l’Université de Mons. La station est complètement isolée des villages avoisinants et est caractérisée par la présence de plusieurs points de résurgence d’eau douce aux environs. Elle est bordée à l’Ouest par une forêt de mangrove et à l’Est par une forêt sèche typique de la région Sud-Ouest de Madagascar. L’analyse des échantillons a été faite à l’Université de Liège.

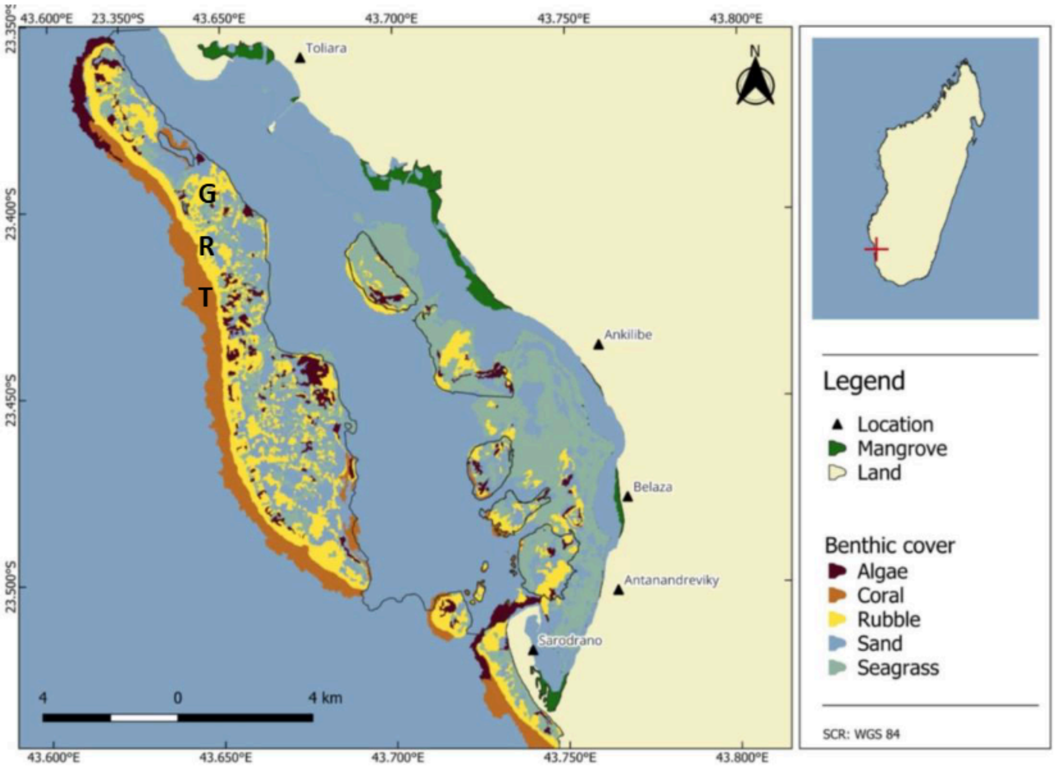

**Figure 2. 1.** Localisation de la zone d'étude

## 2. Description de l'espèce *Siganus sutor*

Cette thèse se porte sur Sigan cordonnier, un poisson des récifs de l'espèce *Siganus sutor* (Valenciennes, 1835) appartenant à la famille des Siganidae (Duray & Southeast Asian Fisheries Development Center, 1998b) (Tab. 2.1). Quatres espèces de Siganidae peuvent être trouvées à Toliara : *Siganus argenteus* (Amboramasaky en malagasy), *Siganus laqueus* (Amboramasaky am-bohony), *Siganus luridus* (kely teraky) et *Siganus sutor* (Amboramasaky) (Fricke et al., 2018) (Voir photos en Annexe 1, page b).

*Siganus sutor* se distingue par un corps ovale latéralement aplati, allant du vert olive au brun, avec des couleurs variables selon l'environnement et l'état de stress. Au repos, il présente des taches sombres pour le camouflage. Les post-larves ont un corps translucide avant de se métamorphosé en juvénile qui a même morphologie et coloration les adultes (Duray, 1998; Lam, 1974) (Fig 2.2). Il peut atteindre une taille maximale de 45 cm (Froese & Pauly, 2000). Sa morphologie comprend une petite bouche en forme de bec, des nageoires robustes et des épines venimeuses (Lam, 1974; Woodland, 1983). Son surnom de « poisson lapin » provient de ses grands yeux et de sa bouche mobile (Duray & Southeast Asian Fisheries Development Center, 1998b). Doté d'une peau à l'aspect du cuir et coriace, *S. sutor* est souvent maladroitement désigné comme étant sans écailles du fait de ses écailles lisses, petites et étroitement adhérentes.

Le *S. sutor* est un poisson tropical endémique de la région l'Ouest de l'océan Indien (Woodland, 1983). Il fréquente les récifs coralliens, herbiers, lagunes, mangroves et fonds rocheux. Les œufs fixés au substrat éclosent en larves planctoniques dérivantes, qui rejoignent les zones côtières en grandissant, coloniser les récifs coralliens (Ben-Tuvia et al., 1972; De Souza, 1988). Les juvéniles s'installent dans les herbiers puis migrent à l'âge adulte vers les récifs coralliens (Duray, 1998). Il a un régime alimentaire principalement herbivore (Almeida-Silva et al., 2015; Duray & Southeast Asian Fisheries Development Center, 1998b; Pitt, 1997), se nourrissant d'algues et de phanérogames, avec parfois des invertébrés et vertébrés marins. Les juvéniles ont un régime plus varié, incluant des proies animales riches en protéines (Ravelohasina et al., 2024), avant de devenir strictement herbivores à l'âge adulte. Leur activité alimentaire est diurne, avec des estomacs vides la nuit (Almeida-Silva et al., 2015).

**Tableau 2. 1.** Classification et noms vernaculaires du Sigan cordonnier *Siganus sutor*

| Classification | |
|---|---|
| Règne | Animalia |
| Phylum | Vertebrata |
| Classe | Actinopterygii |
| Ordre | Perciformes |
| Famille | Siganidae |
| Genre | Siganus |
| Espèce | *Siganus sutor* |
| Noms vernaculaires | Malagasy : Amboramasaky (Vezo), Henjy, Hinta (Sakalava), Fiamalandy (Betsimisaraka), Halalaza (Antanosy)<br>Français : Sigan cordonnier, poisson lapin, Marguerite<br>Anglais : Rabbitfish |

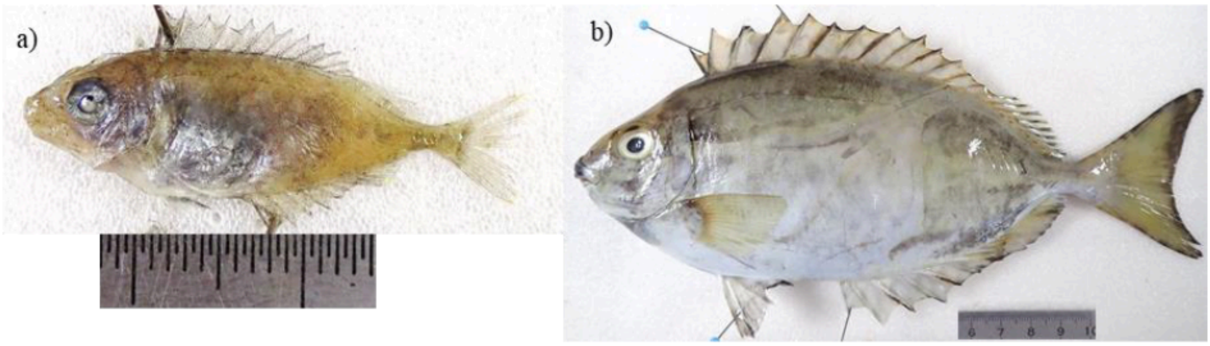

**Figure 2. 2**. Morphologie du *Siganus sutor :* a) post-larve et b) adulte

## 3. Echantillonnage

L'échantillonnage a été effectué en coopérant avec les pêcheurs des villages d'Ankilibe et de Sarodrano. Les juvéniles ont été capturés en utilisant des chaluts à moustiquaire (Fig. 2.3a). La pêche s'est effectuée sur des zones peu profondes (moins de 1,5 m de profondeur) sur la zone des mangroves, la zone des herbiers, la zone intermédiaire, et le platier récifal du GRT. Et du Sud au Nord, les zones ont été comprises entre Ankilibe et Sarodrano. La description et l'emplacement exacte des sites de pêche est illustré dans le chapitre 03. Les pêcheurs sont à bord de pirogue monoxyle à balancer et ils déploient une voile quand les conditions en rapport avec le vent sont favorables. Ils sont composés par deux ou trois personnes par pirogue et une pirogue par station. La pêche se fait à pied durant la période de basse mer des vives-eaux.

Pour l'échantillonnage des adultes et sub-adultes (juvéniles de taille entre 10 et 20 cm), la collaboration a été faite avec des pêcheurs d'Ankilibe et d'Ankiembe (Toliara ville) utilisant le filet maillant comme engin de pêche (Fig 2.3b). L'équipe formée avec les pêcheurs d'Ankilibe pêche sur la zone des herbiers plus profonde (jusqu'à 4.5m de profondeur) en face du village d'Ankilibe. Celle avec les pêcheurs d'Ankiembe part au-delà du GRT sur la pente externe pouvant atteindre 100 m au large du récif à des profondeurs allant jusqu'à 14 m. Ils sont composés de trois à quatre personnes par pirogue avec une pirogue par station. La pêche se fait sur la pirogue et seuls les plongeurs plongent pour libérer le filet en cas de blocage sur le fond. La date et durée d'échantillonnage sont détaillées dans les chapitre 3, 4 et 5.

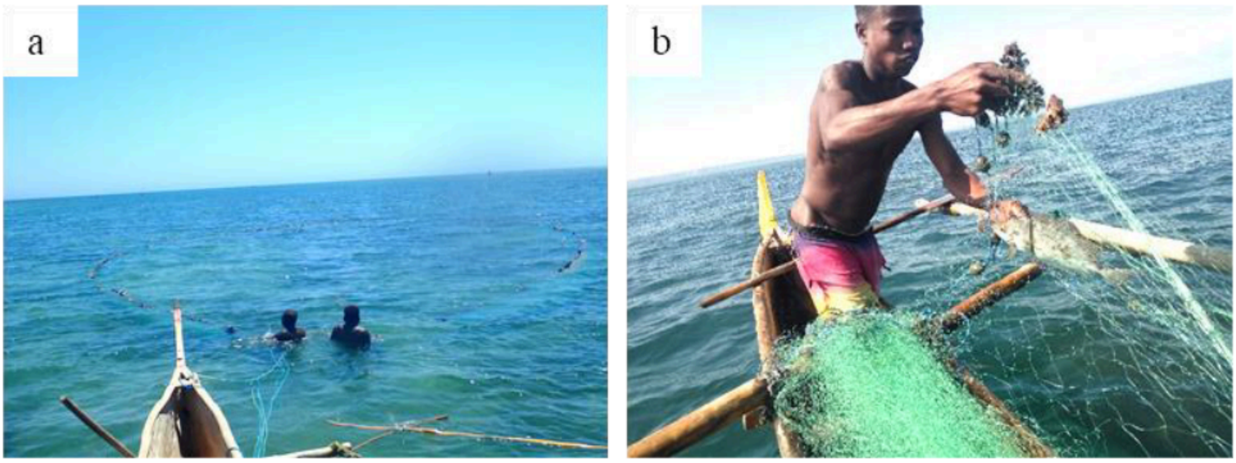

**Figure 2. 3.** Echantillonnage des a) juvéniles de *Siganus sutor* à l'aide de chalut à moustiquaire et b) adultes *Siganus sutor* à l'aide de filet maillant

Les échantillons de *Siganus sutor* capturés sont immédiatement placés dans des glacières contenant de la glace, puis transportés vers l'IH.SM. Une fois au laboratoire, les juvéniles sont comptés et photographiés par groupe. En cas d'effectif trop élevé, un sous-échantillon aléatoire est prélevé pour chaque station, en veillant à ce qu'il représente la gamme de tailles de l'échantillon brut. Pour les adultes, tous les individus capturés serviront pour l'étude (Tab. 2.2). Alors, les adultes et les sou-échantillons de juvéniles sont pris un à un pour être photographié. Ensuite, les longueurs standard (LS : correspondant à la longueur comprise entre le bout du museau et l'insertion de la caudale) et la longueur totale (LT : définie par la longueur entre le bout du museau et l'extrémité de la nageoire caudale) sont mesuré comme décrit par Schreck et al. (1990). Tous les sou-échantillons sont ensuite pesé (poids total) à l'aide d'une balance électrique à 0,01g de précision. La LS est la mesure utilisé dans cette thèse sauf pour le chapitre dédié à la reproduction où la LT est utilisée pour faciliter la comparaison des résultats avec les données disponibles dans la littérature (essentiellement des LT). Ensuite, au cours d'une dissection, le tube digestif est prélevé pour l'analyse des contenus stomacaux. Puis, un échantillon de muscle épaxiale (muscle situé entre la ligne latérale et la nageoire dorsale) est retiré pour l'analyse d'isotope stable. Et enfin la présence de gonade est inspectée visuellement, et en cas de présence, celle-ci est prélevé, photographiée, pesée puis conservé pour l'étude de la reproduction.

Pour l'expérimentation en aquaculture, les post-larves et juvéniles de *S. sutor* ont été capturés avec les pêcheurs sur la zone des herbiers en face du village de Sarodrano. Les échantillons ont été mis dans des bacs avec de l'eau de mer et transportés à la station de Belaza. Durant la capture et le transport les bacs ont été munis d'aérateurs portables (Fig. 2.4).

**Tableau 2. 2**. Résumé du nombre d'échantillon de *Siganus sutor* étudiés

| **Etudes** | **Juvéniles** | **Adultes** |
|---|---|---|
| Distribution spatio-temporelle | 5975 | 127 |
| Contenus stomacaux | 95 | 133 |
| Isotopes stables | 367 | 44 |
| Cycle de reproduction | | 300 |
| Taille à la première maturité sexuelle | 33 | 53 |
| Pré-grossissement | 600 | |
| Grossissement A | 512 | |
| Grossissement B | 512 | |

**Figure 2. 4.** Echantillonnage de post-larves et juvéniles pour l'élevage de *Siganus sutor*

## 4. Analyse des données

Les données de cette thèse sont analysés sur le logiciel R version 4.4.2 (R Core Team, 2024). Les détails des analyses sont décrits dans chaque chapitre.

# Chapitre 3 : Habitat-use during the ontogeny of the shoemaker spinefoot rabbitfish, *Siganus sutor*

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## Résumé

La petite pêche est essentielle pour les moyens de subsistance des communautés côtières en Afrique de l'Est. *Siganus sutor* (Siganidae), un poisson herbivore largement répandu dans l'Indo-Pacifique, figure parmi les espèces les plus ciblées par les pêcheries artisanales, ce qui témoigne de son importance majeure pour la sécurité alimentaire des populations côtières. Dans un contexte de nécessité urgente d'une exploitation durable fondée sur des données scientifiques, notre étude visait à identifier les zones de nourricerie et les habitats des adultes de *S. sutor* dans le récif de Toliara, au sud-ouest de Madagascar. Pendant une année, des données sur la fréquence des tailles et l'abondance ont été collectées dans les mangroves, les herbiers marins, les récifs coralliens et les zones intermédiaires. Les résultats ont révélé deux principales périodes de recrutement pour *S. sutor* : août et janvier. L'abondance et la taille des juvéniles variaient selon les habitats, les herbiers marins en particulier ceux situés loin du récif servant de principales zones de nourricerie. La distance au rivage, la couverture sédimentaire, la densité des herbiers et l'abondance de l'épifaune étaient des facteurs significatifs influençant l'abondance des juvéniles. Les modèles GAM ont expliqué jusqu'à 88 % de la variation observée, avec une grande précision. Les adultes de *S. sutor*, en particulier les individus de plus grande taille, ont été trouvés exclusivement sur le platier externe du récif. Cette étude souligne l'importance des herbiers côtiers pour les juvéniles de *S. sutor* et met en évidence la nécessité de stratégies de gestion spatiale pour assurer l'exploitation durable de cette espèce.

## Abstract

Small-scale fishing is crucial for the livelihoods of coastal communities in Eastern Africa. *Siganus sutor* (Siganidae), a herbivorous fish widespread in the Indo-Pacific, is among the most targeted species by small-scale fisheries, indicating its substantial importance in food security for coastal communities. In the context of an urgent need for science-based sustainable use of this resources, our study aimed at identifying nursery areas and adult habitats for *S. sutor* at Toliara reef, southwest Madagascar. Over a year, size-frequency and abundance data were collected from mangroves, seagrass beds, coral reefs and intermediate zones. Results revealed two main recruitment periods for *S. sutor*: August and January. Juvenile abundance and size varied across habitats, with seagrass beds, particularly those far from the reef, serving as the main nursery area. Distance from the shoreline, sediment cover, seagrass cover, and epifauna abundance were significant factors influencing juvenile abundance. GAM models explained up to 88% of the variation, with high accuracy. Adult *S. sutor*, especially the largest individuals, were found exclusively on the outer reef shelf. This study underscores the importance of nearshore seagrass beds for juvenile *S. sutor* and highlights the need for spatial management strategies to ensure the sustainable use of this species.

## 1. Introduction

Understanding animal space use is crucial for the objectives of biological conservation and sustainable fisheries (Brownscombe et al., 2019; Lima & Zollner, 1996; Morris, 2003). However, animal behavior and spatial patterns are complex and can change significantly over time due to a variety of intrinsic factors (e.g. energy needs and reproductive state) and extrinsic factors (e.g. trophic resources and predation) (Nathan et al., 2008). Specifically, several authors have explained the habitat selection by coastal marine fish species can be influenced by environmental variables such as sea surface temperature, food availability, tidal cycle, proximity to shore and habitat structure (Baumgartner et al., 2003; Goetz et al., 2007; Mendes et al., 2002). Therefore, identifying the mechanisms driving animal movements and space uses is of crucial importance for our understanding of population and ecosystem dynamics and for developing predictive models of their future ecology (Brownscombe et al., 2019; Schlaepfer et al., 2002).

The great majority of coral reef fishes have a bipartite life cycle made of a pelagic dispersal larval stage and a demersal coastal habitat-associated juvenile and adult stages (Lecchini et al., 2017; Macedo-Soares et al., 2009; Planes et al., 2009; Wolanski et al., 1997). It is common for marine fish species to utilize different habitats at various life stages, often spawning in locations that vary from their juvenile settlement areas (Hanson et al., 2013; Tzadik et al., 2017). Understanding fish habitat-use patterns along their ontogeny is helpful to identify key areas for feeding, sheltering and spawning (Jadot et al., 2006) and to detect nurseries (Sabetian et al., 2021), leading to effective protection measures (Welsh & Bellwood, 2012).

A large number of tropical reef fishes heavily depend on mangrove and seagrass habitats during their juvenile phase, where the mangrove prop roots or the leaves of seagrasses create a unique structurally complex underwater environment (Bennett, 1989; Madi-Moussa et al., 2020; Nagelkerken, 2009). Mangrove and seagrass habitats are considered attractive settlement areas for a lot of reef fish larvae from the open ocean due to their high food abundance and low predation pressure (Aguaiza et al., 2024; Parrish, 1989). Lately, those fish species spend their adult stage on coral reefs, and their level of dependence on reef habitat varies greatly among species (Elsdon & Gillanders, 2003; Verweij et al., 2008). However, some fish species may directly settle on corals and remain closely associated with it throughout much of their early life stages (Jones et al., 2004; Wilson et al., 2010). The potential nursery function differed among nearshore habitats (Huijbers et al., 2013; Kimirei et al., 2011) and vary among reef fish species (Dorenbosch et al., 2005a; Dorenbosch et al., 2005b; Gullström et al., 2008).

The rabbitfishes (Siganidae) have a broad spatial distribution across the Indo-Pacific region. They are mainly herbivorous fish and they are known for being an excellent food fish (Duray & Southeast Asian Fisheries Development Center, 1998a). *Siganus sutor* is an endemic species of the Western Indian Ocean (Woodland, 1990). It is largely targeted by the small-scale fishers in Eastern Africa (Grandcourt, 2002; Samoilys et al., 2013) including Madagascar (Ranaivomanana et al., 2023). *Siganus sutor* may therefore play a significant role for food security in coastal zones of the Eastern Africa (Foale et al., 2013). However, *S. sutor* appears to be heavily fished in some countries like Kenya (McClanahan & Mangi, 2004; Robinson et al., 2011; Samoilys et al., 2013). In Madagascar, small scale catches made by using mosquito seine nets in the nearshore habitats comprise of 50% *S. sutor* juveniles (Jaonalison, 2019). This negatively impacts the recruitment of many species and, especially, *S. sutor* (Jaonalison, 2019; Ranaivomanana et al., 2023).

Beyond the negative effect of catching juveniles, intensive fishing activities may lead to habitat degradation that also threat the sustainability of coastal fisheries (Sundblad et al., 2014). The coasts of Madagascar are an active fishing grounds for the small-scale fishers, especially represented by the Vezo, an ethnic group that relies primarily on the sea for their livelihood (Bruggemann et al., 2012; Chaboud, 2006). Fishermen use destructive fishing gears like mosquito net (Jaonalison, 2019) and this situation highlights the need of in-depth studies on the nearshore habitats and associated fishes. Our understanding of the ecological importance of those habitats for fishes remained poorly known in Madagascar.

The present work aims to study the habitats-use of *S. sutor* in the coastal areas from the Western Indian Ocean (WIO). By combining data from fish catches in different habitats over one year with generalized additive models, we described the spatial distribution of *S. sutor* individuals and identified key factors driving abundance and fish size distribution over the coastal ecosystem of the largest barrier reef of the WIO: the Great Reef of Toliara. This information will be of great interest for proposing management measures for the sustainability of *S. sutor* fishery in Madagascar.

## 2. Materials and methods

### 2.1. Study site

This study on *S. sutor* was carried out at the Great Reef of Toliara, SW of Madagascar (Fig. 3.1). The Great Reef of Toliara is a complex ecosystem made of a 18 km barrier reef protecting a lagoon where seagrass meadows, fringing reefs and mangroves are distributed (Clausade et al., 1971). Although the Great Reef of Toliara is highly degraded by human activities, it conserves one of the highest coral and fish diversity of the Western Indian Ocean along Eastern Africa (Botosoamananto et al., 2021; Jaonalison et al., 2022).

The area is characterized by high tidal range during spring tide periods (with a maximum tide range of 3.6m). Mangrove (mainly characterized by *Avicennia marina* and *Sonneratia alba*) and adjacent unvegetated areas are emerged almost every day. Tidal area is colonized by different seagrass beds colonizing soft bottom of both sides of the lagoon according to their emersion tolerance. Monospecific stand of *Halodule pinifolia* and *Halodule uninervis* are found in the upper intertidal area (e.g. Rakotonjanahary et al. 2024). Continuous polyspecific seagrass meadows are found in the lower intertidal to subtidal area (max depth 5-6 m) (Hantanirina & Benbow, 2013; Rakotonjanahary et al., 2024; Vaitilingon et al., 2003). Seagrass beds houses more than 200 fish species as resident adult fish fauna or as juveniles (Jaonalison et al., 2016, 2022).

### 2.2. Sampling and processing methods

Juveniles of *S. sutor* were sampled monthly along four different coastal habitats: (1) mangroves, (2) seagrass meadows on the fringing reef, (3) intermediate area made of patchy reefs mixed with seagrasses, and (4) seagrass meadows on the barrier reef, including internal reef slope. The intermediate sampling zones are located near the outer fringing reef. The sampling zone on the back barrier area of the GRT is dominated by H. *uninervis* or, in the deepest zone by polyspecific seagrass meadow (i.e. *Cymodocea serrulata*, *Cymodocea rotundata*, *Syringodium isoetifolium*, *Thalassia hemprichii*, *H. uninervis*) and monospecific patch of *Thalassodendron ciliatum*, entangled with a low coverage of living and dead coral. The seagrass meadows on the fringing reef is dominated by Halodula uninervis with some area colonized by Syringodium isoetifolium, Thalassia hemprichii and *Thalassodendron ciliatum.* For each habitat, three sampling sites were established reaching a total of 12 sites (Fig. 3.1, Tab. 3.1).

**Table 3.1.** Description of sampling locations in Toliara reef for juveniles and adults of *Siganus sutor*

| **Fish stages** | **Habitats** | **Descriptions** | **Stations** |
|---|---|---|---|
| Juveniles | Mangroves | Flat zones without seagrass vegetation in or near the mangroves | Antoko<br>Ankorohaky<br>Antsanira antety |
| | Seagrasses beds | Seagrass vegetations on the fringing reef near the mangroves with no live or dead corals | Ankily<br>Antsanira<br>Beakio |
| | Intermediate areas | Lagoon reef mixed with high proportion of seagrass vegetation in the shallow water | Ambatomitsanga<br>Norikazo<br>Betsilatsilaky |
| | Reef zones | Seagrass vegetation mixed with coral reef on the barrier reef (less than 1.5m depth) | Kaiasy<br>Andretiky<br>Beantsisy |
| Adults | Lagoon | Fringing reef mixed with seagrass vegetations in water body up to 4.5m depth | Tandeolava<br>Nosimboro<br>Nosy tsena<br>Beambitse<br>Sakatelo<br>Kely nosy |
| | Barrier reef | Outer reef shelf characterized by live coral in 1.5 to 14 m depth up to 100m beyond the barrier reef | Noropasy<br>Fasindava<br>Norondriake<br>Beleja<br>Befy<br>Lazizy<br>Fay<br>Tsakata<br>Ambanevera<br>Nanavina |

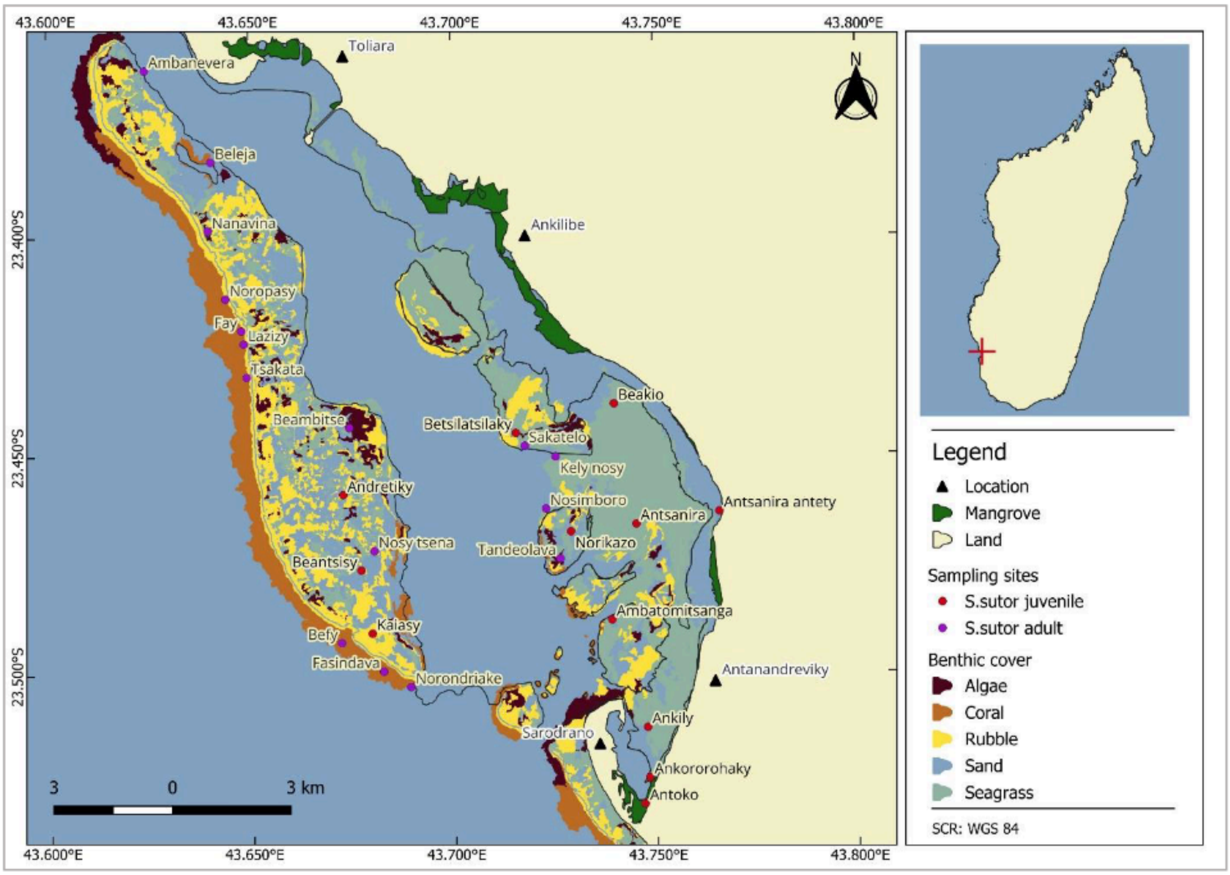

**Figure 3. 1.** Locations of juvenile and adult fish sampling in the Bay of Toliara (original)

Monthly sampling for *S. sutor* juveniles was performed from July 2021 to June 2022 in the four habitats (three sites per habitat). We worked with small-scale fishers who used mosquito trawl nets of 50m length and 2m height. Four samples were collected per day from four different sampling sites, three days each month, across the four habitats. As the sampling lasted 12 consecutive months, we covered the two main seasons in Madagascar (i.e. warm and cool seasons). Being on board of each small-scale fisher canoe, we recorded the sampling effort in terms of fishing haul duration (i.e. the beginning and the end) as well as the local environmental conditions. In the laboratory, samples of juvenile *S. sutor* from mosquito nets were sorted and counted. Then, the samples were photographed in groups on plexiglass fitted with a grid serving as a scale. These photographs were then used to measure the individuals' standard length one by one using ImageJ software.

Adult sampling was performed for three consecutive months (May – July 2023) at 16 fishing sites of *S. sutor* frequented by the local fishers, spread over two different habitats. The first habitat was in the lagoon of Toliara, located on the fringing reef and seagrass meadows of Ankilibe, at a depth ranging between 0.8 to 4.5 meters on low tide. The second habitat was on the outer reef, with depths ranging from 1.5 to 14 meters (Fig. 3.1). We sampled at 6 sites located on the fringing reef in front of Ankilibe and at 10 sites on the barrier reef. The exact geographic position (precision ± 3m) of each fishing site was marked using a Garmin GPS. Samples were collected in collaboration with local small-scale fishermen with two to four fishers per canoe using gillnets of 40m length, 2m height and a 40mm mesh size. Sampling was conducted for three days each month for each habitat. All individuals of *S. sutor* captured during the fishermen's fishing trips were sampled, quantified and measured using a tape measure before giving them back to the fishers.

### 2.3. Characterization of benthic substrates and the epifauna associated with seagrass blades

For each habitat, the benthic substrates were assessed along three transects conducted via scuba diving during periods of neap tides for better visibility and low currents. We used a transect of 50m by laying out 50 × 50cm quadrats each 4m. Each quadrat was photographed, and then analyzed in the software photoQuad, using 40 points randomly spread within the quadrat, and identifying substrate under each point. The substrate was classified into broad morphological categories (sand, rubble, macroalgae, seagrass, dead coral, live coral). An average proportion of each benthic morphological group was calculated for each transect.

The sampling of epifauna associated with the aboveground eelgrass shoots was performed in nine stations where seagrasses were present. We used a 60 µm mesh bag with mouth dimension of 0.15 $m^2$ to collect the eelgrass shoots and associated epifauna, a collection method widely used worldwide (Duffy et al., 2015). The shoot collected through this method can accurately represent the whole shoot of each site (Momota & Nakaoka, 2018). We collected about three samples per seagrass species and per station, by sampling only the dominant monospecific meadow. In the laboratory, epifaunal invertebrates were separated from the seagrass blades and other organisms by scraping with a glass slide. We identified and counted the epifaunal invertebrates after extraction using a 320-µm sieve and preserving with 70% ethanol (Al-Wedaei et al., 2011; Momota & Nakaoka, 2018). Epifauna abundance on the seagrass was measured as the number of individual epifauna per station.

### 2.4. Data analyses

As the effort ranged from 0.18 to 0.81 hours, abundance data was standardized with an equal sampling efforts of 0.5 hour before the analyses using the following equation:

$$\frac{Abundance\ per\ sample\ X\ 0.5\ hour}{Effort(hour)}$$

For both abundance and size data, Shapiro-Wilk test and Levene test were performed to check the normality of the distribution and the homogeneity of the variance, respectively. To identify recruitment periods of *S. sutor*, the temporal distribution of the abundance and the size of juveniles were visualized with barplots and boxplots, respectively. We also tested for hypothetical differences in fish abundance between the observed recruitment periods using Wilcoxon Rank-Sum Test as the data was not normally distributed. To identify the putative nursery ground, we performed spatial analysis of juvenile abundance and size with QGIS 3.36.3 for showing their distributions along the coastal habitats. After verifying the normality of the distribution and the homogeneity of the variance, we tested with ANOVAs the spatial trends of abundance and size of fish to find out any significant differences among habitats. Then, we followed up with post-hoc tests (Tukey's HSD) to determine which habitats differ from each other.

The spatial distribution of abundance and size of *S. sutor* from gillnets, which comprised larger individuals, was also mapped to show the variation among locations in fringing reefs and outer shelf reefs. This allowed to identify the location with the highest concentrations and largest size of *S. sutor*. We classified the adult individuals of *S. sutor* from the medium-sized juveniles or sub-adults using the first sexual maturity size TL 21.7 cm (Ntiba & Jaccarini, 1988). Then, we tested the difference of size and abundance of medium sized/Sub-adults and the adults' fish between both habitats using respectively chi-square and t-test. In addition, size frequency analysis was also conducted and plotted to show the size variation between the fringing and the outer shelf reef.

Two set of explanatory factors (spatial and habitat variables) were used to unravel the spatial distribution of the abundance and size of juvenile fish. The spatial variable was the distance from the shoreline obtained from google earth by using the geographical position of each location. The habitat variables included the cover of benthic substrates (seagrass, macroalgae, "sand", rubble, dead and live coral), the habitat heterogeneity index which indicates the degree of habitat variability by assessing the diversity and the variability of habitat features, and the density of their associated epifauna using the total abundance per square meter. Among the diversity of epifauna observed along the different four habitats, we only retained the preferred food items of juvenile *S. sutor* for the analyses, including copepod, gastropod, foraminifera, decapod crustacean larvae,… (Ravelohasina et al., 2024).

$$Heterogeneity\ Index = \frac{Shannon\ Diversity + Richness + Evenness + Edge\ Density}{4}$$

Where:

- *Shannon Diversity (H') is calculated as:* $H' = -\sum(p_i \cdot \ln p_i)$ with $p_i$ being the proportion of each habitat type.
- Richness is the number of distinct habitat types.
- Evenness was calculated as: $Evenness = \frac{H'}{\log(\text{Richness}+1)}$
- Edge Density represents the density of habitat edges within the spatial landscape

To explore the pattern of size and abundance in relation to habitat and spatial variables, we used Generalized Additive Model (GAM). To avoid model overfitting, the highly correlated explanatory variables (more than 0.85; e.g. the live coral which was positively correlated with the macroalgae) were not integrated in the model. The best fitted models were then selected by using Akaike Information Criterion (AIC). All statistical analyses were performed in the environment R 4.4.0 (R Core Team, 2024) using the packages *mgcv* (version 1.9-1, Wood 2017) for GAM model fitting, *vegan* (version 2.6-4, Oksanen et al. 2022) for ANOVA test and tukeyHSD, and *ggplot2* (version 3.4.1, Wickham 2016) for producing plots.

## 3. Results

### 3.1. Distribution of juvenile fish size and abundance

Our results revealed two clear recruitment periods of *S. sutor* on the reef system of Toliara: one in August and one in January (Fig. 3.2a). Both periods corresponded to the highest observed abundance (Fig. 3.2a) and the lowest observed body sizes where almost 75% of individuals were smaller than 2.5 cm (Fig. 3.2b). Wilcoxon Rank-Sum Test revealed no significant difference (*p-value* > 0.05) between these two recruitment periods.

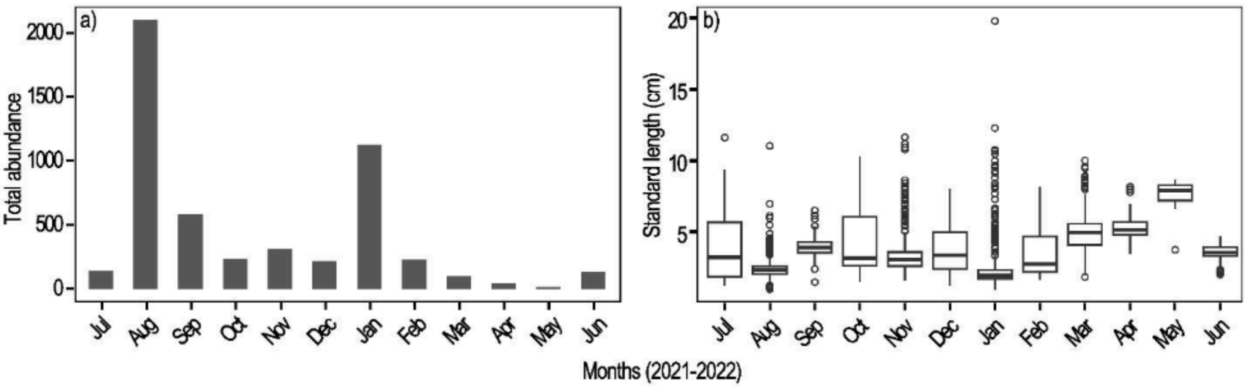

**Figure 3. 2.** Temporal distribution of juvenile fish abundance (a) and size (b), using the monthly standardized total abundance and individual size of fish from all the sampled coastal habitats with 12 samples per month. The lower and upper boundaries of the boxplot correspond to the 25th and 75th percentile, respectively. The horizontal lines within the box correspond to the median values and the vertical lines show the range of values that fall within 1.5 times the interquartile range, individual points correspond to values outside three times of the interquartile range.

We also observed a spatial difference in abundance and size of juvenile *S. sutor* among habitats (Fig. 3.3). The highest abundance was in the seagrass area of the fringing reef (near the coast) and remarkably reduced when approaching the barrier reef or the mangrove and the upper tidal flat. ANOVA revealed that the abundance of small-sized *S. sutor* differed significantly among habitats (*p-value* = 0.013). Post-hoc tests (TukeyHSD) showed that only the abundance of fish observed on the seagrass meadows of the fringing reef differed significantly from the ones observed in the remaining habitats (Tab. 3.2).

The size of *S. sutor* was also significantly different among habitats (ANOVA: *p-value* = 0.002). The smallest fish were located near the coast within mangroves and seagrass beds from the fringing reef (Fig. 3.3b). TukeyHSD tests (Tab. 3.2) revealed that the size of *S. sutor* from the barrier reef habitat was significantly larger than specimens living in mangroves and seagrasses from the fringing reef. Intermediate habitat also sheltered larger juveniles compared to mangrove habitats (Tab. 3.2).

**Table 3. 2. .** Results of Tukey's Honest Significant Difference (TukeyHSD) test comparing the total abundance and mean size among habitats. With diff: the mean difference of habitat group; "*lwr*" and "*upr*" refer to the lower and upper bounds of the 95% confidence interval for the difference between group means; and *p adj*: the adjusted p-value.

| **Variables** | **Habitats** | **diff** | **lwr** | **upr** | **p adj** |
|---|---|---|---|---|---|
| Abundance of juvenile fish | Seagrass *vs* Mangroves | 1391.00 | 249.79 | 2532.21 | **0.019** |
| | Intermediate *vs* Mangroves | 142.67 | 998.54 | 1283.88 | 0.977 |
| | Reef *vs* Mangroves | 73.00 | 1068.21 | 1214.21 | 0.996 |
| | Intermediate *vs* Seagrass | -1248.33 | -2389.54 | -107.13 | **0.033** |
| | Reef *vs* Seagrass | -1318.00 | -2459.21 | -176.79 | **0.025** |
| | Reef *vs* Intermediate | -69.67 | -1210.88 | 1071.54 | 0.997 |
| Size of juvenile fish | Seagrass *vs* Mangroves | 0.27 | -1.45 | 1.98 | 0.958 |
| | Intermediate *vs* Mangroves | 1.73 | 0.02 | 3.45 | **0.048** |
| | Reef *vs* Mangroves | 2.89 | 1.17 | 4.60 | **0.003** |
| | Intermediate *vs* Seagrass | 1.47 | -0.25 | 3.18 | 0.097 |
| | Reef *vs* Seagrass | 2.62 | 0.90 | 4.34 | **0.005** |
| | Reef *vs* Intermediate | 1.15 | -0.57 | 2.87 | 0.217 |

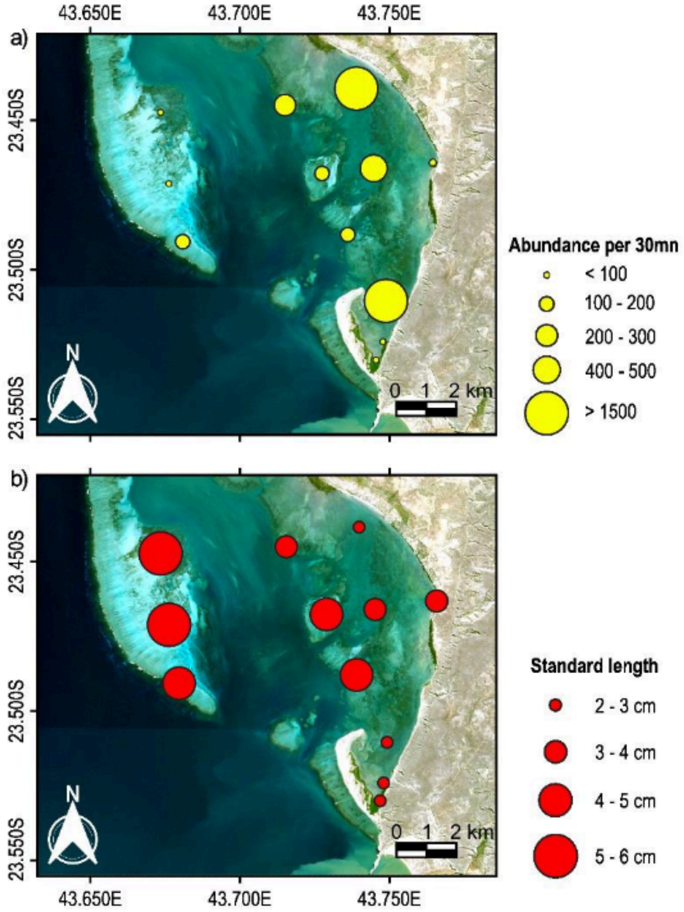

**Figure 3. 3.** Spatial distribution of juvenile fish abundance (a) using the standardized total abundance and the mean size (b)

### 3.2. Distribution of sub-adult and adult fish size and abundance

Our finding revealed that adult (more than 22 cm SL) mainly occurred on the outer reef slope of the barrier reef while medium-sized juveniles or sub-adults (under 20 cm SL) were observed in the lagoon (Fig. 3.4.a). The Chi-square test revealed that there was no significant difference in the abundance of catch in the two sites (*p-value* = 0.16). Subadult could be caught in greater group in the lagoon, from one to 30 individuals per sampling site. On the other hand, adult individuals were caught in small group, not exceeding 10 individuals per sampling sites, for all the studies sites except one site where we found up to 20 individuals. Subadult were also found in the lagoon, near the sampling site of juvenile fish on the fringing reef.

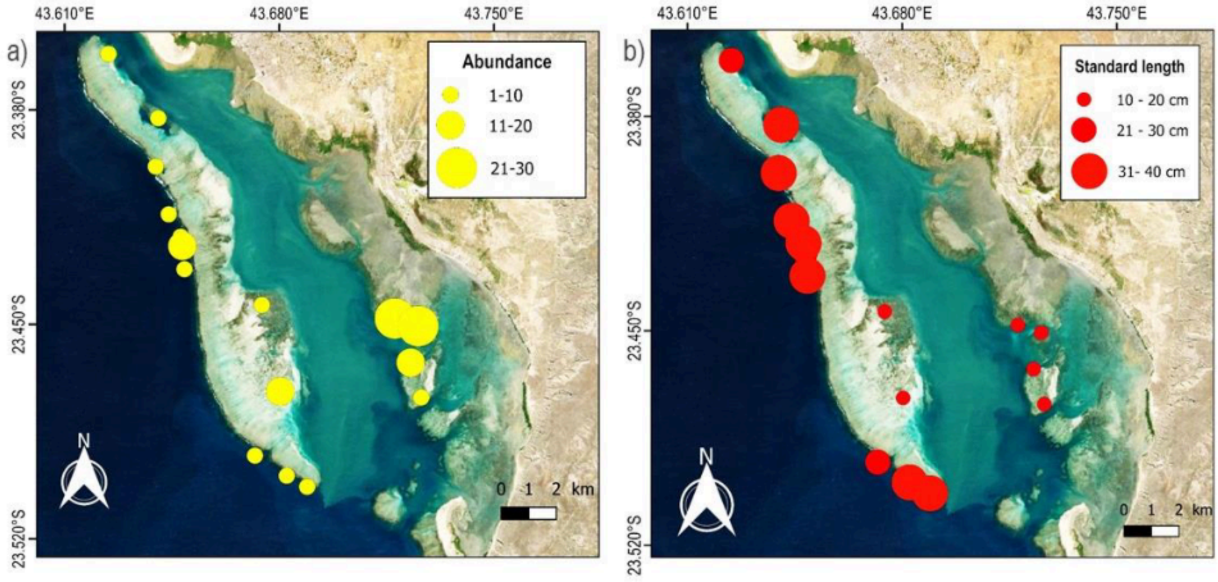

**Figure 3.4.** Spatial distribution of the total adult fish abundance (a) and mean size (b)

We observed that gillnets caught significantly larger individuals on the barrier reef that in the lagoon (T-test, *p-value* $< 2.2x10^{-7}$). We caught a large number of medium-sized juvenile individuals or sub-adult in the lagoon, ranging from 10 to 20 cm (Fig. 3.5). Individuals with SL between 15 and 16 cm occurred the most in the lagoon, while the frequency of individuals with SL between 21 to 38cm appeared to be high on the barrier reef (Fig. 3.5). The maximum body size was 40 cm SL and was observed on the barrier reef. However, the frequency of such large-sized fish in the capture was low.

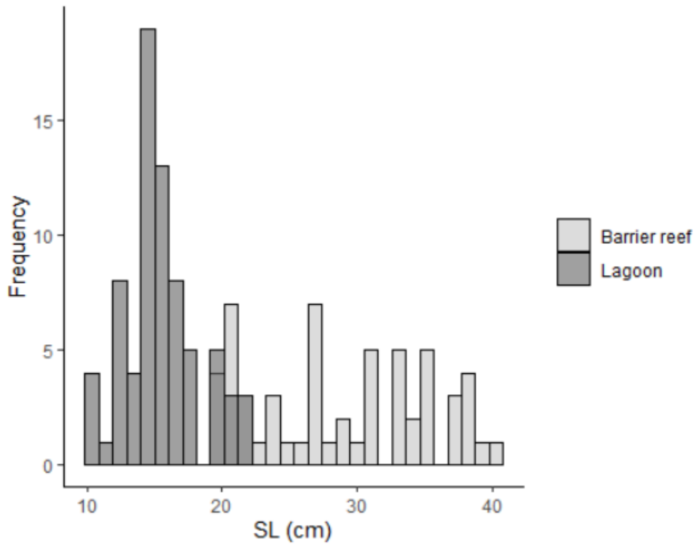

**Figure 3. 5.** Frequency of fish size in the lagoon (in dark grey) and in the barrier reef (clear grey)

### 3.3. Relationship between size/Abundance and habitats variables

GAM found that the combination of the three studied predictors (distance from the shoreline, sediment cover, epifauna abundance, and seagrass cover) produced the best model explaining the spatial variation of juvenile fish abundance (i.e. the lowest AIC value in Tab. 3.3). This combination of variables explained a large proportion of the spatial variation of abundance (pseudo-$R^2$ 87.5%), with important fitting model performance (adj.$R^2$ = 0.7). Both distance from the shoreline, sediment cover and epifauna abundance were significant linear predictors of juvenile fish abundance with a different effect. The abundance of juvenile fish decreased with increasing both distance from the shoreline and sediment cover, while it increased with the increasing epifauna abundance (Fig. 3.6a). In contrast to the distance from the shoreline and epifauna abundance, GAM indicated a significant non-linear relationship between seagrass cover and the abundance of *S. sutor* juvenile (Fig. 3.6a).

**Table 3. 3.** Generalized additive model outputs for abundance and size data of *S. sutor* juvenile obtained from four coastal habitats. AIC: Akaike Information Criterion, pseudo-$R^2$: Deviance explained, adj.$R^2$ relates to fitting model performance, and Signif.: Significance.

| **Responses** | **Predictors combinations** | **AIC** | **pseudo-$R^2$** | **adj.$R^2$** | **Signif.** |
|---|---|---|---|---|---|
| Abundance | Shoreline distance | 2460.19 | | | |
| | Shoreline distance+ Sediment | 1669.79 | | | |
| | Shoreline distance+ Sediment+ Epifauna abundance | 1308.01 | | | |
| | Shoreline distance+ Sediment+ Epifauna abundance + Seagrass cover | **1245.26** | 87.5 | 0.7 | <0.0001 |
| Size | Shoreline distance | **25.56** | | | |
| | Shoreline distance+ Dead coral | **25.01** | | | |
| | Shoreline distance+ Dead coral+ Debris | **24.72** | 87.9 | 0.833 | 0.0002 |

GAM revealed that the combination of distance from the shoreline, dead coral and debris cover were the best predictors explaining a large proportion of variance in the size of *S. sutor* (adj.$R^2$ =0.83, pseudo-$R^2$=87.9%; Tab. 3). This model suggested a significant relationship between the distance from the shoreline and the size of the *S. sutor* juvenile (*p-value* < 0.0001). GAM indicated a positive effect of distance from the shoreline on *S. sutor* size which increased with the increasing distance from the shoreline (Fig.3.6b). The effect of dead coral and debris cover also followed similar pattern (Fig.3.6b), but their linear relationships with the size of *S. sutor* were not significant (with p-value=0.128 and 0.231 for the dead coral cover and debris, respectively).

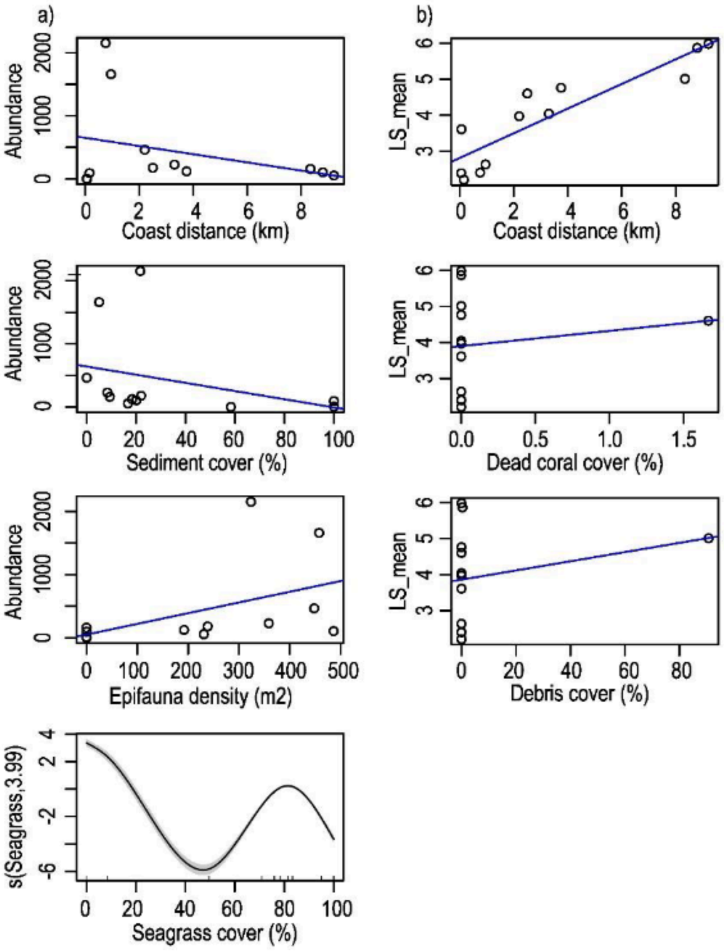

**Figure 3. 6.** Relationship between response variable "Abundance" (a) and "sizes" (b) with the best predictors. (Distance from the shoreline, 1.753)" indicates that the relationship "Distance from the shoreline" and the size is non-linear, with an estimated degrees of freedom of approximately 1.75. s(Seagrass,3.99) shows that the relationship "Seagrass cover" and the abundance is non-linear, with an estimated degrees of freedom of approximately 3.99.

## 4. Discussion

The present study revealed the major recruitment periods, the main nursery areas as well as the habitat used by adults for *S. sutor* at Toliara Reef. Our findings highlighted the important role of habitat geographical position and the benthic characteristic structures in shaping the ecological preferences and spatial distributions of juvenile *S. sutor*, emphasizing the critical importance of the diversity of habitat types, especially seagrass beds, along the shoreline. Hereafter, we also discuss about the importance of the species for the small-scale fishing in the region as well as the possible management proposals considering the ecological trait of the species and the local contexts.

The high densities of juvenile during cool and warm periods has been suggested as the primary recruitment period of coral reef fish species (Kimirei et al., 2011). Here, we also discuss two major recruitment periods: in warm (January) and in cool (August) season. These periods corresponded to the highest small-sized abundance of *S. sutor*, with nearly 75% of individuals measuring less than 2.5 cm. Previous study conducted on the Great Reef of Toliara (GRT) during the warm season found that the highest larval supply of *S. sutor* occurred in November and December (Jaonalison, 2019). This appears in line with our findings as the recruitment in juvenile were detected one or two months later during the same season. In Kenya, two periods of recruitment were also detected for *S. sutor* : one in February/March for the warm season and one in September for the cool season (Ntiba & Jaccarini, 1990). The recruitment period of *Siganus rivulatus* is characterized by a single annual peak. In this species, recruitment occurs during the summer, specifically in August, along the eastern side of the Gulf of Suez in the Red Sea (El-Ganainy & Ahmed, 2002). A study conducted in Indonesia indicated that recruitment of *Siganus canaliculatus* can occur throughout the year, with the highest proportion of recruits observed in November (Tresnati et al., 2020). According with these different studies and the present one, it appears that periods of recruitment may vary among siganids and across geographic regions.

Juveniles of reef fish species often select shallow habitats such as mangroves or seagrass beds as favorable shelters for settlement (Aguaiza et al., 2024; Dorenbosch, et al., 2005a; Nagelkerken et al., 2002; Whitfield, 2017). Among other characteristics enhancing survival rates, these habitats are advantageous due to their lower predator abundance (Blader, 1997; Parrish, 1989; Verweij et al., 2008) but also their high prey abundance, such as epifaunal copepods and epiphytes (De Troch et al., 2003; Leliaert & Vanreusel, 2001). These preys seem to be important when juveniles settle in the meadows (Ravelohasina et al., 2024). Later, individuals of *S. sutor* change to a more herbivorous diet (epiphytes, macroalgae and seagrass blades). In the present study, juveniles of *S. sutor* were observed colonizing seagrass meadows as it have been shown by several authors (De la Torre-Castro et al., 2014; Harris et al., 2010; Maina et al., 2013). Particularly, seagrass areas farther from the barrier reef harbored the highest abundance of juveniles *S. sutor*, predominantly consisting of individuals less than 2.5 cm in standard length. Seagrass vegetation close to the barrier reef was found to have a notably lower abundance, likely due to frequent visits by larger reef predators (Asunsolo-Rivera et al., 2023; Mihalitsis et al., 2022; Stallings, 2009). These findings support previous suggestions that seagrass areas isolated from reefs provide greater benefits for smaller fish (Kimirei et al., 2015).

Locations exhibiting high abundance of the smallest individuals of *S. sutor* likely serve as crucial nursery habitats, as they are closely associated with higher relative survival rates (Kimirei et al., 2015).

The results of the Generalized Additive Model (GAM) indicate that the combination of distance from shoreline, sediment cover, epifauna abundance, and seagrass cover forms the best predictive model for explaining the spatial variation in juvenile fish abundance. Among the predictors, we demonstrated that as the distance from the shore and the extent of sediment cover increased, juvenile fish numbers decreased. This could suggest that juveniles prefer shallow, nearshore areas with less sedimentation, possibly due to better food availability, refuge, or favorable environmental conditions for growth and survival. It is worth to note that, here, the closest zones to the shore is almost uncolonized by juveniles *S. sutor*. This is likely an effect of the tidal range, more than 3 m that discover this area almost every day (but see below).

On the other hand, epifauna abundance showed a significant positive linear relationship, indicating that higher densities of epifauna corresponded to increased juvenile fish abundance. This suggests that epifauna could be playing a crucial role for habitat selection as *S. sutor* directly targets the epiphytes growing on the seagrass blades, which serve as a food source (Jones et al., 2021; Ravelohasina et al., 2024; Susilo et al., 2018). Interestingly, seagrass cover exhibited a significant non-linear relationship with juvenile fish abundance. This non-linear relationship suggests that juvenile fish may benefit from moderate seagrass cover, but the effect may taper off or even become less favorable at very high levels of coverage, perhaps due to overcrowding or competition for resources. Some authors have shown the limit accessibility for juvenile fish according to overly higher seagrass cover, it may increase competition for resources, and reduce available open space, leading to a nonlinear response in fish abundance (Heck Hay et al., 2003; Hindell et al., 2000).

It is common for fish species to prefer seagrass beds for nursery areas, as is the case with *S. rivulatus* in Egyptian Red Sea (Abu El-Regal & Ibrahim, 2014) or *S. canaliculatus* in northeastern Philippines (Bobiles et al., 2015). Some author have explained this preference as a result of the proximity of seagrass beds that facilitates trophic transfers and cross-habitat utilization by fishes (Beck et al., 2001). However, some siganids species have been proved to prefer other habitat as nursery area. For example, *Siganus vermiculatus* is known to be more tolerant of changes in temperature, salinity and oxygen levels than any other siganids. Accordingly, this species was found living at least partly in mangrove swamps, a habitat with substantially fluctuating physicochemical parameters (Undermann et al., 1983). The juvenile *S.*

*sutor* was occasionally observed in the mangrove zones. This may be linked to the absence of seagrass vegetation's in the mangroves or may also be associated to the non-permanent access of this habitat due to the tidal variability (Kimirei et al., 2015). The variation in water parameters in the mangrove can be one of the reasons influencing the choice of species in this habitat as a nursery zone (Abu El-Regal & Ibrahim, 2014). Evans et al. (2014) were among the first to observe that juvenile siganids (*Siganus spp*) select macroalgal beds as their preferred nursery habitat. The canopy of macroalgae not only offers protection from predators and a direct food source for herbivorous but also supports a diverse community of prey species consumed by invertivores (Mantyka & Bellwood, 2007; Yamada et al., 2012). In our study, subadult were very abundant in the back reef habitat. This area is characterized by a mosaic of habitats including seagrass beds but also rubbles with many macroalgae growing on them.

Seagrass meadows appeared as important for both juveniles and adults *S. sutor* (Ebrahim et al., 2020b; Gell & Whittington, 2002; Kimirei et al., 2011). The nearshore shallow water habitats seem to be a transient habitat for the juveniles of *S. sutor* (Duray & Southeast Asian Fisheries Development Center, 1998a; Maina et al., 2013). Individuals gradually colonise area closer to the barrier reefs, quitting the fringing reef for the back of the barrier reef. Our finding revealed that the adult *S. sutor* were only found on the barrier reef, a habitat characterized by coral cover with macroalgae and patches of seagrass meadows. This is in line with the findings in Tanzania where no reproductive fish was observed in the shallow water habitats such as mangroves and seagrasses (Kimirei et al., 2015).

*Siganus canaliculatus* has very similar ontogenetic habitat shifts between seagrass beds and coral reefs (Tomascik et al., 1997). This confirms that juvenile and adult siganids inhabit a wide variety of shallow water environments over their ontogeny but also they are segregated according to their size among these habitats. This is particularly remarkable that juvenile recruited in August replace individuals recruited in January those have already move to other habitats closer to the barrier reef. This is potentially a way to alleviate the potential competition between different cohorts of *S. sutor*.

*Siganus sutor*, as other siganids, is locally an important commercial fishes in the Indian Ocean (Darsono, 1993; Duray & Southeast Asian Fisheries Development Center, 1998a). It is one of the most commonly caught species by the small scale fishing and the most consumed fish in SW Madagascar (Jaonalison et al., 2020; Laroche & Ramananarivo, 1995; Ranaivomanana et al., 2023). The availability of *S. sutor* ensuring a consistent source of protein for the local community may directly impact food security. Beyond nutrition, the fishery of this species supports numerous households, with individuals engaged in various stages of the fishing supply chain, including catching, processing, and selling (Gough et al., 2020). The economic activities generated by *S. sutor* fishing contribute to the overall economic resilience of the community, allowing for investments in education, healthcare, and other essential services. This shed light on the importance of the small-scale fishing that play a vital socio-economic role underpinning both the economic stability and food security of the coastal region (Brenier et al., 2012; Jerry & Razanoelisoa, 2024), where the coastal communities is pronounced to rely on marine resources for their livelihood (Brenier et al., 2012).

Fishery resources on the GRT is experiencing overfishing (Gough et al., 2020; Laroche & Ramananarivo, 1995; Ranaivomanana et al., 2023). Species with similar ecological traits to *S. sutor* are supposed to be more vulnerable to overfishing (Robinson et al., 2011) as the nursery areas (seagrass meadows from the fringing reef) and the adult habitats (barrier and fringing reefs) are both in vicinity to the coast and are thus more exposed to human pressure (Hughes et al., 2009; Basset et al., 2013). Furthermore, overfishing poses another critical threat, as unsustainable fishing practices deplete fish populations, disrupt food webs, and damage the physical structure of reefs (Gough et al., 2020). This factor creates a challenging environment for marine species on the GRT, threatening their survival and the livelihoods of local community dependent on marine resources.

Although *S. sutor* is still listed as least Concern on the IUCN red list (Yahya et al., 2017), the conjunction between the ecological importance of the coastal habitats and their importance for the coastal communities as a fishing ground highlight the urgent needs of effective management for *S. sutor* fishery. Implementing marine protected areas, seasonal closures, and restrictions on destructive fishing gear are the commonly known as vital strategies to ensure the sustainability of these populations (Goreau & Hilbertz, 2005). To do so, data-driven decision making by integrating scientific research will be helpful for adaptive and effective management practices (Agardy, 1997). Considering the findings related to the nursery areas, the recruitment periods as well as the habitat beyond the barrier reef with high concentration of adult *S. sutor* appears to be important for policy makers. The protection of key nursery and adult habitats is crucial as they are essential for the survival and the reproduction of *S. sutor* populations (Agembe, 2012), and taking into consideration the recruitment periods can be helpful for the non-permanent measures. The involvement of coastal communities is one of the main keys in effective conservation efforts, and these communities must be informed about sustainable practices and the benefits of conservation (Carvalho et al., 2021; Patterson et al., 2009; Potempa et al., 2021).

In conclusion, our study successfully identified the preferred sites for both juvenile and adult fish of *S. sutor*. It highlighted two distinct recruitment peaks and established the quality of seagrass beds as the primary factor influencing the presence of juveniles. Future research should focus on identifying the specific reproduction sites of adults and understanding the daily movements of fish between their "rest" and "fishing ground" sites to further enhance our knowledge of their behavior and habitat use.

# Chapitre 4 : Spatio-temporal and ontogenetic variation in the diet of the spinefoot shoemaker rabbitfish *Siganus sutor*

## Résumé

Comprendre la variation du régime alimentaire de *Siganus sutor* est essentiel pour évaluer son rôle écologique dans les écosystèmes récifaux et pour appuyer les stratégies de gestion durable, incluant la conservation des habitats et le développement de l'aquaculture. Ce chapitre explore la composition et la variation spatio-temporelle et ontogénétique du régime alimentaire du *Siganus sutor*, en combinant les analyses de contenus stomacaux et les isotopes stables ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$), afin de mieux comprendre ses interactions trophiques et son positionnement dans les réseaux alimentaires récifaux. Les résultats montrent que *S. sutor* est principalement herbivore avec une préférence marquée pour les macroalgues (43,1%) et les phanérogames (29,4%), mais ils consomment également une proportion non négligeable de proies animales benthiques mobiles (crustacés, mollusques, foraminifères,…) représentant 21,7% de l'abondance des aliments. Cette composante animale du régime alimentaire diminue progressivement avec la croissance, indiquant un changement ontogénique vers un régime plus strictement herbivore à l'âge adulte. Les valeurs isotopiques confirment cette tendance : les $\delta^{15}N$ relativement élevés chez les juvéniles traduisent une position trophique légèrement supérieure, alors que les $\delta^{13}C$ et $\delta^{34}S$ suggèrent un ancrage progressif aux sources benthiques et au forçage local des habitats côtiers. La variabilité des signatures isotopiques selon les sites et les saisons indique également une plasticité trophique spatiale et temporelle, possiblement influencée par la disponibilité des ressources, la compétition alimentaire et la structure des habitats (présence d'herbiers, turbidité, pression anthropique). Ces résultats soulignent l'importance de considérer la diversité des stades de vie et des habitats dans les études écologiques de *S. sutor*, espèce souvent utilisée comme indicateur écologique ou ressource potentielle en aquaculture. Ils apportent aussi des éléments utiles à la gestion durable des stocks sauvages et à la mise en place de stratégies d'élevage adaptées, tenant compte des besoins nutritionnels à chaque stade de développement.

## Abstract

Understanding the variation in the diet of *Siganus sutor* is essential for assessing its ecological role in coral reef ecosystems and for supporting sustainable management strategies, including habitat conservation and aquaculture development. This chapter explores the composition and the spatio-temporal and ontogenetic variation in the diet of *Siganus sutor*. We used the combination of stomach content analysis with stable isotope measurements ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$), in order to better understand its trophic interactions and position within reef food webs. The results show that *S. sutor* is primarily herbivorous, with a marked preference for macroalgae (43.1%) and seagrasses (29.4%), but they also consume a significant proportion of mobile benthic preys (crustaceans, molluscs, foraminifera,…) representing up to 21.7% of abundance of food categories. This animal component of the diet progressively declines with growth, indicating an ontogenetic shift toward a more strictly herbivorous diet in adulthood. The isotopic values confirm this trend: relatively high $\delta^{15}N$ values in juveniles reflect a slightly higher trophic position, while $\delta^{13}C$ and $\delta^{34}S$ suggest a progressive reliance on benthic sources and the influence of local coastal habitat conditions. The variability in isotopic signatures across sites and seasons also indicates spatial and temporal trophic plasticity, likely influenced by resource availability, feeding competition, and habitat structure (such as the presence of seagrasses, turbidity, and anthropogenic pressure). These findings highlight the importance of considering both life-stage diversity and habitat heterogeneity in ecological studies of *S. sutor*, a species often used as an ecological indicator or considered as a potential resource for aquaculture. They also provide valuable insights for the sustainable management of wild populations and the development of appropriate farming strategies that account for the species' nutritional requirements throughout its ontogeny.

## 1. Introduction

The health of coral reef ecosystems is largely maintained by herbivorous organisms including fish, which play a key role in controlling algae, preventing it from overwhelming corals and competing for light and space, which supports coral recruitment and maintains reef structure (Cheal et al., 2013; T. Hughes et al., 2007; Knoester et al., 2019; Plass-Johnson et al., 2015). By breaking down algae, herbivorous fish contribute to nutrient cycling, releasing essential nutrients back into the environment, which benefits corals and other benthic organisms. This regulation of algal levels helps maintain biodiversity, as open spaces allow diverse marine species to thrive (Bellwood et al., 2004; T. Hughes et al., 2007). After disturbances like coral bleaching, herbivorous fish are essential for reef recovery; their grazing limits algae, giving corals more chance to regenerate and reclaim habitats (Mumby, 2009; Adam et al., 2015). Furthermore, herbivorous fish transfer energy from plants to higher trophic levels, shaping plant community structure and promoting ecosystem resilience (Meekan, 1997; Tebbett et al., 2017).

Despite the ecological importance of herbivorous fish on coral reefs and associated coastal ecosystems, this trophic guild counts a relatively low number of reef fish species (Bakus, 1967; Randall, 1963, 1967). At Toliara reef (SW Madagascar), for example, herbivorous reef fish represented only 9% of species diversity (Harmelin-Vivien, 1981). The herbivorous reef fishes are distributed in nine different families including the conspicuous Acanthuridae (surgeonfishes), Pomacentridae (damselfishes), Labridae (parrotfishes), Siganidae (rabbitfishes) and Kyphosidae (sea chubs) (Choat, 1991). Herbivorous fish exhibit differential utilization of available food resources on marine habitat (Dromard et al., 2015). Herbivorous coral reef fish exhibit diverse feeding strategies, which shape their movement patterns and behaviour (Choat & Bellwood, 1985). Some surgeonfishes, parrotfishes and rabbitfishes forage over extensive areas, often forming mixed feeding schools with minimal aggression toward other species (Duray & Southeast Asian Fisheries Development Center, 1998a; Green & Bellwood, 2009). Additionally, herbivorous fish families employ a variety of feeding strategies that influence the structure and balance of reef ecosystems. Acanthuridae mainly graze on turf algae (Lilkendey et al., 2024) while Scarinae (parrotfishes) scrape algae from corals, aiding reef maintenance (Burkepile & Hay, 2008). Siganidae consume both macroalgae and seagrasses (Wu et al., 2022), and Kyphosidae specialize in macroalgae (Morales-de-Anda et al., 2024).

In the Mediterranean Sea, the sparid *Sarpa salpa* primarily feeds on seagrass (Ahmed et al., 2014; Buñuel et al., 2020; Havelange et al., 1997). This species shows an ontogenetic variation in the composition of its diet during growth, with an increase proportion of algae in the diet during fish growth (Havelange et al., 1997). Large individuals (over 39 cm of total length) feed exclusively on algae, while seagrass was entirely absent from their diet. Conversely, the proportion of animal prey, such as crustaceans and Polychaeta, decreased as fish size increased. Size-related dietary variation have also been observed in the herbivorous damselfish *Chrysiptera annulata* on the Great Barrier Reef of Toliara (Lepoint et al., 2016).

In addition to ontogenetic variation, spatial dietary variation has been documented in the herbivorous parrotfish *Leptoscarus vaigiensis* in Kenya. For this species, niche breadths were broader in protected sites during the northeast monsoon, whereas higher values were observed in fished sites during the southeast monsoon season (Locham et al., 2015). A study conducted on the Brazilian coast, at three sites extending from 17°S to 27°S, showed a decrease of a factor of 10 from the north to the south of the consumption of herbivorous fish on the benthos (Longo et al., 2014). However, only few studies investigated the diet variation in herbivorous fish although their ecological and economical importance like the case of the rabbitfish (Siganidae).

The whitespotted spinefoot rabbitfish *Siganus sutor* (*S. sutor*)is widely distributed in the Indian Ocean, particularly along the East African coast (Ebrahim et al., 2020a; Samoilys et al., 2013). It inhabits shallow coastal areas, especially coral reefs and seagrass beds, where it feeds primarily on algae (De la Torre-Castro et al., 2014). Their life cycle and reliance on shallow coastal habitats make them important to coral reef ecosystems and local fisheries in these regions (Ebrahim et al., 2020a). In Madagascar, *S. sutor* is a much targeted species. It is localised along the west coast of Madagascar and is very appreciated around the country. Unfortunately, it is fished abundantly from its juvenile stages as it represent a high proportion among the fished juvenile by mosquito net (Behivoke et al., 2021; Jaonalison et al., 2022; Ranaivomanana et al., 2023). Despite the importance of herbivorous fish and the increase of fishing pressure, the trophic ecology of herbivorous fish in Madagascar remains poorly understood. In the Great Reef of Toliara (GRT), studies on fish assemblages have mainly focused on the trophic diversity of a few families, such as Pomacentridae (Frédérich et al., 2009) and Apogonidae (Frédérich et al., 2017). Some authors have also addressed specific topics, including intraspecific competition (Frédérich et al., 2010) and trophic diversity in herbivorous damselfishes (Lepoint et al., 2016).

The great majority of siganids are herbivorous, primarily feeding on macroalgae and seagrass, with occasional ingestion of detritus or small invertebrates while grazing (Horn, 1989; Woodland, 1983). Their diet varies by species, habitats, and resource availability, influencing their ecological role in controlling algal growth in coral reef and seagrass ecosystems (AI-Ghais, 1993; Duray & Southeast Asian Fisheries Development Center, 1998a). It is generally assumed that juvenile siganids consume small benthic invertebrates in addition to algae (Ebrahim et al., 2024b; Ravelohasina et al., 2024) when adults primarily graze on macroalgae and seagrasses (Fox & Bellwood, 2013). However, detailed studies of their diet are sparse, with only few studies conducted in the Western Indian Ocean (Ebrahim et al., 2020b; Ravelohasina et al., 2024). In Toliara, one preliminary study illustrated trophic variation across time and space in juveniles *S. sutor* by combining stomach contents and isotopic analyses (Ravelohasina et al., 2024). However, further detailed research is required to investigate dietary variation throughout the entire life cycle of this species.

A commonly used approach to study fish diet is gut content analyses. This method involves examining the gut contents of fish to identify specific prey items or food types consumed recently before fish sampling. It provides a detailed, immediate view of diet composition, allowing to determine the types, quantities, and sometimes nutritional value of food items ingested (Baker et al., 2014; Hyslop, 1980). Gut content analysis is particularly useful for studying dietary shifts, prey preferences, and feeding strategies over short timescales (Baker et al., 2014; Scharf et al., 2000). However, it may be limited by rapid digestion rates and the absence of information on prey eaten long before sampling and possible changes in diet (Cocheret De La Morinière et al., 2003). This lack can lead to underrepresentation of certain dietary components.

Stable isotope analyses are another widely recognized technique for investigating fish diet. Typically, we examine the isotopic composition of fish tissues to infer their trophic position and primary food sources over longer timescales (Bouillon, 2011; Jardine et al., 2003). The study of carbone stable isotope identifies the origin of carbon in fish's diet, helping to distinguish between benthic and pelagic food sources. Nitrogen stable isotope provides information about trophic level, as nitrogen becomes progressively enriched at each step of the food chain. Sulfur stable isotope ratio to distinguish fish living mainly on the external slope from fish living preferentially in the lagoon(Gajdzik et al., 2016). While stable isotope analysis is highly informative, it does not offer details about prey items without additional reference data. Since isotopes integrate dietary information over weeks to months, this method complements gut content analysis by providing a broader view of feeding ecology and habitat use (Davis et al., 2012).

The present study focuses on the dietary variation of *S. sutor* by combining gut content and stable isotope analyses. The study aims to investigate spatial, temporal, and ontogenetic variations in the diet of *S. sutor*. The specific objectives are: i) to explore ontogenetic changes in the diet of *S. sutor* by identifying shifts in food sources and trophic position across life stages (juvenile and adult); ii) to examine diet differences of *S. sutor* across various habitats and locations within the Toliara lagoon; iii) to analyze short-term dietary variation of *S. sutor* across different months; and iv) to analyse the possible link between diet variation and phenotype variation by analysis ontogenetic variation on gut length.

## 2. Materials and methods

### 2.1. Sampling

Sampling was performed in Toliara bay in collaboration with local fisher. Details about the sampling stations are describes in the chapitre 3 (Fig. 3.1).

Juveniles of *S. sutor* were sampled across five distinct lagoonal habitats in the south part of the GRT (Ankilibe): (1) mangroves, (2) seagrass meadows on the fringing reef, (3) areas made of patchy reefs mixed with seagrasses, (4) seagrass meadows on the inner reef slope, and (4) inner reef Three sampling sites were established within each type of habitat, resulting in a total of 15 sampled sites. The sampling was carried out every month from July 2021 to June 2022. Adults were sampled exclusively on the outer reef slope of the GRT, their main habitat. Sampling was performed from October 2021 to September 2022. Both juveniles and adults were caught in collaboration with local small-scale fishermen. Juveniles were collected by using mosquito nets when the adults were captured with gill nets with a 40 mm mesh size.

Fish caught were then directly placed in coolers with ice and transported to the laboratory for processing. Once in the laboratory, specimens of *S. sutor* were sorted, and a representative subsample covering the size range of the captured individuals was selected. This subsample was subsequently used for analyses to assess the dietary variation of the species.

### 2.2. Morphological analyses

Each individual was measured for standard length (SL) and weighed to the nearest 0.01 g using a precision balance. The digestive tract was carefully removed, and the total gut length (GL), measured from the stomach's anterior to the rectum, was recorded to the nearest millimetre.

### 2.3. Gut content analysis

The entire digestive tract was removed, opened, and the contents were identified in a petri dish under a binocular microscope. Each prey was identify to the order level of taxonomic classification. To quantify fish diet, we used the approach developed by Wilson and Bellwood (1997). Gut contents were spread evenly on a Petri dish, with a 15 × 15 grid (comprising 5 × 5 mm squares) placed beneath the dish for analysis. A total of 50 quadrants were randomly selected, and for each quadrant, the dominant food item, determined by its area, was recorded. Any additional material present in the same quadrant was also documented to provide a complete overview of the gut contents. The prey items were subsequently grouped into seven food categories: phytoplankton, macroalgae, seagrass, zooplankton, mobile benthic prey, sessile benthic prey, and an "others" category for rubble and unidentified food items. Next, we determined the contribution of each food category to the gut contents, expressed as the percentage of quadrants where that category was dominant (i.e. numerical percentage). Additionally, we calculated the percentage of occurrence for each of the seven food categories (Hyslop, 1980).

### 2.4. Stable isotope analysis

For each fish individual, a sample of lateral muscle was collected and subsequently dried at 60°C for 72 hours. The dried muscle tissues were then ground to a fine and homogeneous powder (Lepoint et al., 2016). Carbon, nitrogen and sulfur stable isotopes were measured using an isotope ratio mass spectrometer (IsoPrime 100, Elementar UK, United Kingdom) coupled to an elemental analyzer (microVario, Elementar, Germany). Isotopic ratios were expressed using the commonly used δ (delta) relative notation (Coplen, 2011). Certified materials were IAEA-N1 ($\delta^{15}N$ =+ 0.4 ± 0.2‰) and IAEA C-6 (sucrose) ($\delta^{13}C$ = –10.8 ± 0.2‰). Glycine was placed every 15 samples as secondary reference material (in lab reference) with $\delta^{15}N$ = +2.25± 0.3‰ and $\delta^{13}C$ = –47.5 ± 0.3‰. The standard deviations for replicated measurements (0.3‰ for both $\delta^{13}C$ and $\delta^{15}N$) were measured on an in-house standard (seabass muscle) placed every 15 samples in each batch.

### 2.5. Data analysis

The relative gut length (RGL) was determined by calculating the ratio of gut length to body length.

$$\text{GRL} = \frac{\text{Gut length (cm)}}{\text{Standard length (cm)}}$$

To visualize the frequency (presence/absence) of food item across sampling months and habitat type, a Non-metric Multidimensional Scaling (NMDS) was performed after a standardized the frequency data using a Hellinger transformation with the decostand function (Legendre & Gallagher, 2001). Then, to assess the differences in variation of the frequency of food item a Bray-Curtis distance matrix was calculated with vegdist and a Permutational Multivariate Analysis of Variance (PERMANOVA). In case of a significant difference, we performed a post-hoc pairwise comparison using the pairwise_adonis function to assess the differences between each pair of factors (months or habitats) (Anderson, 2001).

In term of food abundance, the significant difference in food category abundance across months was tested using an Aligned Rank Transform (ART) ANOVA (Leys et al., 2019; Wobbrock et al., 2011). In case of a significant effects, a Dunn's post-hoc test is performed to identify the specific months that showed differences in abundance across food categories (Dinno, 2015). The relation between SL and abundance of food categories in one hand, and the relation between SL and GL or RGL in other hand were tested using linear regression models. Then, the significance of correlation was tested using Pearson test if applicable.

Variation of the isotopic niche parameters were tested by using SIBER (Stable Isotope Bayesian Ellipses in R) from the R-package SIAR (Jackson et al., 2011). For juvenile sample, a SIBER object of the data was first created to visualize isotopic niche variation across months or habitat (Jackson et al., 2011; Parnell et al., 2010). Next, data were plotted a using ggplot2, adding convex hulls to illustrate the isotopic space occupied by different tested group. I then calculated Layman's metrics, including the Total Area (TA) of the convex hull, to compare niche breadth (Layman et al., 2012; Turner et al., 2010). To analyse the temporal variation of adult stable isotopic ratios, standard ellipses were plotted to visualize core isotopic niches. A Bayesian Standard Ellipse Areas (SEAB) were computed and a density plot was generated to visualize SEAB variations across months.

To statistically test differences in stable isotope ratios (of juvenile and adult) between groups (months or habitats types) a Kruskal-Wallis test was perform followed by a pairwise comparisons using Wilcoxon rank sum test with Bonferroni correction. The difference in TA across groups was tested using Kruskal-Wallis test, followed by analysis of probability of difference by a Bayesian pairwise overlap of Wilcoxon rank sum test with Benjamini-Hochberg adjustment. To illustrate a possible correlation between isotopic ratio and individual SL (juvenile and adult combined), a regression curve was plotted. The significance of the correlation was then tested using the Spearman test.

## 3. Results

### 3.1. Tropic ecology of *Siganus sutor*

While assessing the diet of *S. sutor* in both juveniles and adults the most frequent food categories found in their stomach was macroalgae (27.5%), followed by seagrass (26.8%) and mobile benthique preys (25.8%) (Fig. 4.1 a). These three main food categories remained the most important in terms of food abundance (Fig. 4.1b).

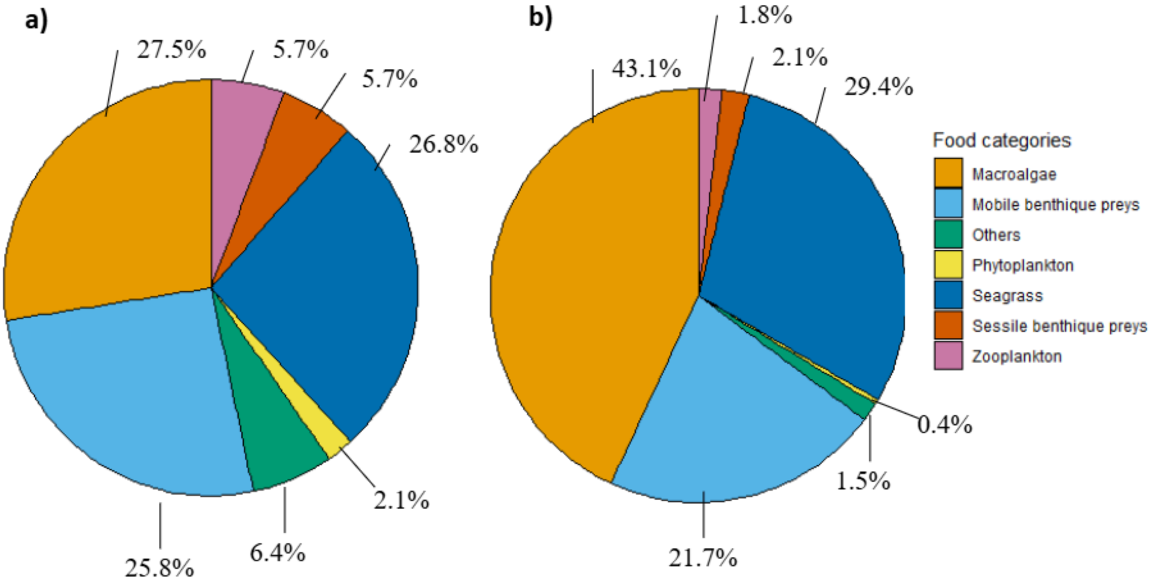

**Figure 4. 1.** Pie chart representing the percentage of a) frequency and b) abundance of food categories in *Siganus sutor*

The stable isotope analysis revealed a notable variation in the isotopic composition of *S. sutor*. Carbon stable isotope values ($\delta^{13}C$) ranged from –12‰ to –20‰ (Fig.4.2). Nitrogen stable isotope values ($\delta^{15}N$) varied between 6‰ and 10‰. Sulfur stable isotope values ($\delta^{34}S$) ranged from 9‰ to 18‰.

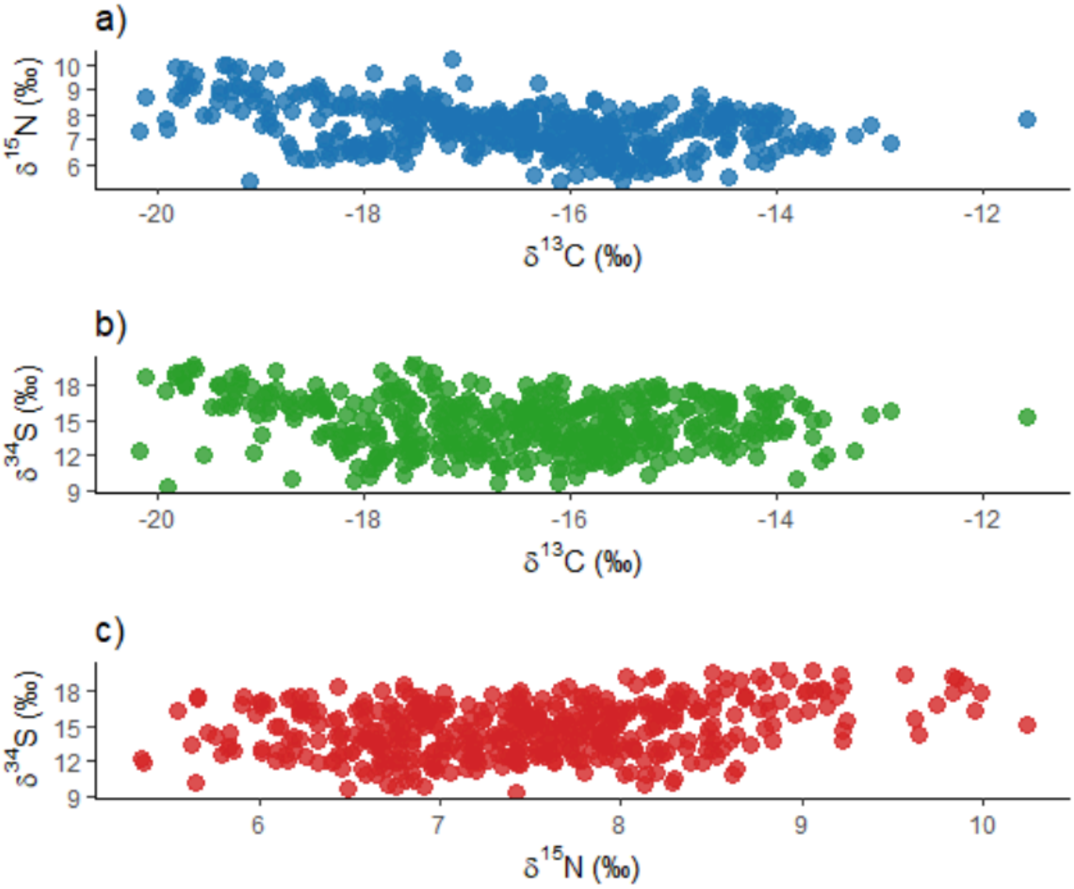

**Figure 4. 2.** Variation in isotopique ratio of *Siganus sutor*

## 3.2. Diet variation in adult *Siganus sutor*

### 3.2.1. Size distribution

A total of 133 adults samples were used for gut content analysis. The number of sample varied from 17 to 20 per month (Fig. 4.3). The SL of adult range from 19 to 37.5cm with a mean of 26.65 ± 4.17cm.

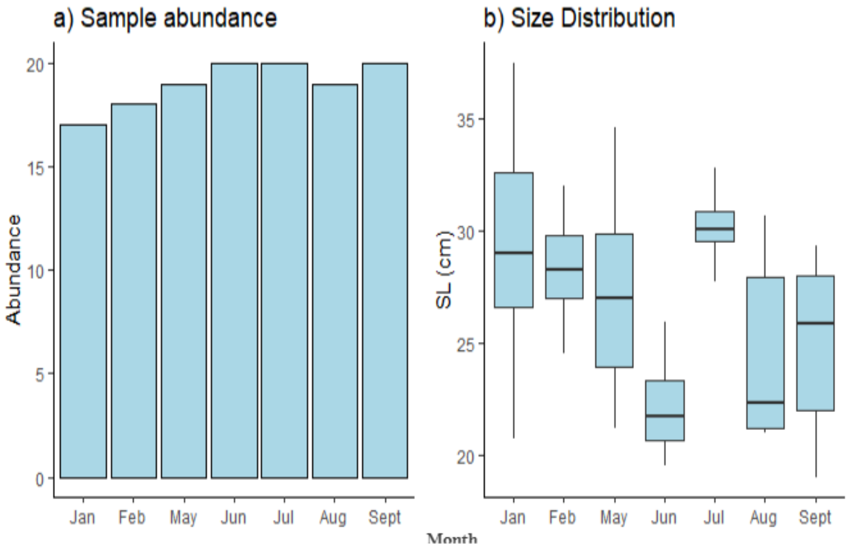

**Figure 4. 3.** a) abundance and b) Size distribution of adult *Siganus sutor* across the sampling months from January to September 2022

### 3.2.2. Percentage of occurrence of food items

We identified 24 food items in adult gut content with a domination of macroalgae and seagrass (Tab. 4.1). Zooplankton were still the less frequent food category despite its presence in each month.

**Table 4. 1.** Percentage of occurrence (%F) of all food items in adult *Siganus sutor*

| **Phylum** | **Food items** | **Jan. 2022** | **Feb. 2022** | **May 2022** | **June 2022** | **July 2022** | **August 2022** | **Sept. 2022** |
|---|---|---|---|---|---|---|---|---|
| | **Phytoplankton** | **17.65** | **0** | **5.26** | **15.00** | **10.00** | **15.79** | **5.56** |
| | **Algae** | **100.00** | **100.00** | **100.00** | **95.00** | **100.00** | **94.74** | **94.44** |
| | **Seagrass** | **100.00** | **100.00** | **89.47** | **95.00** | **100.00** | **94.74** | **94.44** |
| | **Zooplankton** | **5.88** | **2.22** | **2.11** | **1.00** | **6.00** | **5.26** | **3.33** |
| **Chaetognatha** | Chaetognath | 5.88 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Retaria** | Jellyfish | 11.76 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Cnidaria** | Siphonophore | 0 | 0 | 0 | 0 | 15 | 15.79 | 5.56 |
| **Cnidaria** | Copepod | 0 | 5.56 | 0 | 0 | 15 | 0 | 5.56 |
| **Arthropoda** | Decapod larvae | 11.76 | 5.56 | 10.53 | 5 | 0 | 10.53 | 5.56 |
| | **Mobile benthic preys** | **12.19** | **16.67** | **10.60** | **13.50** | **15.52** | **16.16** | **10.67** |
| **Foraminifera** | Foraminifera | 23.06 | 10.23 | 21.05 | 15 | 10.2 | 12.63 | 44.44 |
| **Annelida** | Polychaete | 23.53 | 5.33 | 6.84 | 20 | 15 | 10.53 | 27.78 |
| **Mollusca** | Cladocerean | 11.76 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Mollusca** | Gastropod | 10.59 | 77.78 | 8.42 | 55 | 65 | 84.21 | 4.44 |
| **Mollusca** | Bivalve | 5.88 | 6.67 | 11.79 | 20 | 10 | 15.79 | 5.56 |
| **Arthropoda** | Amphipod | 17.65 | 27.78 | 26.32 | 5 | 35 | 26.32 | 11.11 |
| **Arthropoda** | Hydracarian | 5.88 | 16.67 | 5.26 | 0 | 5 | 0 | 5.56 |
| **Arthropoda** | Crustacean decapod | 11.76 | 11.11 | 0 | 0 | 5 | 6.84 | 5.56 |
| **Arthropoda** | Isopod | 5.88 | 11.11 | 21.05 | 20 | 10 | 5.26 | 2.22 |
| **Arthropoda** | Ostracod | 5.88 | 0 | 5.26 | 0 | 0 | 0 | 0 |
| | **Sessile benthic preys** | **5.71** | **16.67** | **6.16** | **2.50** | **12.50** | **6.05** | **13.89** |
| **Chordata** | Tunicata | 0 | 0 | 0 | 0 | 0 | 5.26 | 11.11 |
| **Cnidaria** | Scleractinia | 11.41 | 33.33 | 12.31 | 5 | 25 | 6.84 | 16.67 |
| | **Other** | **2.94** | **0.00** | **7.89** | **5.00** | **5.00** | **9.21** | **6.94** |
| | Fish scale | 5.88 | 0 | 15.79 | 5 | 10 | 15.79 | 22.22 |
| | Mollusk shell | 5.88 | 0 | 10.53 | 15 | 5 | 15.79 | 5.56 |
| | Operculum | 0 | 0 | 5.26 | 0 | 5 | 0 | 0 |
| | Spicule | 0 | 0 | 0 | 0 | 0 | 5.26 | 0 |
| Number of food items | | **20** | **14** | **18** | **15** | **19** | **19** | **19** |

There was no significant difference in food frequency across months in adult *S. sutor* (PERMANOVA, $p = 0.48$). The NMDS plot (Fig. 4.4) visually represents the dissimilarity in food composition among months."

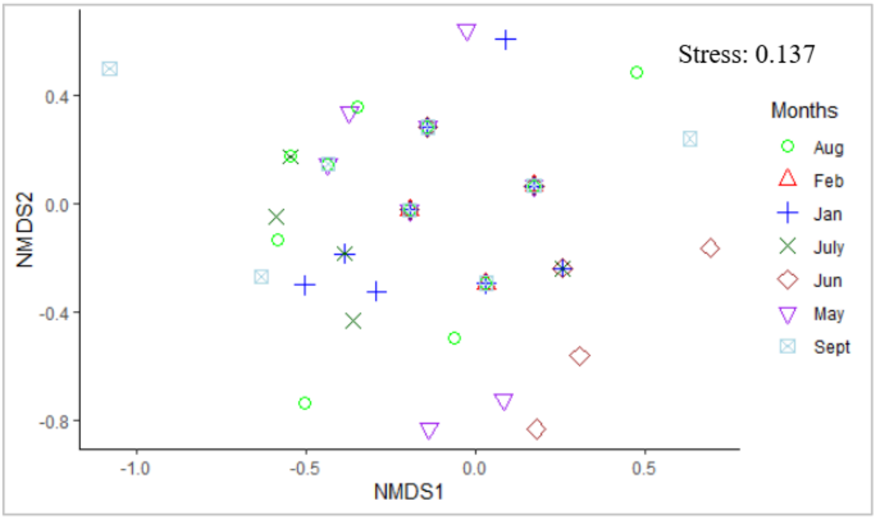

**Figure 4. 4.** NMDS plot of food category frequencies across sampling months in adult *Siganus sutor*

### 3.2.3. Abundance of food category

Macroalgae are the most abundant food category in adult *S. sutor* over the seven-month study period, followed by seagrass and mobile benthic prey (Fig. 4.5). Sessile benthic prey and zooplankton are less abundant with a presence in all sampling months. Phytoplankton were only present in small abundance in January 2022.

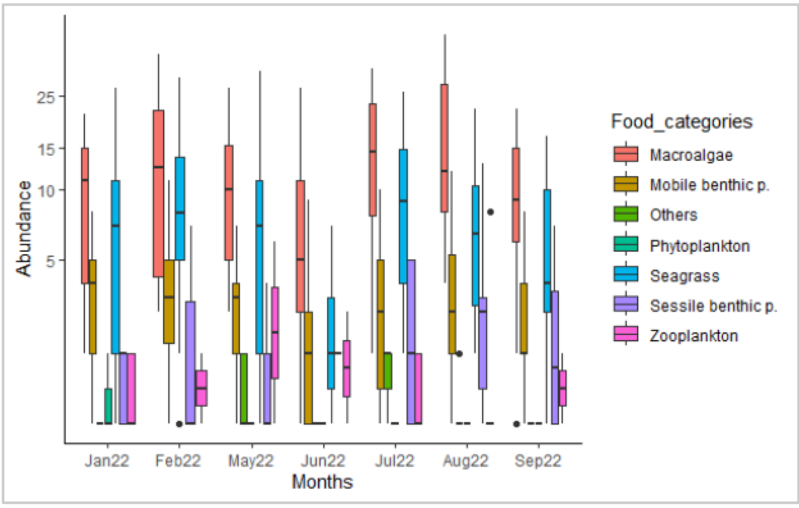

**Figure 4. 5.** Variation in the abundance of diet categories in adult *Siganus sutor*

The ART ANOVA test ($p < 2.22 \times 10^{-16}$) revealed a significant difference in the abundance of food categories, indicating that certain categories are more prevalent than others. Abundance also varies significantly across months ($p < 2.22 \times 10^{-16}$), highlighting temporal fluctuations. Additionally, a significant interaction between food category and month ($p < 2.22 \times 10^{-16}$) suggests that the abundance of certain food categories changes differently over time, rather than following a uniform trend across all months. The Dunn's post-hoc test revealed seven significant difference after a pairwise comparison among the sampling months (Tab. 4.2).

**Table 4. 2.** Results of Dunn's post-hoc test comparing the abundances of different food categories in adult *Siganus sutor* across sampling months. Significant differences are shown in bold.

| | Jan. 2022 | Feb. 2022 | May 2022 | Jun. 2022 | Jul. 2022 | Aug. 2022 | Sep. 2022 |
|---|---|---|---|---|---|---|---|
| **Jan.** | | 0.939 | 0.772 | **0.007** | 0.662 | 0.294 | 0.145 |
| **Feb.** | | | 0.83 | **0.008** | 0.601 | 0.253 | 0.161 |
| **May.** | | | | **0.013** | 0.452 | 0.169 | 0.23 |
| **Jun.** | | | | | **0.001** | **0.0001** | 0.183 |
| **Jul.** | | | | | | 0.52 | **0.048** |
| **Aug.** | | | | | | | **0.009** |
| **Sep.** | | | | | | | |

### 3.2.4. Stable isotope

For stable isotope analysis, sample of 82 adult *S. sutor* were used for stable isotope analysis. Samples came from seven sampling months: October and November (2021), as well as January, May, June, August, and September (2022). Samples from June and September 2022 were the most abundant compared to the other sampling months (Fig. 4.6a). The SL ranged from 21 to 38 cm, with a mean SL of 29.63 ± 4.25 cm (Fig. 4.6b).

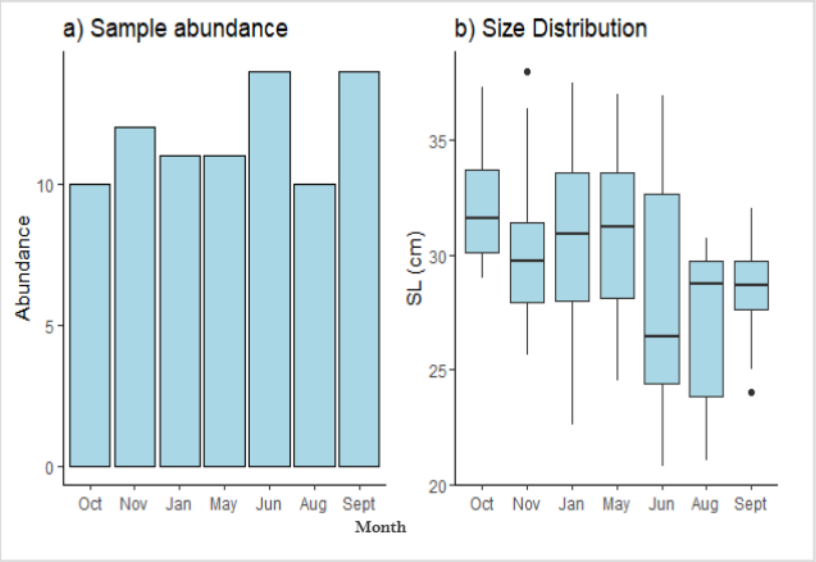

**Figure 4. 6.** a) Abundance and b) size distribution of adult *Siganus sutor* across the sampling months from October 2021 to September 2022.

There was overlaps in the ellipses representing the isotopic niche of tested samples from several months (Fig. 4.7: a.1, b.1, c.1). Samples from May and September 2022 represented the largest ellipses areas (Fig. 4.6: a.2, b.2, c.2). A gnificant temporal variation of carbon ($p = 0.03$) and nitrogen ($p = 0.0001$) stable isotope was observed in adult sample. However, there was no significant variation in sulfur stable isotope across the sampling months (p = 0.34). The Kruskal-Wallis test highlighted pairwise differences between months (Tab. 4.3). The pairwise comparison revealed that differences mainly occurred between samples from warm and cool season.

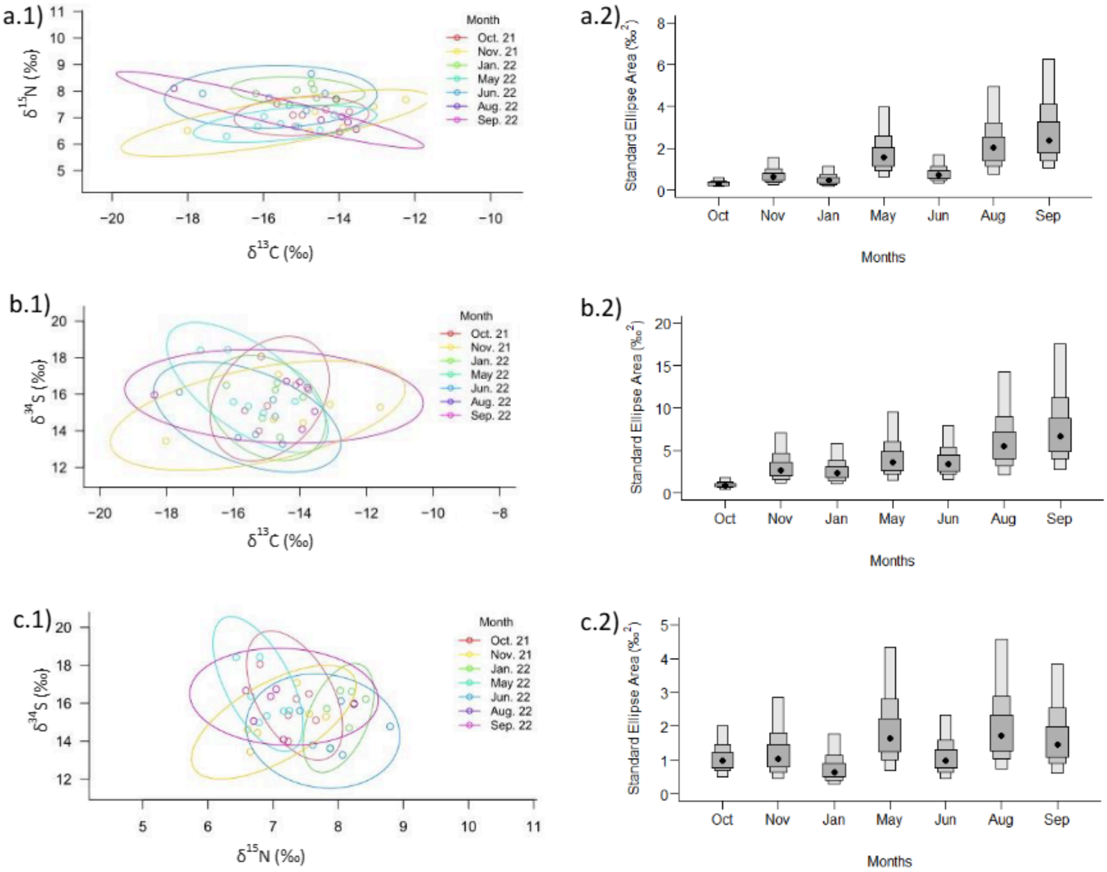

**Figure 4. 7.** Ellipses representing the carbon, nitrogen and sulfur isotopic niche space of adult *Siganus sutor* for each sampling months (a.1, b.1, c.1) and their associated Bayesian Standard Ellipses Areas (SEA) (a.2, b.2, c.2). Dark, median and light grey boxes are respectively the 50%, 75% and 95% credibility intervals of the probability of density function distributions of the model solutions, and black dots are the modes of these distributions.

**Table 4. 3.** Pairwise comparison of stable isotopes (C, N) across months in adult *Siganus sutor*

| $\delta^{13}C$ | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Oct. 2021 | Nov. 2021 | Jan. 2022 | May 2022 | Jun. 2022 | Aug. 2022 | Sep. 2022 |
| Oct. 2021 | | 0.38 | **0.022** | **0.01** | **0.014** | **0.035** | 0.95 |
| Nov. 2021 | | | 0.95 | 0.6 | 0.45 | 0.46 | 0.46 |
| Jan. 2022 | | | | 0.46 | 0.58 | 0.33 | 0.55 |
| May 2022 | | | | | 0.95 | **0.031** | 0.38 |
| Jun. 2022 | | | | | | 0.31 | 0.38 |
| Aug. 2022 | | | | | | | 0.95 |
| Sep. 2022 | | | | | | | |

| $\delta^{15}N$ | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Oct. 2021 | Nov. 2021 | Jan. 2022 | May 2022 | Jun. 2022 | Aug. 2022 | Sep. 2022 |
| Oct. 2021 | | **0.0373** | 0.3077 | 0.9186 | **0.0022** | **0.0429** | **0.0373** |
| Nov. 2021 | | | **0.0091** | **0.0373** | **0.0429** | 0.2695 | 0.7727 |
| Jan. 2022 | | | | 0.6364 | **0.0082** | 0.0664 | **0.0091** |
| May 2022 | | | | | **0.0082** | 0.0664 | **0.0373** |
| Jun. 2022 | | | | | | 0.7329 | 0.7329 |
| Aug. 2022 | | | | | | | 0.9372 |
| Sep. 2022 | | | | | | | |

## 3.3. Diet of juvenile *Siganus sutor*

### 3.3.1. Sample size

A total of 95 individuals of juvenile *S. sutor* were used for gut content analysis. Sample are from four months (July 2021, September 2021, November 2021 and March 2022) and are distributed according to the five different types of habitat. Sample from mangrove were less represented while those from seagrass meadow were the most represented (Fig. 4.8a). Size (SL) of analysed juvenile range from 1.9 to 11cm with a mean of 5.12 ± 1.9cm (Fig. 4.8b).

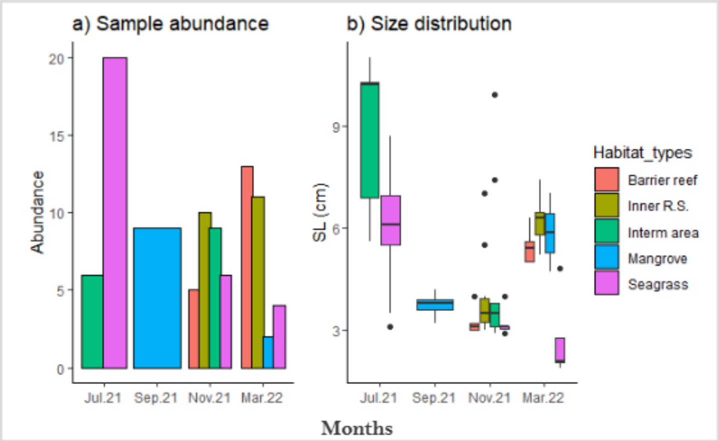

Figure 4. 8. a) Abundance and b) size distribution of juvenile *Siganus sutor* from five habitats across the sampling sampling months. Inner R. S. refers to the inner reef slope.

### 3.3.2. Percentage of occurrence of food items

For all the 95 analyzed individuals, only one empty stomach was found. The analysis of gut content in juvenile *S. sutor* revealed a total number of 25 food items composed by vegetal and animal prey in the gut of juvenile *S. sutor* (Tab. 4.4). Plant-based preys, including macroalgae and seagrass, were the most frequently encountered food items with a percentage of occurrence that can reach 100%. Zooplankton were the less frequent food category found in juvenile gut content.

**Table 4. 4.** Percentage of occurrence (%F) of all food items in juvenile *Siganus sutor*

| Phylum | Food items | July 2021 | Sept. 2021 | Nov. 2021 | March 2022 |
|---|---|---|---|---|---|
| | **Phytoplankton** | **7.69** | **0** | **6.90** | **0** |
| | **Algae** | **100.00** | **100.00** | **100.00** | **100.00** |
| | **Seagrass** | **100.00** | **77.78** | **89.66** | **100.00** |
| | **Zooplankton** | **5.38** | **0.00** | **5.52** | **0** |
| **Chaetognatha** | Chaetognath | 0 | 0 | 3.45 | 0 |
| **Retaria** | Radiolarian | 0 | 0 | 0 | 3.33 |
| **Cnidaria** | Jellyfish | 0 | 0 | 3.45 | 0 |
| **Cnidaria** | Siphonophore | 7.69 | 0 | 0.00 | 0 |
| **Arthropoda** | Copepod | 7.69 | 0 | 13.79 | 0 |
| **Arthropoda** | Decapod larvae | 11.54 | 0 | 6.90 | 0 |
| **Arthropoda** | **Mobile benthic preys** | **27.40** | **19.81** | **14.25** | **16.00** |
| **Foraminifera** | Foraminifera | 38.46 | 46.12 | 13.79 | 23.33 |
| **Annelida** | Polycheta | 15.38 | 11.11 | 3.45 | 13.33 |
| **Mollusca** | Cladocerean | 0 | 0.00 | 33.12 | 3.33 |
| **Mollusca** | Gastropod | 61.54 | 55.56 | 48.28 | 63.33 |
| **Mollusca** | Bivalve | 26.92 | 0 | 3.45 | 20.00 |
| **Arthropoda** | Amphipod | 11.54 | 42.11 | 17.24 | 23.33 |
| **Arthropoda** | Hydracarian | 32.46 | 0 | 0 | 6.67 |
| **Arthropoda** | Crustacean Decapod | 37.89 | 0 | 12.87 | 0.00 |
| **Arthropoda** | Isopod | 7.69 | 11.11 | 6.90 | 6.67 |
| **Arthropoda** | Ostracod | 42.16 | 32.11 | 3.45 | 0.00 |
| | **Sessile benthic preys** | **5.13** | **0** | **5.75** | **4.44** |
| **Chordata** | Tunicata | 0 | 0 | 3.45 | 0.00 |
| **Cnidaria** | Scleractinia | 11.54 | 0 | 13.79 | 6.67 |
| | **Other** | **13.46** | **5.56** | **5.17** | **7.50** |
| | Sponge | 0 | 0 | 0 | 3.33 |
| | Fish scale | 46.15 | 22.22 | 6.90 | 3.33 |
| | Eggs | 0 | 0 | 3.45 | 6.67 |
| | Mollusk shell | 7.69 | 0 | 10.34 | 16.67 |
| **Number of food items** | | **19** | **7** | **21** | **19** |

The results of the PERMANOVA analysis revealed a significant difference in the composition of food categories across the sampling months ($p = 0.018$). This suggests that the month is a significant factor influencing the variation in food category frequency within the samples. The NMDS plot illustrates the variation in food category frequency across months based on Bray-Curtis dissimilarity (Fig. 4.9). This visualization supports the findings from the PERMANOVA analysis and highlights the seasonal differences in dietary composition. The significant differences were specifically observed between samples from July 2021 and November 2021 ($p = 0.046$), July 2021 and March 2022 ($p = 0.03$), and September 2021 and March 2022 ($p = 0.03$).

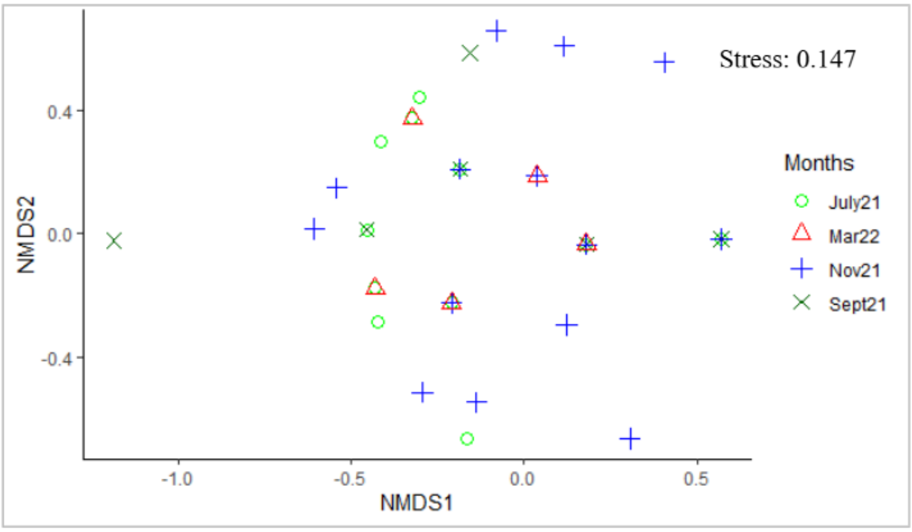

**Figure 4. 9.** NMDS plot of food categories across sampling months in juvenile *Siganus sutor*

The NMDS plot illustrate the dissimilarity between frequencies of food item in juvenile *S. sutor* (Fig. 4.10). The PERMANOVA analysis revealed no significant difference in food frequency according to habitat type ($p = 0.144$).

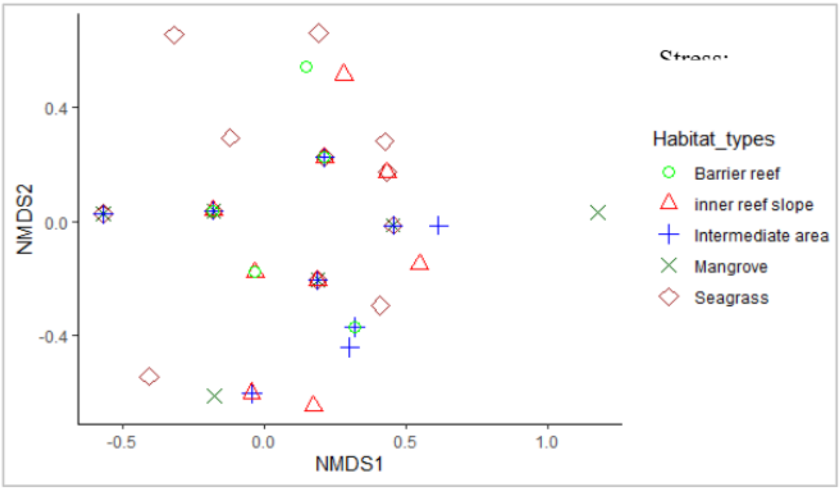

**Figure 4. 10.** NMDS plot of food categories across habitat type in juvenile *Siganus sutor*

### 3.3.3 Abundance of food categories

The analysis of abundance showed a high abundance of macroalgae over three months except in September, which was dominated by mobile benthic preys (Fig. 4.11). The mobile benthic preys represented the second most abundant food category followed by the seagrass. Phytoplankton are the less abundant in the four compared months.

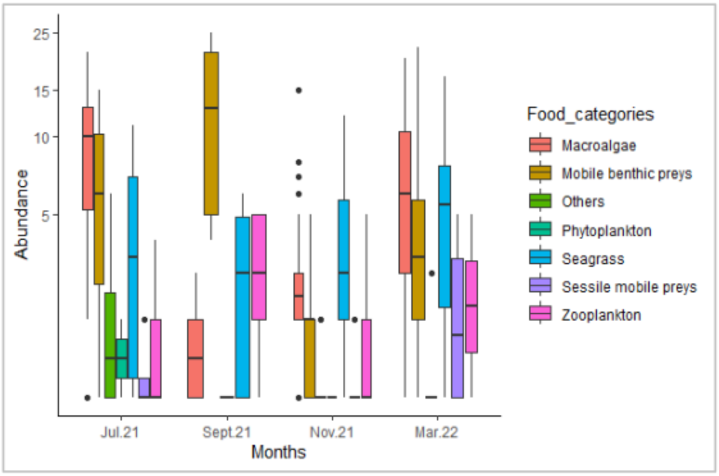

**Figure 4. 11.** Temporal variation in the abundance of diet categories in juvenile *Siganus sutor*

The ART ANOVA revealed a significant effect of food category abundance ($p < 2.22 \times 10^{-16}$), indicating that globally certain food categories are more abundant than others. A significant effect of month ($p < 2.22 \times 10^{-16}$) suggests temporal variations in food availability. Additionally, the significant interaction between food category and month ($p < 2.22 \times 10^{-16}$) indicates that changes in abundance are not uniform across all food categories, but rather vary depending on the sampling period. Pairwise comparisons using Dunn's post-hoc test revealed a significant difference between July and November 2021 ($p = 0.0002$; Tab. 4.5). This difference is primarily driven by the variation in macroalgae abundance (Dunn test, $p = 2.28 \times 10^{-6}$). Another significant difference was observed between November 2021 and March 2022 ($p = 0.007$), influenced by variations in the abundance of both macroalgae ($p = 1.67 \times 10^{-4}$) and mobile benthic prey ($p = 6.45 \times 10^{-5}$).

**Table 4. 5.** Results of Dunn's post-hoc test comparing the abundances of different food categories in juvenile *Siganus sutor* across sampling months. Significant differences are shown in bold.

| | **Jul. 2021** | **Sept. 2021** | **Nov. 2021** | **Mar. 2022** |
|---|---|---|---|---|
| **Jul.** | | 0.135 | **0.0002** | 0.278 |
| **Sep.** | | | 1 | 1 |
| **Nov.** | | | | **0.007** |
| **Mar.** | | | | |

Analysis of variation of abundance of food categories in juvenile from the different sampling habitat also revealed the predominance of macroalgae in the gut content of sample from the five habitats (Fig.4.12). The food diversity is less diversified in samples from mangrove and the barrier reef. There is no significant difference in the abundance of food categories between the tested habitat (Kruskal-Wallis, p = 0.8981).

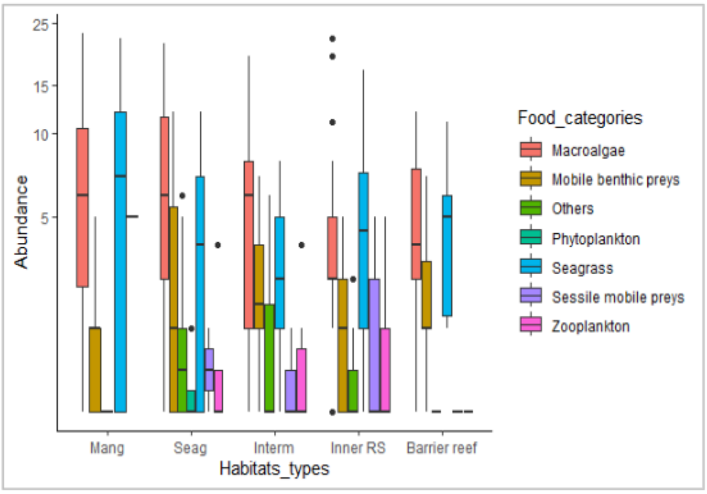

**Figure 4. 12.** Spatial variation in the abundance of diet categories in juvenile *Siganus sutor*

### 3.3.4. Stable isotope

For the stable isotope analysis, 407 juveniles *S. sutor* were analysed. Those subsamples are from seven sampling months Samples from July, August, September, and November (2021), as well as January, February, and March (2022). The most abundant subsample was found in November 2021 (Fig. 4.13a). Fish size ranged from 3 to 13 cm, with an average SL of 4.77 ± 2.03 cm (Fig.4.13b).

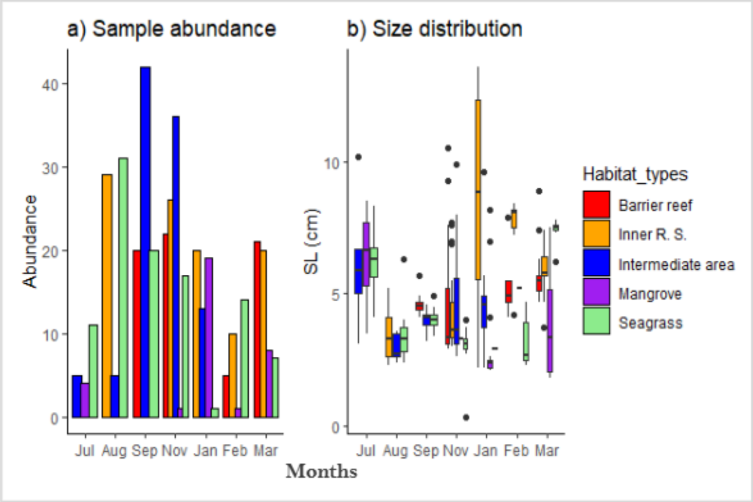

**Figure 4. 13.** a) Abundance and b) size distribution of juvenile *Siganus sutor* from five habitats across the sampling months (July 2021 to March 2022). Inner R. S. refers to the inner reef slope.

### 3.3.4.1. Spatio-temporal variation of stable isotope ratios

A certain degree of variability in the isotope ratios was observed in juveniles, depending on the month of sampling (Fig. 4.14: a.1, b.1, c.1). There was slight overlap between the convex hulls representing the isotopic values of the groups being compared. The slight overlap observed between the hulls indicates some degree of isotopic niche overlap, suggesting potential similarities in dietary sources among the samples from several sampling months. Only sample from August 2021 presented no overlaps with the other samples. There was a significant difference between Bayesian posterior densities of total isotopic niche areas across months (Kruskal-Wallis, $p = 0.01$) (Fig. 4.14: a.2, b.2, c.2).

A strong significant difference was observed in the stable isotope ratios of both carbon, nitrogen and sulfur across the sampling months (Kruskal-Wallis, $p<2.2 \times 10^{-16}$). The results of pairwise comparisons showed several differences in the of stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) across months in juvenile *S. sutor*, based on the Wilcoxon rank sum test (Tab. 4.6). Difference mainly occurred between samples from warm season (September, November, January and February) and samples from cool season (June, July and August).

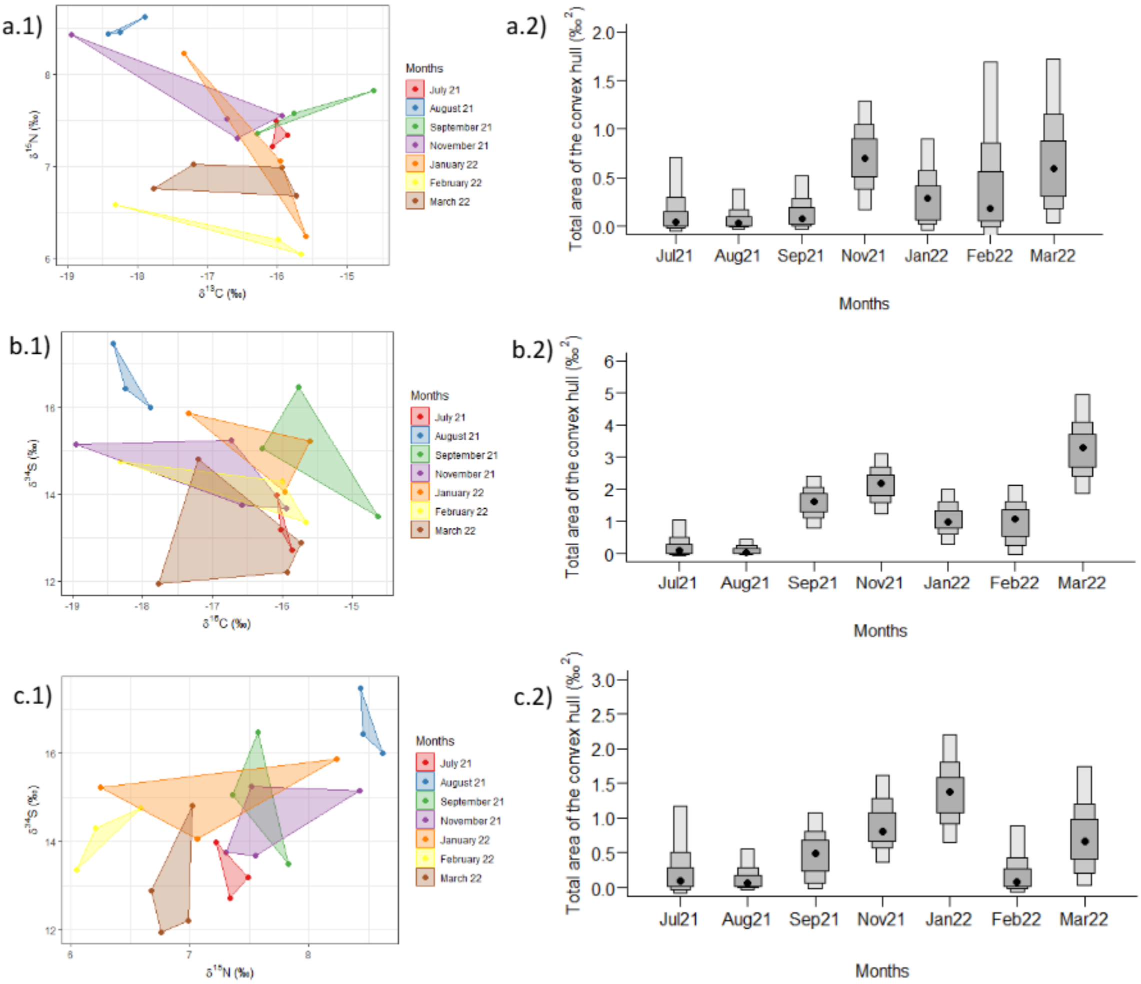

Figure 4. 14. Convex hull plot of carbon, nitrogen, and sulfur isotopic niche space of juvenile *Siganus sutor* across sampling months (a.1, b.1, c.1). Each dot represents the mean isotopic ratio per habitat type, with colors indicating the sampling month. The associated Bayesian posterior densities of total isotopic niche area are shown in (a.2, b.2, c.2). Dark, median, and light grey boxes represent the 50%, 75%, and 95% credibility intervals of the probability density function distributions of the model solutions, while black dots indicate the modes of these distributions

**Table 4. 6**. Pairwise comparison of stable isotopes (C, N, S) across months in juvenile *Siganus suto*r. Significant differences are showed in bold.

| **13C** | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Jul. 2021 | Aug. 2021 | Sep. 2021 | Nov. 2021 | Jan. 2022 | Feb. 2021 | Mar. 2022 |
| Jul. 2021 | | **1.80E-08** | 0.31019 | **0.00056** | 0.33025 | 0.15748 | **0.00553** |
| Aug. 2021 | | | **3.60E-15** | **3.80E-06** | **6.40E-08** | **0.00119** | **4.10E-07** |
| Sep. 2021 | | | | **8.50E-08** | **0.00833** | **0.00015** | **2.60E-05** |
| Nov. 2021 | | | | | 0.14093 | 0.75899 | 0.6521 |
| Jan. 2022 | | | | | | **0.01671** | 0.15748 |
| Feb. 2021 | | | | | | | 0.18965 |
| Mar. 2022 | | | | | | | |
| **15N** | | | | | | | |
| | Jul. 2021 | Aug. 2021 | Sep. 2021 | Nov. 2021 | Jan. 2022 | Feb. 2021 | Mar. 2022 |
| Jul. 2021 | | **2.30E-07** | **0.019** | 0.129 | 0.701 | **3.70E-08** | **2.80E-07** |
| Aug. 2021 | | | **8.90E-12** | **4.50E-10** | **7.10E-08** | **6.90E-13** | < 2e-16 |
| Sep. 2021 | | | | 0.644 | 0.414 | **9.80E-12** | **6.70E-13** |
| Nov. 2021 | | | | | 0.081 | **7.40E-13** | **1.10E-12** |
| Jan. 2022 | | | | | | **0.01** | 0.274 |
| Feb. 2021 | | | | | | | **1.00E-06** |
| Mar. 2022 | | | | | | | |
| **34S** | | | | | | | |
| | Jul. 2021 | Aug. 2021 | Sep. 2021 | Nov. 2021 | Jan. 2022 | Feb. 2021 | Mar. 2022 |
| Jul. 2021 | | **2.20E-08** | **3.50E-05** | 0.07101 | **0.002** | **0.01353** | 0.24796 |
| Aug. 2021 | | | **0.00038** | **1.40E-05** | **0.02944** | **2.70E-05** | **8.70E-14** |
| Sep. 2021 | | | | 0.07266 | 0.72631 | **0.04159** | **1.40E-09** |
| Nov. 2021 | | | | | 0.06324 | 0.73432 | **3.50E-05** |
| Jan. 2022 | | | | | | **0.07451** | **3.00E-06** |
| Feb. 2021 | | | | | | | **0.00017** |
| Mar. 2022 | | | | | | | |

### 3.3.4.2. Spatial variation

While assessing the variation across the habitats types, the Kruskal-Wallis test revealed a significant difference in stable isotope of carbon ($p = 8.853 \times 10^{-16}$), nitrogen ($3.587 \times 10^{-07}$) and sulfur ($p = 1.576 \times 10^{-05}$) (Fig. 4.15: a.1, b.1, c.1). Additionally, Kruskal-Wallis test showed a significant difference in the Bayesian posterior densities of total isotopic niche areas ($p=0.023$) (Fig. 4.15: a.2, b.2, c.2). This highlights the variations in isotopic composition across the tested sampling habitats with a relative wider trophic niche in samples from seagrass and the inner reef slope. The results of the pairwise comparisons revealed significant differences in the stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) across habitat types in juvenile *S. sutor* (Tab. 4.7). The barrier reef was the habitat that differs the most from other habitat types. Samples from this habitat had a stable isotopic ratio that is significantly different from those of all other habitats. Additionally, the inner reef slope also showed some differences compared to the mangrove and seagrass habitats.

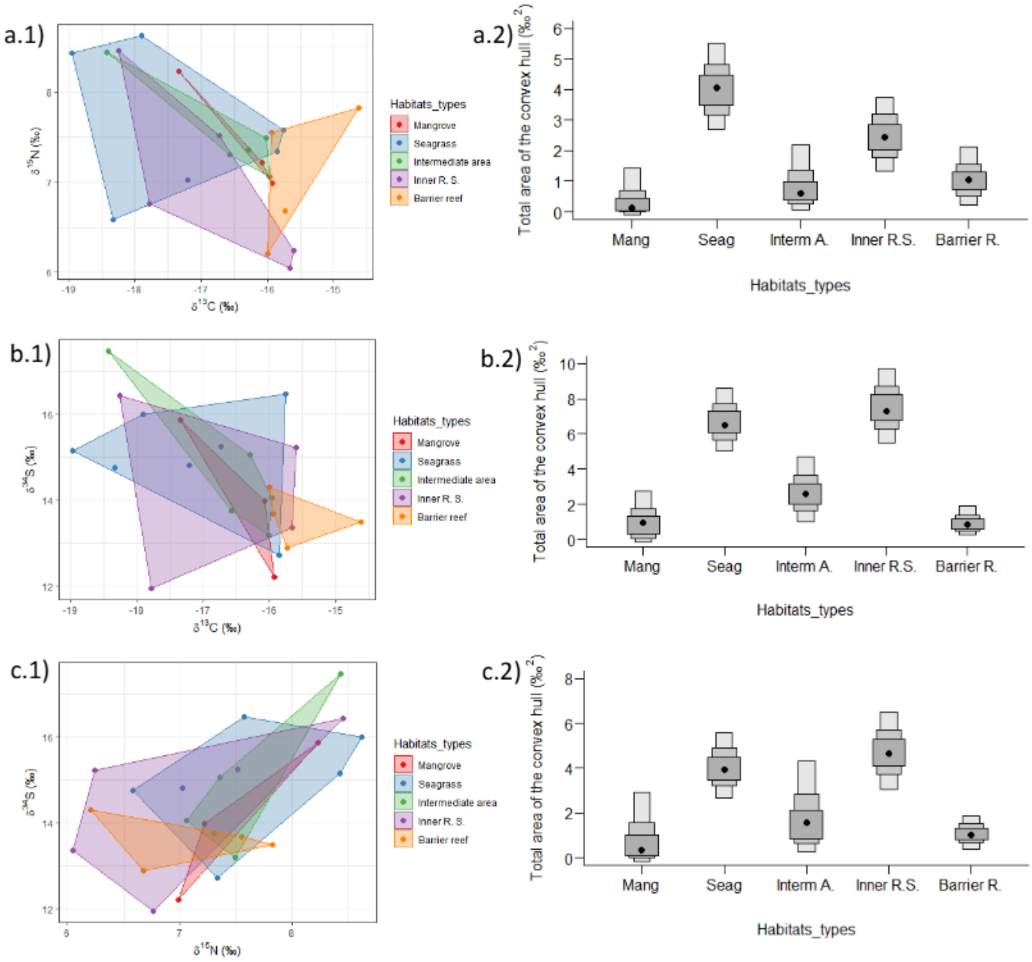

**Figure 4. 15.** Convex hull plot of carbon, nitrogen, and sulfur isotopic niche space of juvenile *Siganus sutor* across different habitats types (a.1, b.1, c.1). Each dot represents the mean isotopic ratio month, with colors indicating the habitat type. The associated Bayesian posterior densities of total isotopic niche area are shown in (a.2, b.2, c.2). Dark, median, and light grey boxes represent the 50%, 75%, and 95% credibility intervals of the probability density function distributions of the model solutions, while black dots indicate the modes of these distributions.

**Table 4. 7.** Pairwise comparison of stable isotopes (C, N, S) across habitats types in juvenile *Siganus sutor*. Interm area and Inner RS refers to Intermediate area and Inner reef slope.

| **$\delta^{13}C$** | | | | | |
|---|---|---|---|---|---|
| | Mangrove | Seagrass | Interm area | Inner RS | Barrier reef |
| Mangrove | | **0.0051** | **0.0357** | 0.5575 | **$2.40\times10^{-06}$** |
| Seagrass | | | **$2.40\times10^{-06}$** | **0.0167** | **$8.50\times10^{-12}$** |
| Interm area | | | | **0.0014** | **$2.40\times10^{-06}$** |
| Inner RS | | | | | **$9.80\times10^{-11}$** |
| Barrier reef | | | | | |
| **$\delta^{15}N$** | | | | | |
| | Mangrove | Seagrass | Interm area | Inner RS | Barrier reef |
| Mangrove | | 1 | **0.02164** | **0.00967** | **0.00426** |
| Seagrass | | | **0.00135** | **0.00023** | **0.0005** |
| Interm area | | | | 0.14114 | 0.50258 |
| Inner RS | | | | | 0.50258 |
| Barrier reef | | | | | |
| **$\delta^{34}S$** | | | | | |
| | Mangrove | Seagrass | Interm area | Inner RS | Barrier reef |
| Mangrove | | 0.2365 | 0.8952 | 0.8474 | 0.1583 |
| Seagrass | | | **0.0099** | 0.167 | **$3.60\times10^{-07}$** |
| Interm area | | | | 0.3529 | **0.0133** |
| Inner RS | | | | | **0.0014** |
| Barrier reef | | | | | |

## 3.4. Ontogenetic diet variation

### 3.4.1. Variation of gut content

Pearson's correlation analysis revealed significant relationships between fish size (SL) and the abundance of different food categories in *S. sutor* (Fig. 4.16). A positive correlation was observed between SL and the abundance of macroalgae ($p = 5.08 \times 10^{-12}$) and seagrass ($p = 1.53 \times 10^{-10}$). In contrast, a negative correlation was found between SL and the abundance of benthic mobile preys ($p = 1.96 \text{ x } 10^{-07}$). There was no significant correlation between SL and abundance of phytoplankton and zooplankton.

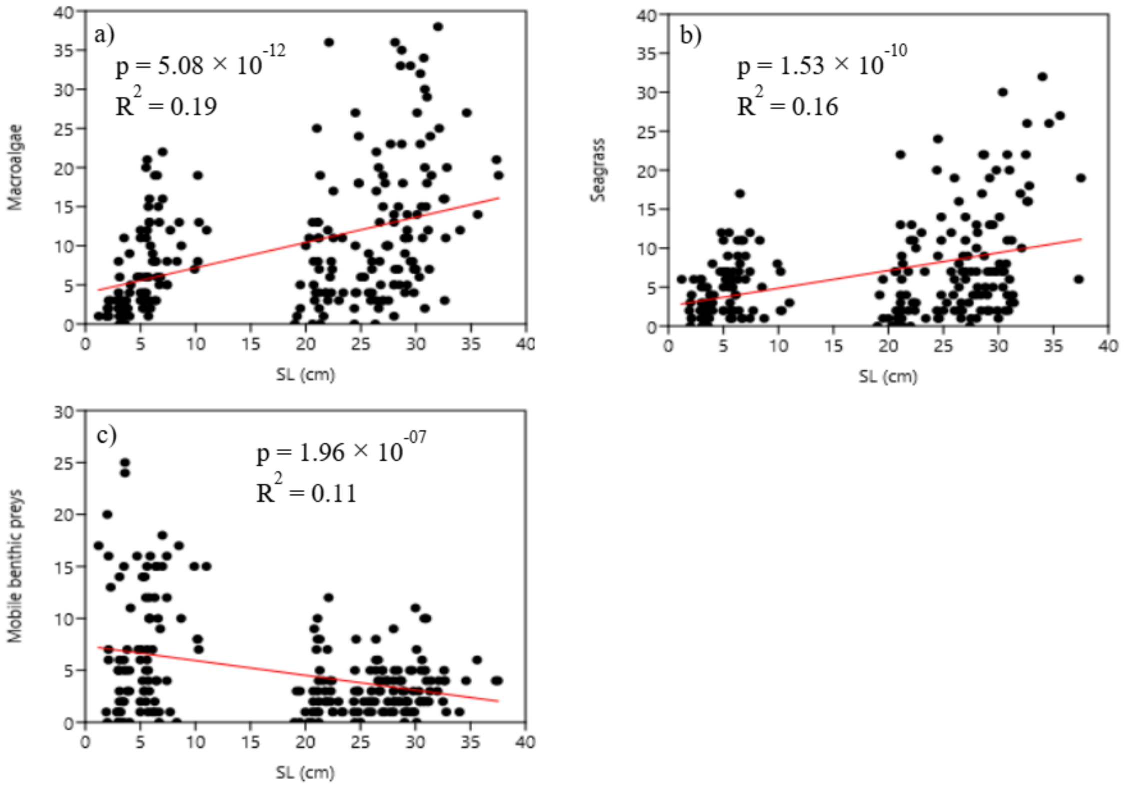

**Figure 4. 16.** Correlation between size (SL) of *Siganus sutor* and abundance of food categories: a) macroalgae, b) seagrass and c) mobile benthic preys

### 3.4.2. Variation of stable isotope ratio

A significant positive correlation was observed between standard length (SL) and carbon stable isotope ratios ($\delta^{13}C$) (Spearman's rank correlation, $p = 0.0001$) (Fig. 4.17), indicating that smaller individuals exhibit lower $\delta^{13}C$ ratios compared to larger individuals. In contrast, the correlation between SL and nitrogen stable isotope ratios ($\delta^{15}N$) was negative but weaker (Spearman's rank correlation, $p = 0.013$). No significant correlation was found between SL and sulfur stable isotope ratios ($\delta^{34}S$).

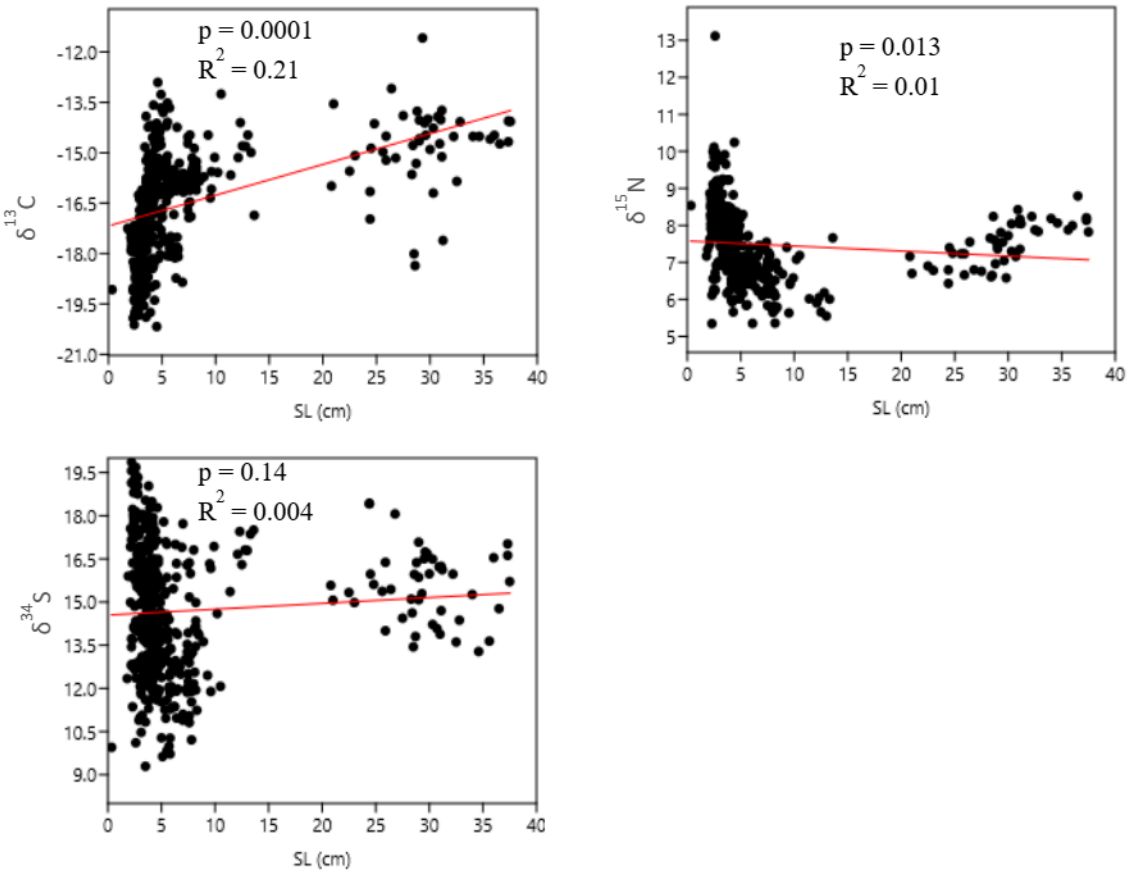

**Figure 4. 17.** Relationship between body size (SL) and stable isotope ratios in *Siganus sutor*

### 3.4.3. Variation of gut length

The results revealed a positive significant correlation between SL and GL in *S. sutor* (Pearson, $p = 2.05 \times 10^{-159}$) (Fig. 4.18). We observed a high correlation with a $R^2 = 0.95$. This relationship indicates that as individuals grow, their digestive tract proportionally increases in length.

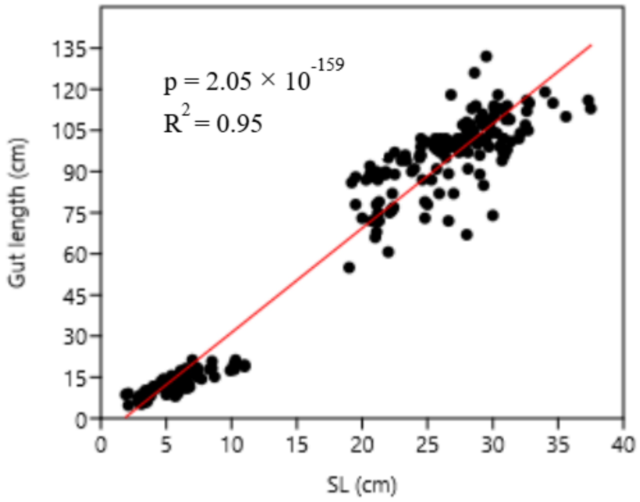

**Figure 4. 18.** Correlation between fish size and gut length in *Siganus sutor*

The mean RGL is 3.1 ± 0.79 for *S. sutor.* There was a significant increase in RGL from 1.5 in smaller individuals to 4.7 in bogger samples. (Pearson correlation, $p = 1.09 \times 10^{-38}$) (Fig. 4.19). This finding indicates that adults have a significantly higher RGL up to four times the body size compared to juveniles.

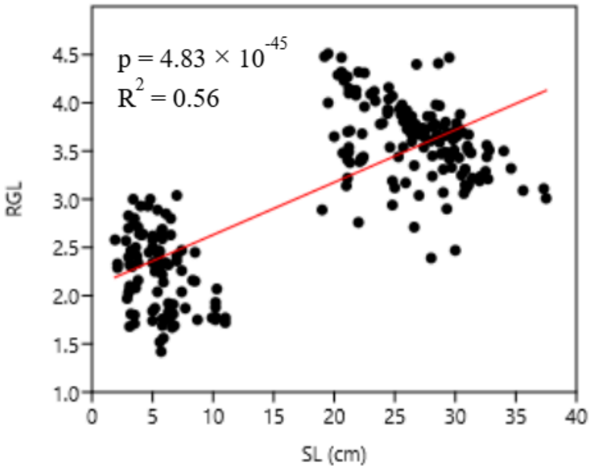

**Figure 4. 19.** Correlation between fish size (SL) and regressive gut length (RGL) of *Siganus sutor*

## 4. Discussion

The gut content analysis revealed the presence of 25 food items in juvenile *S. sutor* and 24 in adults, with a predominance of macroalgae and seagrass. Animal prey was also observed in the gut, with mobile benthic organisms being more common than zooplankton, which were rarely found. All seven food categories were present in both juvenile and adult samples, with the abundance of the primary categories varying throughout the ontogeny of the species. For instance, the abundance of plant-based categories, such as macroalgae and seagrass, increased with fish size, while the abundance of mobile benthic prey decreased proportionally. A significant positive correlation was observed between fish length and gut length, with relative gut length (RGL) ranging from 1.42 in smaller individuals to 4.58 in larger ones. Temporal variation in food abundance was observed in both juvenile and adult fish, a trend that was corroborated by stable isotope ratio analysis. In juvenile *S. sutor*, stable isotope ratios also varied according to habitat types, reflecting significant differences in trophic niche across sampling habitats.

### 4.1. Diet of *Siganus sutor*

The stable isotope values of carbon ($\delta^{13}C$) in *S. sutor* ranged from -17‰ to -13‰. This relatively narrow range is typical of marine primary production sources, particularly benthic macroalgae and seagrass-based food webs. Less negative $\delta^{13}$C values (closer to -13‰) suggest a stronger reliance on benthic or nearshore carbon sources, whereas more negative values (around -17‰) may indicate some contribution from pelagic or phytoplankton-based sources.

Nitrogen isotopic values ($\delta^{15}$N) varied from 6.5‰ to 8.5‰. This range indicates low to moderate trophic level variation among the individuals sampled. The relatively narrow $\delta^{15}$N range suggests that most individuals occupy similar trophic positions, likely functioning as primary consumers or low-level omnivores feeding on algae and detritus. Slight differences in $\delta^{15}$N may reflect seasonal or spatial differences in nitrogen sources or feeding behavior.

Sulfur isotope values ($\delta^{34}$S) ranged from 14‰ to 18‰, indicating a predominant reliance on marine sulfur sources. These values are consistent with a marine sulfate origin, typical of organisms feeding in environments with minimal influence from freshwater or sediment-derived sulfur, such as mangroves or anoxic seafloor zones. Slight variations may suggest some differences in habitat use (e.g., more seagrass-associated vs. more coral reef-associated individuals) or microhabitat sulfur dynamics.

### 4.2.Diet variation in juvenile *Siganus sutor*

Temporal variation in diet of juvenile *S. sutor* can be interpreted as seasonal variation, as differences typically occur between months corresponding to warm and cool seasons. Variations in gut content were observed between samples from November (warm and dry season) and those from March (intermediate and rainy season) and July (cool season). The difference is due to the variation of abundance of main food categories like macroalgae. Stable isotope ratios further confirmed this seasonal variation, with significant differences in carbon, nitrogen, and sulfur isotopic values between samples from September, November, January, and February compared to those from July and August. The isotopic niche of juvenile *S. sutor* fluctuates over time, potentially due to environmental changes, seasonal resource availability, or growth-related dietary shifts (Earl et al., 2011; St. John, 2001). Temporal variation in the diet of juvenile *S. sutor* can also occur between years, as observed in the dietary differences between samples from December 2017 and December 2018 in the lagoon of Toliara (Ravelohasina et al., 2024).

Seasonal diet variationin was also observed in 3 species of herbivorous reef fishes: doctorfish Ac*anthurus chirurgus* (Acanthuridae), endemic grey parrotfish *Sparisoma axillar* (Labridae) and brassy chub Kyphosus vaigiensis (Kyphosidae) in in subtropical rocky reefs in Brazil. Gut content analysis revealed that the 3 species present a seasonal diet variation but variation was not reflected in isotopic variation. This may suggest a balanced intake of isotopically distinct food sources to meet nutritional needs or consumption of different food items that share similar isotopic signatures (Cardozo-Ferreira et al., 2023). Other study have also proven a temporal variation in the trophic ecology of the temperate hemiramphid, *Hyporhamphus melanochir* with a difference in food composition between autumn and winter. This variation is influenced by the difference in day-length that affect the feeding behaviour of the specie (Earl et al., 2011).

The spatial variation of diet in juvenile *S. sutor* had only seen in the stable isotope ratio. Samples from barrier reef present different stable isotope value with a higher $\delta^{13}C$ ratio compared to the samples from the other habitats. Additionally, most of the differences occurred between samples from intermediate area and inner reef slope compared to those from the habitats near to the shoreline like mangrove and seagrass. Gajdzik *et al.* (2016) have shown influence of coral reef habitat morphological features on the trophic ecology of Pomacentridae in Moorea with difference in food preference according to the habitat type. This variation was reflected in the $\delta^{34}S$ ratio of samples.

The absence of spatial variation in gut content analysis but its detection in stable isotope analysis, as in this study, suggests differences in dietary assimilation rather than direct ingestion. Gut content analysis provides a short-term snapshot of recently consumed food, which may be similar across habitats due to opportunistic feeding behaviour (Baker et al., 2014; Cocheret De La Morinière et al., 2003). In contrast, stable isotope analysis reflects long-term dietary assimilation, integrating trophic interactions over weeks to months. This discrepancy implies that while juvenile *S. sutor* individuals in different habitats may consume similar food items at a given moment, differences in resource availability, or habitat-specific nutrient composition influence the long-term assimilation of dietary components, leading to spatial variation in isotope ratios (Chouvelon et al., 2012; Deudero et al., 2004; Gaston & Suthers, 2004).

### 4.3.Diet variation in adult *Siganus sutor*

Diet of adult *S. sutor* varies in and between season, likely influenced by changes in food availability between the warm season (September, January and February) and cool season (June and July). This variation likely reflects changes in the abundance of specific food sources, such as seagrass, macroalgae, and mobile benthic preys, which fluctuate with seasonal shifts. For example, during the warm season, higher water temperatures and increased sunlight may promote greater algal growth and seagrass productivity, leading to a richer and more diverse diet. And in the cool season, primary production may be lower, potentially limiting available food resources and influencing dietary shifts (Ferreira et al., 1998; Hajisamae & Ibrahim, 2008). So, adult *S. sutor* can adapt its feeding habits based on resource availability. This flexibility could be essential for sustaining populations in environments with strong seasonal differences. As it have been proved in Australia where *Siganus fuscescens* presented a seasonal diet variation according to algal availability (Pillans et al., 2004).

Stable isotope analysis to confirm that trophic level shifts occur between seasons. Indeed, seasonal dietary variations in adult *S. sutor* are well captured by carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes but not by sulfur ($\delta^{34}S$) stable isotopes. This can be explain that $\delta^{13}C$ and $\delta^{15}N$ track changes in food sources and trophic level (Hobson & Welch, 1992; Kang et al., 1999; Layman et al., 2012; Lepoint et al., 2004), showing shifts in seagrass, macroalgae, or animal preys consumption between seasons. However, $\delta^{34}S$ remains stable because it primarily reflects the sulfur source in the environment, which likely does not vary significantly across months (Fry, 1988; Peterson & Fry, 1987; Robinson, 2001). This suggests that while *S. sutor* adjusts its diet based on seasonal food availability, it continues to feed within the same general ecosystem, rather than shifting to different habitats.

### 4.4.Ontogenetic variation of diet

The study found that the abundance of plant-based food (macroalgae and seagrass) increases proportionally with fish size. Conversely, the abundance of mobile benthic prey showed a negative correlation with fish SL, illustrating a decrease in animal prey consumption during growth. This result highlights an ontogenetic shift in the diet of *S. sutor*, where juveniles rely more on animal prey, while larger individuals increasingly consume plant-based food. Younger fish often require more protein-rich diets to support rapid growth and development, which could explain their higher consumption of animal preys. As fish grow, their energy demands may shift toward sustaining body mass rather than rapid growth, making plant-based food a viable and abundant resource (Dunic & Baum, 2017; Pilati & Vanni, 2007). A study in the comparison of diet of four siganid species, found significant dietary differentiation as the fish matured, suggesting that developmental stage influence dietary adaptation strategies (Pitt, 1997). Moreover, siganids are known that juvenile and adult Siganids occupy different habitats (Duray & Southeast Asian Fisheries Development Center, 1998a; Nanami, 2018). As the case in this study where all juvenile where caught in the lagoon when adult were all caught in the outer reef slope. In consequent, smaller individuals might reside in areas where benthic invertebrates are more accessible, while larger fish may frequent seagrass beds or algal-dominated zones, leading to a higher intake of plant material.

This correlation was reflected in the isotopic ratio of fish muscle by a significant positive correlation between SL and $\delta^{13}C$. This indicates that larger fish tend to consume food with higher carbon isotopic signatures, possibly due to dietary or habitat shifts as they grow. It may be influenced by the diet of adult *S. sutor*, which tends to be more herbivorous, as plant-based foods (macroalgae and seagrass) have higher $\delta^{13}C$ values. This trend have been observed in surgeonfish *Acanthurus triostegus* where larger fish shift to feeding on more carbon-enriched food sources, while smaller fish tend to rely on planktonic or less carbon-enriched sources (Frédérich et al., 2012). Similar results have been seen in the herbivorous hemiramphid *Hyporhamphus regularis ardelio* indicating that larger individuals consume more carbon-enriched food sources compared to smaller ones (Carseldine & Tibbetts, 2005).

In contrast, the correlation between SL and nitrogen stable isotope ratios ($\delta^{15}N$) was negative. This is due to the difference in trophic level, because nitrogen isotopes become enriched as species move up the food chain. In fact, smaller fish tend to have higher $\delta^{15}N$ due to trophic enrichment as they feed both in plant-based food and in animal preys with enriched nitrogen (Britton & Busst, 2018; Busst & Britton, 2016). Inversely, larger fish have a lower $\delta^{15}N$ due to the low proportion of animal prey ingested and a high proportion of primary producer with lower nitrogen value (Mill et al., 2007). This negative correlation have been seen in sugeonfish (Frédérich et al., 2012) and in parrotfish *Scarus zelindae* (Pereira et al., 2016). However, no significant correlation was found between SL and sulfur stable isotope ratios ($\delta^{34}S$), implying that sulfur isotopes are not influenced by size, possibly reflecting an absence of drastic dietary shift across fish sizes.

### 4.5.Gut length variation

A mean RGL of 3.1 ± 0.79 suggests that the gut is around three times the body length, which is typical for fish with some level of herbivory, but not as extreme as in fully specialized herbivores (e.g., some surgeonfish with $RGL > 4$) (Montgomery & Pollak, 1988). Additionally, research on cyprinid fish has shown that species with long relative gut lengths ($RGL \geq 4$) are adapted to extract nutrients from aquatic plants and algae, suggesting a similar adaptation in herbivorous fish like surgeonfish (Liu et al., 2022). Study on feeding habits and digestive morphology of *Siganus spinus* provided insights into the species' dietary preferences with a digestive system adaptation to efficiently process various food types, reflecting potential dietary adaptation strategies (Bryan, 1975). This characteristic is specific to herbivorous fish species. In contrast, carnivorous species have a relatively low RGL. For example, the Atlantic blue fin tuna (*Thunnus thynnus*), a fast-swimming carnivore, has an RGL of approximately 0.5-0.7, which is typical for large carnivorous fish with a diet consisting primarily of other fish and squid (Olson et al., 2014).

The results indicated a significant increase in RGL from 1.42 to 4.58 in *S. sutor*. This ontogenetic shift suggests a progressive adaptation to a more specialized herbivorous diet with increasing body size (Duque-Correa et al., 2024; Karachle & Stergiou, 2010). Juveniles, characterized by a shorter gut, may exhibit a more opportunistic feeding strategy, potentially incorporating a mix of animal and plant material that requires less extensive digestion. Juveniles prioritize quick energy intake over prolonged digestion, allowing them to reach a size that reduces predation risk. In contrast, the longer gut observed in adults is consistent with the increased consumption of fibrous plant material, such as macroalgae and seagrass, which necessitates greater digestive surface area and prolonged retention time for efficient nutrient extraction (German et al., 2004; German & Horn, 2006; Leigh et al., 2018). This adaptation supports a shift to digesting more fibrous plant material, which requires a longer gut for better nutrient extraction. Shorter guts are associated with faster food processing and higher assimilation efficiency, which may be beneficial for rapid growth at early life stages (Benavides et al., 1994; Berumen et al., 2011). This pattern aligns with the well-documented relationship between gut length and dietary specialization in herbivorous reef fishes, supporting the hypothesis that *S. sutor* undergoes a dietary transition as it matures.

The present study permits to highlight the spatio-temporal and ontogenetic dietary shifts in *S. sutor*, revealing that juveniles have a mixed diet, including animal prey, while adults rely more on macroalgae and seagrass. Stable isotope analysis confirms significant seasonal and habitat-related variations in the trophic niche, with juveniles showing distinct isotopic signatures across habitats. Gut morphology analysis supports this dietary transition, as the relative gut length increases with size, a typical trait of herbivorous fish. These findings emphasize the importance of conserving key feeding and nursery habitats for fisheries management. Additionally, those results can be applied to sustainable aquaculture to optimize feeding strategies by incorporating natural dietary components and assessing how ontogenetic dietary shifts influence growth and survival in cultured individuals. However, comparative studies with other Siganidae species or across different geographical regions would further clarify the adaptability of *S. sutor* and provide insights into broader ecosystem dynamics. Furthermore, future research should explore the implications of dietary variation in *S sutor* for fisheries management, particularly how habitat degradation and fishing pressure affect food availability and population resilience. Understanding the species’ response to environmental stressors, such as climate change, pollution, and extreme weather events, is also crucial for conservation strategies.

# Chapitre 5 : Reproductive biology of *Siganus sutor* in Toliara: spawning cycle and maturity size

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## Résumé

La compréhension des mécanismes reproducteurs de *Siganus sutor* est essentiel pour garantir la gestion durable de cette espèce clée, fortement exploitée par la petite pêche et jouant un rôle crucial dans la sécurité alimentaire des communautés côtières. Ce chapitre explore les caractéristiques de la reproduction de *Siganus sutor* en se basant sur l'étude du cycle de reproduction et de la taille à la première maturité sexuelle de cette espèce. L'analyse histologique des gonades a permis de déterminer les stades de maturation, tandis que l'indice gonado-somatique a révélé une concentration de l'effort reproductif à des moments précis de l'année. L'étude met en évidence une saisonnalité dans la reproduction de l'espèce, avec des pics de ponte coïncidant à la saison chaude (Décembre à Mars) et à la saison fraiche (Juillet). Chez cette espèce, la taille à la première maturité sexuelle est déterminée à 20,84 cm (longueur totale) chez les femmelles et 21,38 cm chez les mâles. Ces résultats soulignent la vulnérabilité de *S. sutor* à la surpêche durant les périodes de reproduction et appellent à une meilleure gestion saisonnière et spatiale de la ressource. Ce chapitre apporte ainsi des éléments fondamentaux pour la mise en place de mesures de conservation comme la mise en œuvre de périodes de fermeture de pêche et de taille minimale exploitable.

## Abstract

Understanding the reproductive mechanisms of *Siganus sutor* is essential for ensuring the sustainable management of this key species, which is heavily targeted by small-scale fisheries and plays a crucial role in the food security of coastal communities. This chapter explores the reproductive characteristics of *Siganus sutor*, focusing on the study of its reproductive cycle and size at first sexual maturity. Histological analysis of the gonads allowed for the identification of maturation stages, while the gonadosomatic index revealed a concentration of reproductive effort at specific times of the year. The study highlights a seasonal pattern in the species' reproduction, with spawning peaks occurring during the warm season (December to March) and the cooler season (July). In this species, the size at first sexual maturity was determined to be 20.84 cm (total length) for females and 21.38 cm for males. These findings underscore the vulnerability of *S. sutor* to overfishing during reproductive periods and call for improved seasonal and spatial management of the resource. This chapter thus provides fundamental insights to support the implementation of conservation measures such as the establishment of fishing closure periods and minimum catch size regulations.

## 1. Introduction

Fish exhibit the most diverse life cycle patterns among vertebrates, with a wide range of reproductive strategies influenced by environmental factors (Belova, 2008; Blanck et al., 2007; Winemiller & Rose, 1992). Studies on reproductive biology of fish species is crucial for understanding their life history and ensuring the sustainable use of fish resources (Ali & Kadir, 1996; Brewer et al., 2008; Ezenwaji, 1998; Muchlisin et al., 2010). Understanding species' reproductive patterns provides a fundamental basis for developing effective conservation and management strategies for fisheries, and for the development of sustainable aquaculture practices and its diversification (Grandcourt et al., 2009; Gui, 2015; Muchlisin et al., 2004; Muchlisin et al., 2010; Muchlisin, 2014).

Reproductive cycle and size at first sexual maturity are two key characteristics that best define species' reproductive patterns. These factors determine the timing and frequency of reproduction, influencing population renewal and sustainability (Ezenwaji, 1998; Park et al., 2022; Stockley et al., 1996). Two common methods used to assess fish reproduction are the gonadosomatic index (GSI) and histological analysis (Ali & Kadir, 1996; Brewer et al., 2008; Eyo et al., 2014; Gómez-Robles & Saucedo, 2009). The GSI provides a macroscopic measure of reproductive activity by relating gonad weight to body weight, allowing for the identification of spawning periods (Pereira et al., 1993; Kabir et al., 1998; Kaur et al., 2012; Pandit & Gupta, 2019). Histological analysis, on the other hand, offers microscopic insights into gonadal development, enabling precise determination of maturity stages and reproductive cycles (Alvarado et al., 2017; Carvalho-Saucedo et al., 2015; Cinquetti & Rinaldi, 1987; Couillard & Brulotte, 2020; López-Peraza et al., 2013; Lotz et al., 1996). The combination of these methods enhances the accuracy of reproductive assessments and provides a comprehensive understanding of fish reproductive dynamics (Brewer et al., 2008; Louiz et al., 2009; Nunes et al., 2011; Stockley et al., 1996).

A study of the reproductive biology of the albacore Tuna (*Thunnus alalunga*) sampled from different regions of the western Indian Ocean revealed that the maturity size for females was estimated at 85.3 ± 0.7 cm (Fork Length: FL), with the spawning season occurring from November to January (Dhurmeea et al., 2016). It is frequent to have two main reproduction peaks in marine fish. It have been proved in a comparative study of reproductive biology of some economically important fish species from Ghana where major peaks of GSI of females were noted in February – March and June – July (Akongyuure, 2020). For herbivorous fish, a study on the white-spotted spinefoot (*Siganus canaliculatus*) in the southern Arabian Gulf found that spawning occurred primarily in April and July, with a secondary, less distinct spawning event in November. The mean size and age at first sexual maturity were estimated at 21.5 cm (FL) for males and 25.7 cm (FL) for females (Grandcourt et al., 2007). A similar study on *S. canaliculatus* along the Arabian Sea coast of Oman reported that males reached sexual maturity at a total length (TL) of 22.6 cm, while females matured at 23.9 cm TL (Al-Marzouqi et al., 2011).

However, reproductive biology traits within a single species can vary across different locations due to the influence of multiple environmental factors such as water temperature, photoperiod, habitat conditions, fishing pressures… (Araújo et al., 2019; Servili et al., 2020). Differences in temperature and photoperiod are known to significantly influence sex differentiation as well as the timing and phenology of spawning in various fish species (Servili et al., 2020). Various authors have demonstrated that a smaller size at maturity serves as an indicator of stress in fisheries, with fishing pressure being one of the primary contributing factors (Andersen et al., 2007; Trippel, 1995). This was observed in the spiny dogfish (*Squalus acanthias*) in the Western North Atlantic, where the maturity size for females decreased by more than 7 cm compared to data reported two decades earlier (Bubley et al., 2013). This high sensitivity necessitates recent, site-specific studies to enhance our understanding of local resources especially for commercially important fish species.

Among coral reef fishes, the whitespotted rabbitfish (*Siganus sutor*) is of particular ecological and economic significance, serving as a valuable resource for fisheries in the Western Indian Ocean (Agembe, 2012b; Ebrahim et al., 2020a; Samoilys et al., 2017). Additionally, as a herbivorous fish, it plays a crucial role in maintaining the health of coral reef ecosystems (Burkepile & Hay, 2008; Knoester et al., 2019; Lewis, 1985; Plass-Johnson et al., 2015). For example, in the coastal waters of Toliara (SW Madagascar), *S. sutor* plays a vital role in local small-scale fisheries, providing food security and livelihoods for fishing communities. In addition, this species, as the majority of Siganidae, has an interest in fish aquaculture, an efficient solution for the sustainable use of this species (Ateweberhan et al., 2018; Darsono, 1993; Jaikumar et al., 2011; Syah et al., 2020). However, increasing fishing pressure and environmental changes threaten the sustainability of this resource (Jaonalison et al., 2022; Ranaivomanana et al., 2023). A thorough understanding of its reproductive biology is crucial for developing informed management strategies that balance ecological conservation with socio-economic needs.

Previous studies on the reproductive biology of *S. sutor* from different regions have shown variability in both spawning frequency and maturity size, likely influenced by environmental factors. Research has indicated that the spawning peaks of *S. sutor* in the Western Indian Ocean generally occurs once during the warm season, with a second peak during the colder season (Agembe, 2012; De Souza, 1988; Kamukuru, 2009; Ntiba & Jaccarini, 1990). However, the intensity and the duration of these spawning periods may vary among populations. Variation in the size at first sexual maturity have also been reported across different locations. In Kenya, *S. sutor* has been found to mature at sizes ranging from 21.7 cm TL (Ntiba & Jaccarini, 1988) to 28.2 cm TL (Agembe, 2012), suggesting potential regional differences in growth rates and environmental conditions. In Tanzania, Kamukuru (2010) reported maturity sizes of 21.7 cm TL for males and 22.7 cm TL for females, indicating a slight sexual dimorphism in maturity size. These variations highlight the importance of studies on local populations to improve fishery management strategies and to develop an efficient aquaculture at regional scales.

Currently, detailed knowledge regarding the reproductive cycles and the size at first sexual maturity of *Siganus sutor* in the South-West of Madagascar remain unknown. Investigating these parameters in the Toliara Reef will provide valuable insights into the species' reproductive strategy and contribute to a better understanding of their populations. This study aims to fill knowledge gaps regarding the reproductive biology of *S. sutor* in Toliara. Specifically, the research focuses on: i) determining the reproductive cycle of *S. sutor* using GSI and histological analysis; ii) identifying the size at first sexual maturity; iii) evaluating the implications of our findings for conservation and local fisheries management. Therefore, these findings may contribute to sustainable practices in fisheries such as the definition of minimum catch sizes and seasonal fishing restrictions, to prevent overexploitation and ensure long-term population viability.

## 2. Material and methods

### 2.1. Study area

The study was conducted in the coastal waters of the Great Reef of Toliara, located in southwestern Madagascar along the Mozambique Channel. This region is part of the tropical western Indian Ocean and is known for its rich biodiversity and complex coastal ecosystems, including coral reefs, seagrass beds, and mangroves (ref).

### 2.2. Sampling

Sampling was performed in Toliara bay. Small individuals of *S. sutor* were catched in the lagoon while bigger individuals were collected on the outer reef slope (Chapitre 1-Fig. 3.1). For studying the spawning cycle of *S. sutor,* only potentially adult individuals larger than 20 cm TL were targeted during sampling. The size limit was determined by previous studies conducted in Kenya (Ntiba & Jaccarini, 1988) and Tanzania (Kamukuru, 2009). So, 20 adult individuals (minimum Total Length (TL) of 22cm) were sampled monthly from January 2022 to March 2023. Fish were sampled with collaboration with fishermen using gill net in the outer slope of the Great Barrier Reef of Toliara. For the maturity size analysis, individuals ranging from 10 cm to 31 cm (TL) were sampled in January 2024. Samples were grouped into sets of minimum 10 individuals, with a size interval of 2 cm.

### 2.3. Gonadosomatic index (GSI) analysis

In the laboratory, the standard length (SL) and total length (TL) were measured to the nearest millimetre using a vernier calliper. Then, the total body weight (BW) was recorded using a precision balance to the nearest 0.01 g. During dissection, the abdominal cavity was carefully opened, and the presence or absence of gonads was assessed macroscopically. If gonads were present, they were removed and analyzed to determine the sex of the specimen. The gonad weight (GW) was then weighed to the nearest 0.01 g.

### 2.4. Histological analysis

Gonads were fixed using a Bouin solution for 24h and then conserved in a 70° alcohol for analysis. All the gonads were transported to the laboratory at the University of Liège for microscopic analysis. For the analysis, samples were prepared according to the protocols developed by Luna (1968). Gonads were first placed in an absolute ethanol bath for 24 hours, followed by immersion in butanol for another 24 hours. Subsequently, they were embedded in three successive paraffin baths for a duration of 24 hours. A cross-section was then prepared for each sample and mounted on cassettes for microtome sectioning of 5 µm. The tissue sections were stained with eosin and hematoxylin before being examined under a light microscope. Gonadal development stage were identified and classified based on description of Ntiba & Jaccarini (1990) and Agembe (2012).

### 2.5. Data analysis

GSI was calculated as the ratio of gonad weight (GW) to the body weight (BW):

$$\text{GSI (\%)} = \frac{\text{GW (g)}}{\text{B W (g)}} * 100$$

The normality of the distributions and the homogeneity of variances were tested using the Shapiro–Wilk test and Levene's test, respectively. For the determination of spawning cycle, a chi-square test of independence was performed to examine whether the proportion of male and female individuals varied significantly across months. To assess the effects of sex, month, and their interaction on total length (TL), a two-way fixed-effects analysis of variance (ANOVA) was performed. The factor "Sex" included two levels (male and female) and the factor "Month" included fourteen levels corresponding to the sampling months. While considering the whole sample, a Wilcoxon rank-sum test was performed to compare the total length between female and male individuals across all months. The correlation between TL and body weight was analysed using a linear regression of Pearson. Kruskal-Wallis tests were performed to assess difference in gonad weight and GSI values between sexes and across the month when the assumptions of normality and homogeneity of variance were not met.

The size at first sexual maturity ($L_{50}$) was identified using logistic regression, a statistical method that models the probability of an individual being mature based on its length (TL) (Torrejon-Magallanes, 2016). First, individuals were classified as mature (1) or immature (0) based on gonadal development, determined through combination of macroscopic observation, GSI threshold and histology. Logistic regression was then applied, where the probability of maturity was modelled as a function of TL, typically using a binomial generalized linear model (GLM). The resulting logistic curve showed the increasing likelihood of maturity with TL. The $L_{50}$ was estimated as the TL at which the probability of maturity reaches 50%, indicating the size at which half of the population has reached reproductive maturity (Fontoura et al., 2009; Roa et al., 1999). A Generalized Additive Model (GAM) was used to explore the non-linear relationship between GSI and TL of fish using the mgcv package.

## 3. Results

### 3.1. Gonadal development and maturation process

Gonads in immature individuals of *S. sutor* are translucent and formed of one homogenous piece or start to be composed by two lobes (Fig. 5.1). At this stage, males and females are hard to differentiate. In mature individuals, ovaries and testes consist of two elongated lobes. In both females and males, one lobe is typically wider: wider lobe (WL) while the other is narrower: narrower lobe (NL). This difference in lobe size is being most pronounced in mature individuals. The gonadal lobes are positioned horizontally. In *S. sutor*, as in most of teleost fishes, gonads are suspended within the abdominal cavity by a membranous structure known as the mesogonad, which serves as a support and conduit for blood vessels and nerves (Cole, 2003; Mazzoni & Grassiotto, 2017). The narrower lobe lies on the ventral side of the cavity, while the wider lobe is positioned above it. In mature females, the ovaries appear yellow to orange due to the presence of developing oocytes, whereas male testes are whitish and firm. The gonads are highly vascularized, with visible blood vessels (especially in females) running along their surface, supporting gamete development.

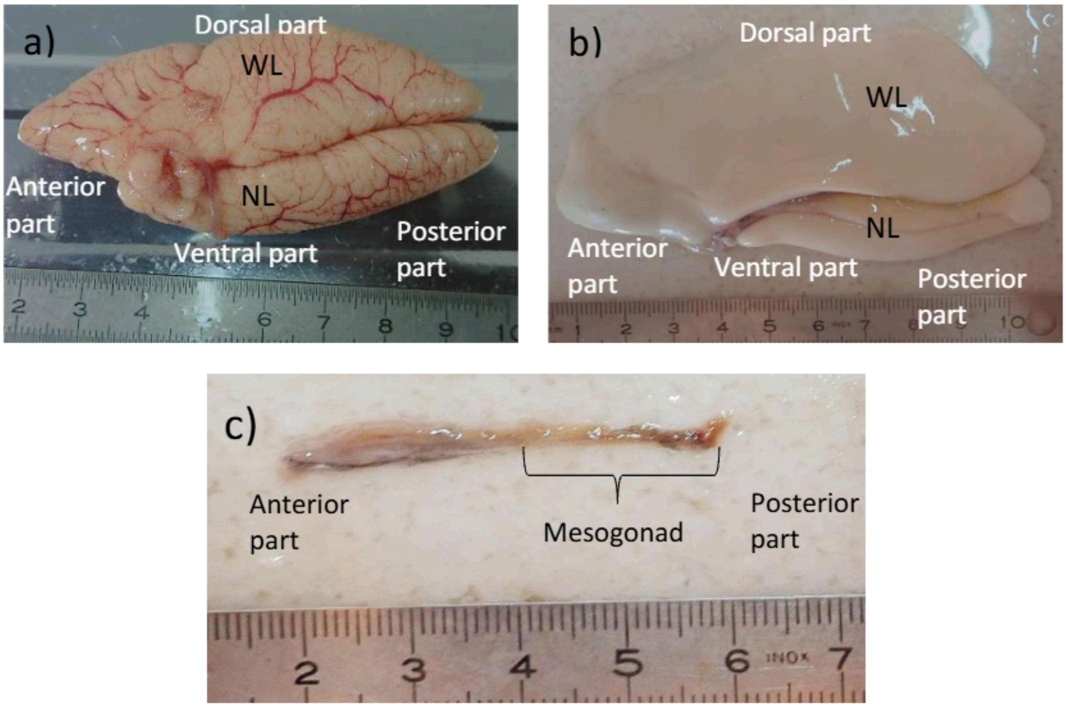


**Figure 5. 1.** Morphological aspect of mature a) female, b) male and c) immature Siganus sutor gonads. WL: wider lobe, NL: narrower lobe

Different gonadal maturation stages were found in female and male of *S. sutor*. The determination was made based on previous descriptions (Agembe, 2012; De Souza, 1988; Ntiba & Jaccarini, 1990; Samejima & Tachihara, 2022). For female *S. sutor*, five distinct stages of gonadal development were identified (Fig. 5.2). Each stage represented a specific phase in the maturation of oocytes and it was revealed by histological changes contributing to the reproductive cycle of this species. These stages included: the immature stage, the maturing stage, the mature stage, the spawning-active stage, and the spent stage (Fig. 5.2).

Stage I – the immature stage represented the beginning of reproductive development, where the ovaries were in the early stages of development and only oogonia and primary growth oocytes were present. These oocytes were characterized by large pink nuclei, indicating the early stages of growth. As the ovaries progressed to the maturing stage, secondary growth oocytes appeared alongside the primary growth oocytes and oogonia. This stage marked the transition from the early growth phase to the more advanced stages of oocyte development.

Stage II – the maturation is marked by the development of oocytes. It was represented by the appearance of yolk granules within the secondary growth oocytes signifying the accumulation of nutrients necessary for the development of viable eggs. At this point, primary growth oocytes and oogonia were still present, but the focus shifts to the yolk-filled secondary growth oocytes.

Stage III – the mature stage was represented by the presence of fully matures oocytes. This stage saw the development of final growth oocytes, with no longer visible nucleus as it disintegrates. This stage indicated the near readiness of oocytes for spawning.

Stage IV – the spawning active stage was marked by the presence of oocytes ready for release. At this point, final growth oocytes were present. In addition, post-ovulatory follicles, that are the remnants of ovarian follicles that recently released mature eggs appeared. This stage was marked by the presence of primary growth oocytes and post-ovulatory follicles, indicated the decline of gonadal activity after egg release.

Stage V - the post-spawning stage was marked by the presence of post-ovulatory follicles. Their presence confirmed that spawning has occurred recently. The appearance of primary growth oocytes that were not ready for maturation yet marks the beginning of the next reproductive cycle. This stage indicated a post-spawning decline in gonadal activity.

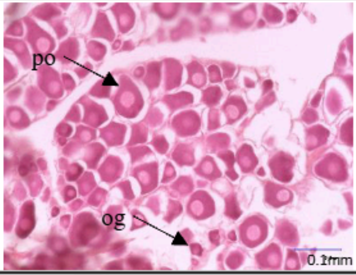
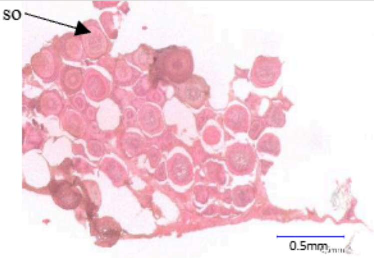
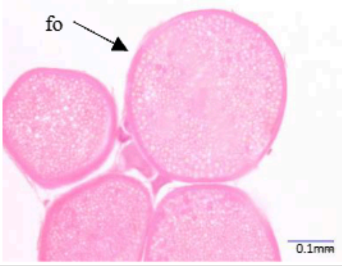
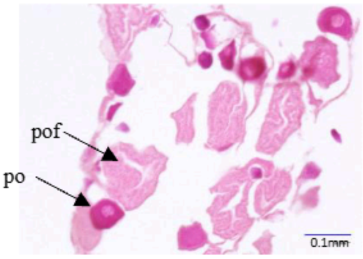
| | |
|---|---|
| **Stage I: Immature**<br>Only oogonia (og) and primary growth oocytes (po) with large pink nuclei are present. |  |
| **Stage II: Maturing**<br>Secondary growth oocytes containing yolk granules (yg), primary growth oocytes and oogonia are present. |  |
| **Stage III: Mature**<br>Final growth oocytes (fo). The nucleus has disintegrated and is no longer visible. |  |
| **Stage IV: Spawning active**<br>Presence of final growth oocytes (fo) and post ovulatory follicles (pof). Primary growth oocytes (po) start to appear. |  |
| **Stage V: Post-spawning**<br>Presence of post ovulatory follicles (pof). Primary growth oocytes (po) start to appear. |  |

**Figure 5. 2.** Gonadal development stages of female *Siganus sutor*

Males of *S. sutor* undergoes a somewhat simpler than females but equally important progression of gonadal development through four distinct stages (Fig. 5.3). It was characterised by the same gonadal maturity stages as found in females but there was no histological distinction between mature and spawning active individuals.

Stage I - the immature stage represented the early phase of testicular development, where spermatogenesis had not yet begun. The testes were in a relatively undifferentiated state, with little structural complexity.

Stage II - the maturing stage is characterized by the growth and differentiation of spermatocytes for spermatogenesis. Spermatocytes started to differentiate and the testes became more structurally organized. This stage marked the onset of sperm production, setting the stage for fertilization.

The stage III mature and the stage IV spawning active: the testes were fully developed, with active spermatogenesis taking place. The mature testes were capable of producing viable sperm, preparing the male for spawning.

Stage V: the post-spawning stage represented the post-spawning period, where spermatogenesis declined, and the testes begin to shrink. This stage signalled a decline in gonadal activity following spawning and the end of the reproductive cycle for that season.

For both females and males, the phase “immature” was only found in juveniles used for the determination of maturity size. The analysis of gonadal development stages in adults showed that, after the spent stage, gonads entered directly into the developing (maturing) phase in preparation for the next reproductive cycle.

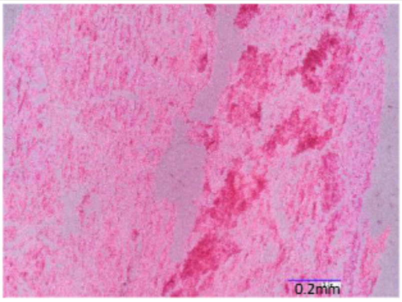
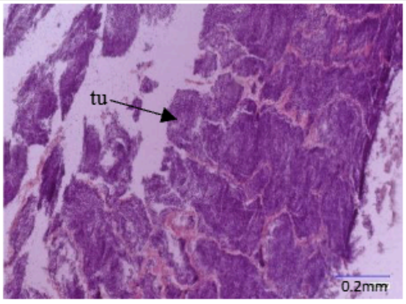
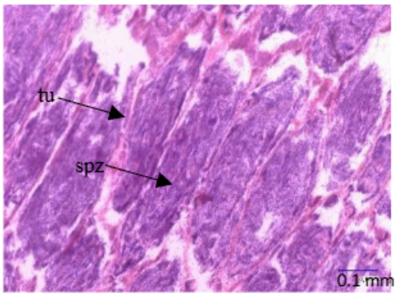
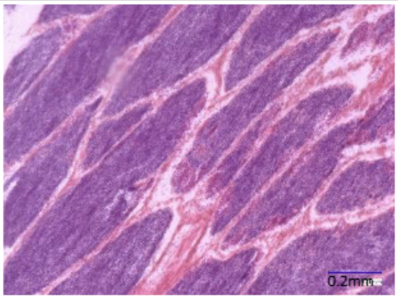
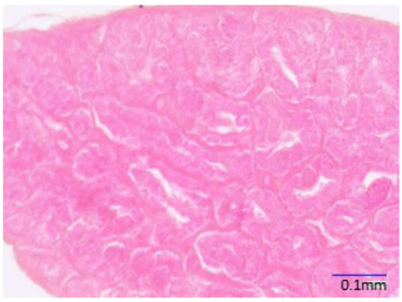
| | |
|---|---|
| **Stage I: Immature**<br>The tubulate structure is not developed |  |
| **Stage II: Maturing**<br>The tubulate (tu) structure start to develop. |  |
| **Stage III: Mature**<br>Tubules (tu) completely developed. Spermatozoa (spz) completely occupy the tubules |  |
| **Stage IV: Spawning active**<br>Tubules (tu) completely developed. Spermatozoa (spz) completely occupy the tubules |  |
| **Stage V: Post-spawning**<br>Residual sperm may be present in some tubules. A new line of germ cells are produced. |  |

**Figure 5. 3.** Gonadal development stages of male *Siganus sutor*

## 3.2. Spawning cycle of *Siganus sutor*

### 3.2.1. Sex ratio and dimorphism between sexes

A total of 300 individuals of *S. sutor* were collected over 15 months, with 20 samples taken per month. The sex ratio was 0.93 (with 84 females and 90 males) and there was no significant difference in the abundance of males and females across months (Chi-square, p = 0.248). Size (TL) of captured adults varied from 22 to 46.7 cm with an average length of 31.62 ± 4.12 cm (Fig. 5.4a). Weight varied between 170.17 g and 1,656.43 g with an average of 654.93 ± 281.58 g (Fig. 5.4b). The two-way ANOVA revealed a significant effect of month on total length (F = 15.084, p < 0.001), and a significant interaction between sex and month (F = 1.738, p = 0.048). However, no significant main effect of sex was detected (F = 1.084, p = 0.299). The differences in fish size are therefore strongly influenced by sampling month and sex-related differences vary depending on the time of sampling. Because the focus was on adults, any natural monthly size variation among adults was likely seen as normal or not relevant to the main question of the study, so it wouldn't distort the findings.

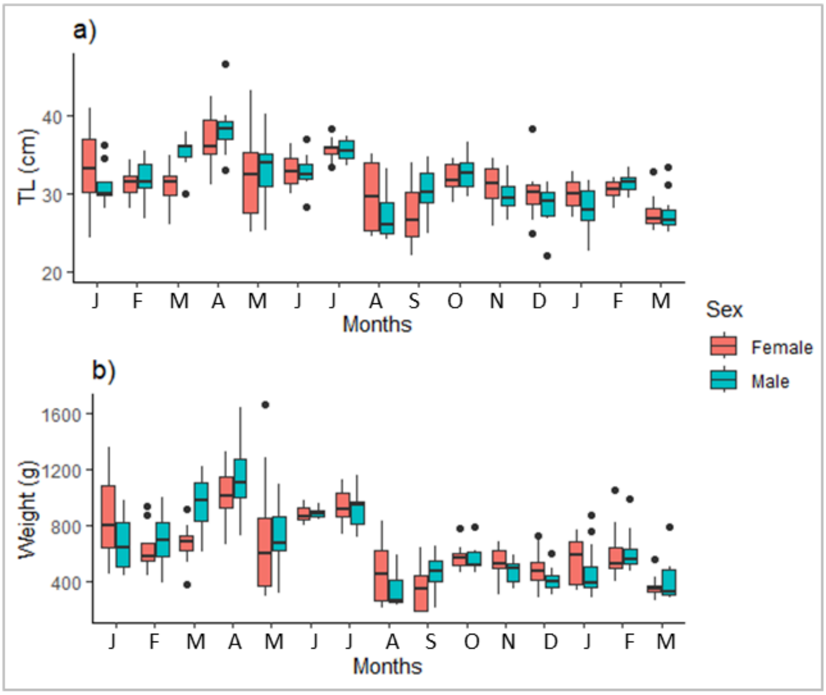


**Figure 5. 4.** Variation of a) Total length and b) weight of female and male *Siganus sutor* according to sampling month

While considering the whole sample, there was no significant difference in TL (Wilcoxon, W = 11416; p = 0.69) and weight (Wilcoxon, W = 11544; p = 0.57) between females and males. The relation between fish length and weight presented a very strong and reliable linear relationship. The correlation between TL and weight was highly statistically significant (Pearson, R = 0.93; p < 0.001), with an R value of 0.93 (Fig. 5.5).

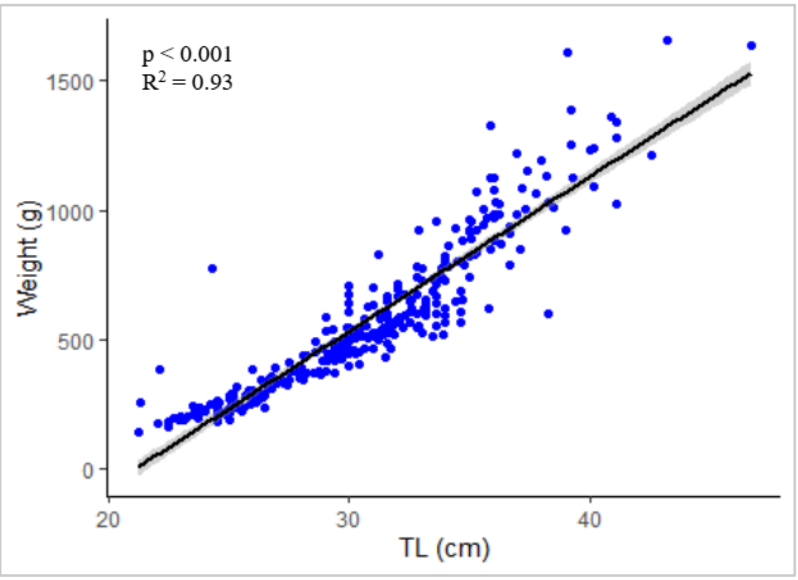


**Figure 5. 5.** Correlation between total length (TL) and weigth of captured *Siganus sutor*

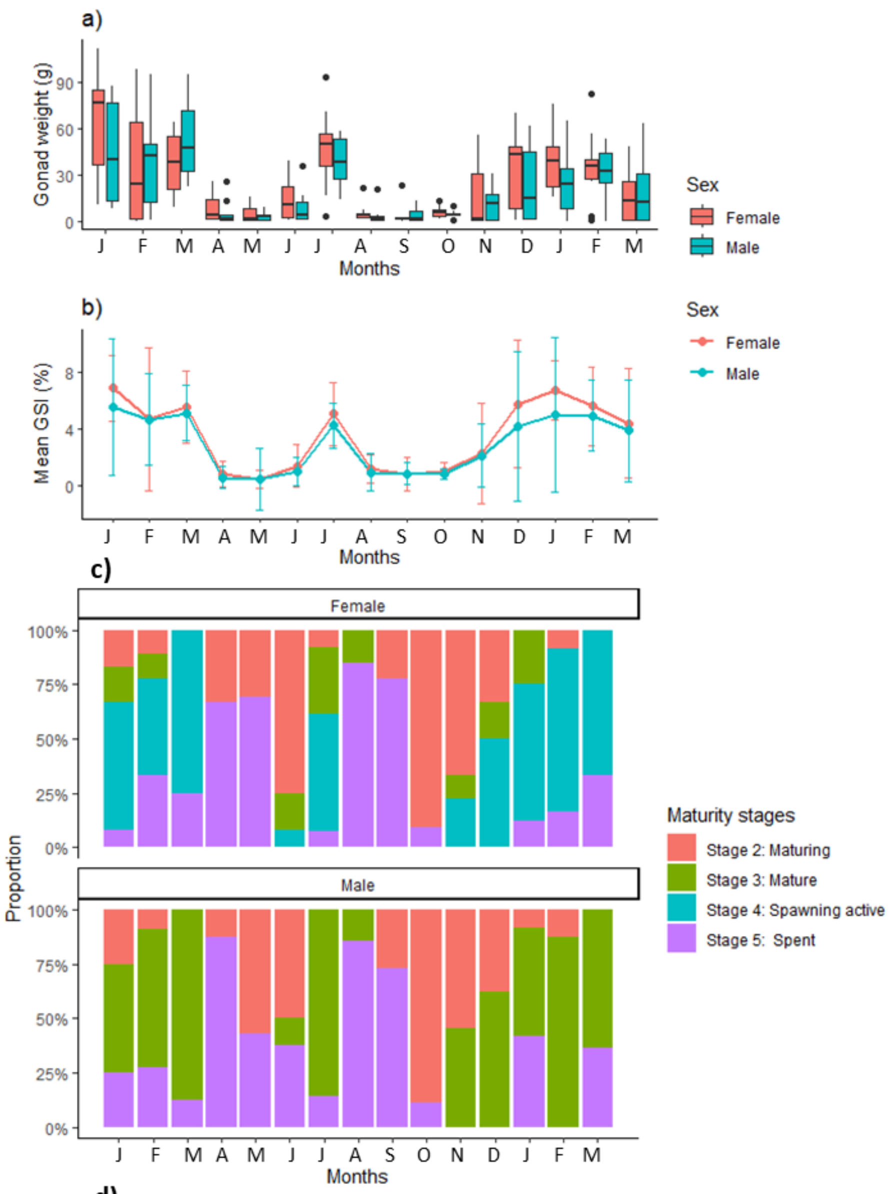
### 3.2.2. Determination of the spawning cycle of *Siganus sutor*

The gonad weight of *S. sutor* ranged from 0.03 g to 112.02 g (Fig. 5.6a), this biggest one was recorded in a 1,358 g female captured in January 2022. The average gonad weight varied significantly depending on the sampling month (Kruskall-Wallis, $p < 2.2 \times 10^{-16}$) with a non-significant difference according to sex (Kruskall-Wallis, $p = 0.25$). Higher gonad weights were observed from January to March, July and December 2022 with an average weight ranging from 24.02 ± 25.72 g to 64.85 ± 33.29 g. In the other months, gonad weight remained relatively low, with average values not exceeding 15 g.

The monthly variation in the GSI of *S. sutor* indicated a distinct seasonal reproductive cycle. Indeed, the GSI values differed significantly across months (Kruskall-Wallis, $p < 2.2 \times 10^{-16}$). There was no significant difference in GSI of female and male *S. sutor* (Kruskall-Wallis, $p = 0.23$). The highest GSI values occurred from December to March, with peaks in January 2022 (Female: 6.82 ± 2.16 %, Male: 5.55 ± 3.35 %) and December 2022 (Female: 5.77 ± 3.7 %, Male: 4.19 ± 3.81 %), suggesting this period is the main spawning season (Fig. 5.6b). A sharp decline in GSI from April to June (April: Female 0.67%, Male 0.13%) marked a post-spawning phase, during which gonads regress and fish recover from spawning. Interestingly, a moderate increase in July (Female: 5.69, Male: 4.61) may indicate a secondary reproductive effort, corresponding to a second GSI peak. The lowest GSI values were observed from August to November, suggesting a resting phase where reproductive activity was minimal.

The monthly variation in the proportion of individuals at different gonadal maturity stages also illustrated the spawning cycle of adult *S. sutor*. The maturity stages were classified as maturing, mature, spawning capable, and spent and their relative proportions were assessed for each month over the studied period (Fig. 5.6c). This analysis provides insights into the timing of reproductive activity and the peak of spawning period. For both females and males, the proportion of mature and spawning active individuals is close to 50% or above from January to March as well as in July and December 2022. It was also the case from January to March 2023 (Fig. 5.6c).

The reproductive cycle of *S. sutor* followed a well-defined annual pattern. Females were actively spawning from January to March, followed by a spent stage in April and May (Fig. 5.6c). Gonads began maturing in June, leading to a second spawning peak in July. Another spent stage occurred in August and September (Fig. 5.6c). Maturation resumed in October and November, marked by an increase in mature individuals. Finally, a new spawning period extended from December to March. Males *S. sutor* were mature from January to March, followed by a spent stage in April . Maturation began again in May and June, with males reaching maturity in July. A second spent stage was observed in August and September. From October to November, males entered a new maturation phase, reaching maturity in December, which persisted until March. By combining results of gonad weight, mean GSI values and monthly variation of proportion of each gonadal maturity stage the reprodutive cycle of *S. sutor* can be defined as follow. Adults *S. sutor* started maturing in June when first spawning peak occurred in July. Then August and September corresponded to post-spwaning stage. They start to maturing again from October to November for a more extended spawning from December to March (Fig. 5.6d).



d)

| **Months** | J | F | M | A | M | J | J | A | S | O | N | D | J | F | M |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Stages** | S | | | P | | M | S | P | | M | | S | | | |

**Figure 5. 6.** Monthly variation of a) gonad weight, b) mean Gonadosomatic index (GSI) ± SD, c) proportion of gonadal maturity stages and d) reproductive stages *Siganus sutor*. With M: maturing, S: spawning active (+mature), P: post-spawning stages

## 3.3. Maturity size of *Siganus sutor*

### 3.3.1. Samples characteristics

A total of 139 samples were analysed for the determination of *S. sutor* maturity size. After the macroscopic observation of gonads and the analysis of GSI, samples were classified into 54 females, 51 males, and 33 immature individuals. Total length (TL) of samples ranged from 11.9 to 31 cm (Fig. 5.7a). Their body weight varied from 60.86 to 152.76 g (Fig. 5.7b).

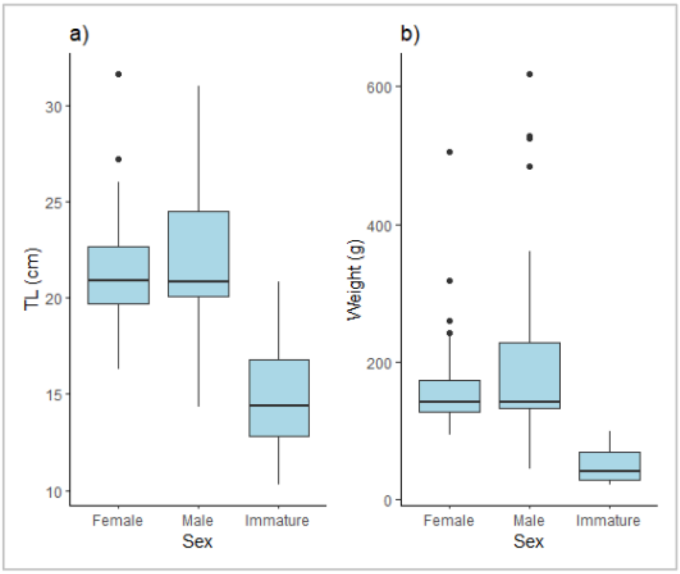


**Figure 5. 7.** a) Size and b) weight of analysed female, male and immature individuals *Siganus sutor*

### 3.3.2. Determination of the size at first sexual maturity of *Siganus sutor*

Gonad weights ranged from 0.02 to 28.12 g (Fig. 5.8a). Gonad weight did not exceed 1 g in immature individuals while it started at around 5 g in mature individuals. The GSI of *S. sutor* varied according to the maturity stage of the fish. Immature individuals exhibited a low GSI, below 1% and ranging from 0.04% to 0.98% (Fig. 5.8b). In contrast, mature individuals had a higher GSI, ranging from 1% to 7%. Specifically, females had a GSI ranging from 1.03% to 6.9%, and males had a GSI ranged from 1.19% to 6.08%.

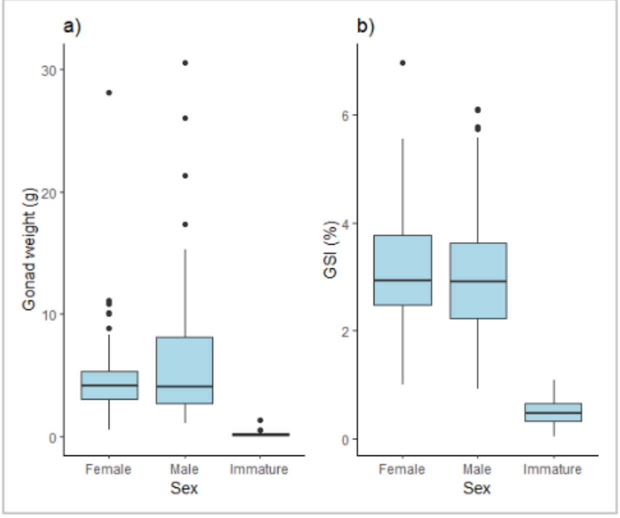


**Figure 5. 8**. a) gonad weight and b) Gonadosomatic index of analysed female, male and immature individuals *Siganus sutor*

For the determination of the size at first sexual maturity, samples were grouped as immature and mature based on gonad weight, GSI and histological analysis. The size at first sexual maturity ($L_{50}$) was then estimated using a logistic regression. The $L_{50}$ is estimated at 20.84 cm for females (Fig. 5.9a) and 21.38 cm for males (Fig. 5.10a), indicating that males tend to reach sexual maturity at a slightly larger size compared to females. The GAM analysis revealed a strong positive relationship between TL and GSI. For females, the model revealed a significant non-linear relationship between GSI and TL (edf = 3.63, F = 41.16, $p < 0.001$), explaining approximately 52% of the variation in GSI (adjusted $R^2 = 0.519$). (Fig. 5.9b). For males, the GSI varied significantly with TL, following a nonlinear relationship (edf = 6.78, F = 19.14, $p < 0.001$). The model explained a substantial portion of the variation (62%) (adjusted $R^2 = 0.616$).

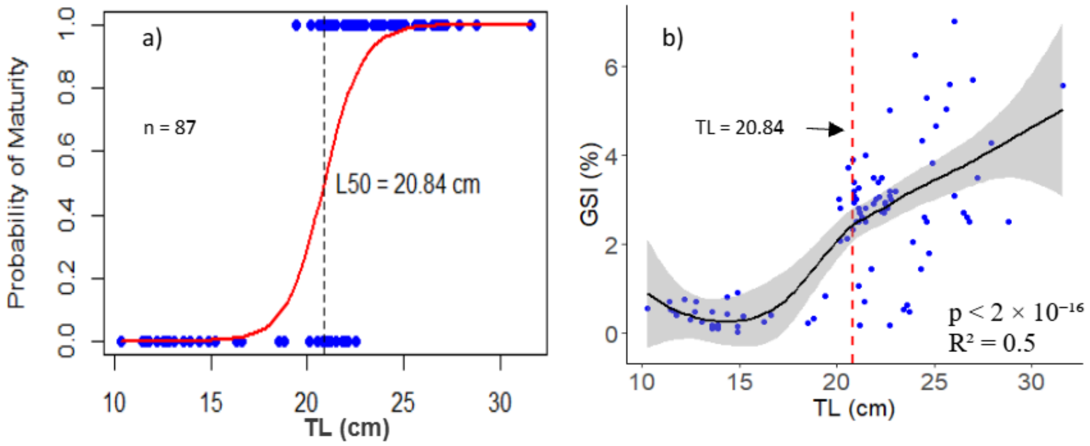


**Figure 5. 9.** a) logistic regression for determining the size at first sexual maturity ($L_{50}$) and b) relationship between gonadosomatic index and total length for female *Siganus sutor*

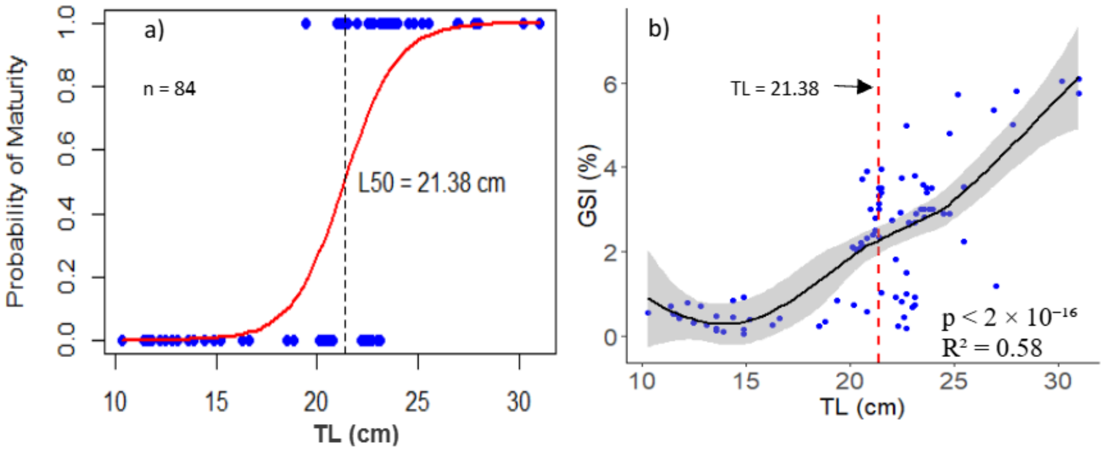


**Figure 5. 10.** a) logistic regression for determining the size at first sexual maturity ($L_{50}$) and b) relationship between gonadosomatic index and total length for male Siganus sutor

## 4. Discussion

As observed in many other fishes (ref), a strong correlation was found between size and weight of *S. sutor* individuals. The size at first sexual maturity for *S. sutor* was estimated at 20.84 cm for females and 21.38 cm for males. Histological study of gonads revealed the presence of five gonadal development stages: immature, maturing, mature, spawning capable, and spent. In males, only four stages were histologically recognized, as the spawning capable stage could not be distinguished from mature stage. The combination of gonad weight variation, GSI fluctuations, and the monthly proportion of mature and spawning-active individuals concluded that female and male *S. sutor* at Toliara start maturing in June for a first spawning peak in July. After this period, they entered into a post-spawning stage in August and September with no spawning activity. Then, they start maturing again from October to November for a second spawning peak from December to March.

### 4.1 Reproduction cycle of *Siganus sutor*

The present study revealed the presence of five clearly identifiable stages of gonadal development in females of *S. sutor*. Conversely, only four gonadal development stages were histological distinguished in males. Indeed the spawning active stage was not distinguished from the mature stage. Ntiba & Jaccarini (1990) found the same gonadal development in females of *S. sutor* from Kenya. However, they also highlighted several differentiations during the maturation phase as developing, early developing and late developing. The difference in the number of gonadal development stages between female and male in the present study can be attributed to biological and histological differences in gametogenesis (egg vs. sperm production) and reproductive behaviour (Dyková et al., 2024; Reading et al., 2018). For example, oogenesis in females is more complex and gradual, with distinct stages that are easily observable in histological examinations (Elkouby & Mullins, 2017; Liu et al., 2022; Sauger et al., 2023). However, spermatogenesis in males tends to be more continuous and less visually distinct, especially between stages like mature and spawning capable (Elisio et al., 2015; Ratty et al., 1989; Schulz et al., 2006). One reason may be that female gonads undergo more noticeable changes due to intermittent spawning. Conversely, males often produce sperm continuously during the breeding season (Aldridge et al., 2020; Chen & Liu, 2022). This phenomenon makes harder to identify the spawning capable stage in males. In addition, the use of more precise markers (histological stain) may help to accurately observe male gonads, which are more difficult to distinguish.

The synchrony between the gonadal development of male and female in *S. sutor* suggests a well-coordinated reproductive strategy aimed at maximizing fertilization success. In this study, both sexes reached maturity during the same periods, indicating that external environmental cues such as temperature or photoperiod may similarly influence gametogenesis in both sexes. Such a synchrony has been observed in *S. canaliculatus* and *S. vermiculatus*, where males and females exhibit aligned maturation and spawning stages (Gundermann et al., 1983; Metar et al., 2023). This alignment is essential in externally fertilizing species like siganids, ensuring that gametes are released simultaneously to increase the chances of successful fertilization and larval development (Popper & Gundermann, 1975). Such reproductive coordination is likely an evolutionary adaptation to seasonal environmental conditions and contributes to the resilience of populations in variable tropical marine habitats (ref).

Our results clearly identified the reproductive period of *S. sutor* at Toliara reef through a combination of various methods. These indicators consistently suggest a bimodal spawning cycle, characterized by two main spawning seasons occurring between December and March with a second peak in July. Males and females are active for reproduction in those periods, as indicated by high gonad weight and GSI values, combined with the high proportion of mature and spawning active individuals. These two breeding peaks appeared during two different seasons: warm season (December to March) and cool season: July. These findings on reproductive peaks align well with the observed peaks in juvenile recruitment (January and August) (Ravelohasina, et al., under review), which occurred approximately one month after each reproductive peak. Since larval development lasts between 30 to 35 days (Woodland, 1990), this timing strongly supports the connection between spawning events and subsequent juvenile arrival in coastal habitats.

Seasonal environmental factors such as water temperature and photoperiod play a critical role in triggering and synchronizing reproductive cycles in many reef fish species. These natural cues act as biological signals that activate hormonal processes leading to gonadal maturation and spawning. Water temperature is one of the main environmental drivers; seasonal increases or decreases can stimulate oocyte maturation and initiate spawning events in several species. For instance, warmer waters have been shown to promote reproductive activity in both marine and freshwater fish populations (Pankhurst & Munday, 2011; Schreck, 2010). Photoperiod also significantly affects reproductive physiology. Changes in photoperiod can influence the onset of reproductive readiness by modulating endocrine responses in fish, as demonstrated in various aquaculture and wild studies (Abdollahpour et al., 2020; El-Sayed & Kawanna, 2007; Polat et al., 2021)

It is common for tropical species to exhibit extended spawning periods throughout the year (Alkins-Koo, 2000; Kahar et al., 2023; Srinivasan & Jones, 2006). It is the case in *Siganus guttatus,* that exhibits a prolonged spawning season with reproductive activity occurring over several months. In tropical environments, spawning may extend nearly year-round with peaks of spawning periods often coinciding with warmer temperatures or lunar cycles (Duray & Juario, 1988). Spawning seasons in Siganidae vary significantly across regions, reflecting adaptations to local ecological conditions such as temperature and photoperiod. For instance, studies in Southeast Asia revealed that *Siganus canaliculatus* spawns from January to April in Philippines and Sigapore, against two distinct spawning peaks in winter (November-January) and summer (April-May) in India (S. V. Metar et al., 2019). In the Mediterranean, *S. luridus* and *S. rivulatus* have summer spawning peaks (Popper & Gundermann, 1975). *Siganus vermiculatus* shows a winter spawning pattern in Fiji (September–February) (Gundermann et al., 1983) and peaks in February–March along the west coast of India (Metar et al., 2023). Some species, like *S. guttatus*, reproduce throughout the year in Philippines (Soletchnik, 1984).

While referring to one species, spawning peak in a defined area may also show interannual variation (Andreasson et al., 2023; Khera et al., 2025; Sun et al., 2020; C. Vincent & Ibáñez, 2024). Various factors may influence this variation: climate change, local perturbations, reproductive plasticity,... For example, while comparing studies on reproduction of *S. sutor* in Kenya, different spawning peaks were identified. Firstly, the spawning peak of this species appeared in January/February and May/June (Ntiba & Jaccarini, 1988). Then, other authors found three different peaks in June, July and October (Agembe, 2012). Another study highlighted only one spawning peak that occurred between November and February (M. A. Samoilys et al., 2023). Another study in Tanzania found a spawning peak of *S. sutor* from December to May (Kamukuru, 2006). In addition, our study defined that the spawning peak of *S. sutor* in Madagascar occured from December to March and in July. This difference suggests spatial variation in spawning synchrony between the sexes, possibly influenced by local environmental factors such as water temperature, food availability, and habitat conditions.

In Toliara reef, the size at first sexual maturity of *S. sutor* was estimated at 20.84 cm for females and 21.38 cm for males. This difference in maturity size between female and male indicated that males tend to reach sexual maturity at a slightly larger size compared to females (Bhatta et al., 2013; Lowerre-Barbieri et al., 2011; Tsikliras & Stergiou, 2014). Interestingly, other studies have shown that males can reach sexual maturity earlier compared to females. Studies in Tanzania have proven it and defined a size at first sexual maturity for *S. sutor* at 21.7 cm and 22.7 cm for male and female respectively (Kamukuru, 2009). This could be related to varied growth patterns, energy allocation strategies, or reproductive investment between sexes (Hüssy et al., 2012; Scott & Heikkonen, 2012; Tsikliras & Stergiou, 2014). Other siganid species reach sexual maturity at a larger size. For example, a study on the reproductive biology of *S. vermiculatus* in the central west coast of India revealed a size at first maturity estimated at 28.13 cm and 32.73 cm for males and females respectively (Metar et al., 2023).

### 4.2 Maturity size of *Siganus sutor*

The estimated maturity size at Toliara is slightly lower than values reported in other regions. In Kenya, for example, authors have found that female *S. sutor* reached the sexual maturity at 28.2 cm (Agembe, 2012). It is knwon that size at first sexual maturity of species shows spatial variation. Such variations might reflect a combination of factors (environmental variability, anthropogenic pressure,…) that influence the species reproductive physiology and behaviour (Alkins-Koo, 2000; Chen & Liu, 2022; Kahar et al., 2023). Fishing pressure have been proved to reduce fish maturity size as highlighted by Andersen *et al.* (2007) in the north-east Arctic cod, the Baltic cod (*Gadus morhua*). These authors suggested that fishing pressure accelerated evolution in an overexploited population.

These results provide essential baseline data for fisheries management and conservation, as they help define appropriate minimum catch sizes to ensure sustainable population dynamics. By identifying the size and maturity stages at which individuals become reproductively active, this information allows to set science-based regulations that prevent the capture of immature individuals. Such measures are critical to maintaining breeding populations, supporting recruitment, and avoiding long-term declines in stock abundance. Moreover, this baseline is particularly valuable in regions with lack of data, where local fisheries often lack robust biological reference points to guide sustainable practices.

Moreover, understanding the reproductive cycle of a species like *S. sutor* is fundamental for establishing effective temporal fishing closures. It is known that fishermen especially target fish aggregation during spawning period as it have been proven in Seychelles (Bijoux et al., 2013) and in Kenya (Maina et al., 2013). This strategy has serious repercussions on fish stocks. By identifying the peak spawning periods, government and fisheries managers can implement seasonal bans that coincide with times of highest reproductive activity, thereby allowing mature individuals to reproduce undisturbed. This strategy helps to maximize the replenishment of fish stocks and maintain the long-term sustainability of the population. In regions like Toliara, where enforcement is limited, aligning closures with locally recognized reproductive events can also improve community compliance and foster participatory management.

In addition to implementing conservation measures aimed at regulating the fisheries of exploited species, aquaculture stands out as a promising and complementary solution. It offers a dual advantage: on the one hand, it contributes to the preservation of wild fish populations by alleviating fishing pressure on natural stocks; on the other hand, it ensures a steady and sustainable supply of fish products to meet the growing demands of human consumption. When developed responsibly and in harmony with local ecosystems, aquaculture can also support coastal livelihoods, promote food security, and play a key role in the transition toward more sustainable and resilient marine resource management.

# Chapitre 6 : Farming potential of the rabbitfish *Siganus sutor* in Toliara

## Résumé

L’intégration des connaissances bio-écologiques de *Siganus sutor* dans les pratiques aquacoles constitue une étape clé pour développer un modèle d’élevage durable adapté aux réalités écologiques et socio-économiques des zones côtières. L’élevage de cette espèce, fortement exploitée par la pêche artisanale, représente une alternative prometteuse pour alléger la pression sur les stocks naturels tout en assurant une source stable de protéines pour les populations locales. Ce chapitre présente les résultats des essais d’élevage en captivité basés sur la capture de juvéniles menés à la station marine de Belaza à Toliara. Un essai de pré-grossissement et deux essais de grossissement ont été réalisés sur une période respective de deux, cinq et quatre mois. La performance d’un aliment industriel est testé contre trois différents aliments expérimentales. Les paramètres de croissance, de survie, et de qualité de l’eau ont été suivis pour évaluer la faisabilité technique et écologique de l’élevage de *S. sutor*. Les résultats montrent une bonne adaptation des *S. sutor* aux conditions de captivité, notamment en termes de taux de croissance et de survie. L’aliment industrielle est le plus performant en terme de croissance (jusqu’à 0,91g/jour de gain de poids moyen). Cependant, il est le moins performant en terme de survie des cheptels avec de faible taux de survie pouvant atteinde 42,19% à la fin de l’expérience.

# Abstract

The integration of bio-ecological knowledge of *Siganus sutor* into aquaculture practices is a key step toward developing a sustainable farming model adapted to the ecological and socio-economic realities of coastal areas. The farming of this species, which is heavily exploited by small-scale fisheries, represents a promising alternative to reduce pressure on natural stocks while providing a stable source of protein for local populations. This chapter presents the results of juvenile capture-based aquaculture trials conducted at the Belaza Marine Station in Toliara. One pre-grow-out trial and two grow-out trials were carried out over periods of two, five, and four months, respectively. The performance of a commercial feed was tested against three different experimental feeds. Growth, survival, and water quality parameters were monitored to assess the technical and ecological feasibility of farming *S. sutor*. The results show good adaptation of *S. sutor* to captive conditions, particularly in terms of growth rate and survival. The commercial feed yielded the highest growth performance, with average weight gains reaching up to 0.91 g/day. However, it showed the lowest survival rates, with stock survival dropping to as low as 42.19% by the end of the experiment.

## 1. Introduction

Marine fisheries have long played a central role in food security, livelihoods, and cultural identity for millions of people around the world. Global per capita fish consumption has more than doubled since 1961, rising from 9.0 kg to 20.2 kg in 2020, fuelled by population growth, dietary shifts, and improved fish supply chains (FAO, 2020). A 2022 report estimated that approximately 576,840 individuals are engaged in the sector of fisheries in Madagascar, including pre- and post-harvest as well as subsistence fishing activities for boh inland and marine fisheries. However, the majority of these persons are involved in the marine small-scale fisheries sub-sector.

However, escalating pressures from overfishing, habitat degradation, and climate change have placed immense strain on global fish stocks in recent decades (Branch et al., 2011; Pauly et al., 1998; Pauly & Zeller, 2014). Wild capture fisheries have reached their maximum potential, producing approximately 92.1 million tonnes annually, a figure that has remained relatively stable over the past three decades. However, this apparent stability conceals a deeper crisis: the depletion of several high-value and ecologically important species, declining catch per unit effort in many regions, and the expansion of fishing activities into previously unfished areas (Pauly et al., 2005). According to the Food and Agriculture Organization of the United Nations (FAO), approximately 35.4% of the world’s fish stocks are currently overexploited, with only 64.6% within biologically sustainable levels (FAO, 2020). While fish continues to represent a key source of animal protein and essential micronutrients, especially in low-income countries, the sustainability of these benefits is increasingly under threat (Rustandi et al., 2019; Smith et al., 2013).

Furthermore, about 2.5 million people in Madagascar depend, at least partly, on fisheries for their livelihoods (Wabnitz et al., 2022). In Madagascar, fish accounts for nearly half of all animal protein consumption, with annual per capita consumption around 21.4 kg (FAO, 2020). Recent assessments suggest that several nearshore fish stocks, particularly those targeted by small-scale fishers, are in decline (Arthur et al., 2022; Bell et al., 2017; Lloret et al., 2018). Additionally, these fisheries often operate in data-poor and weakly regulated environments, which leaves them vulnerable to overfishing and environmental change.

The Bay of Toliara, located in southwestern Madagascar, provides a telling example of these dynamics. This region is home to a diverse coral reef ecosystems and a high concentration of fishing communities, many of whom rely on traditional techniques such as spearfishing, trap fishing, and handline fishing. Over the past decades, fishing pressure in the bay has intensified due to population growth, rising demand, and the lack of alternative livelihoods. The result has been a noticeable decline in catch volumes and a shift toward smaller and lower-value species, which are classic indicators of overfishing (Langley, 2006). Additionally, the degradation of coral reefs and seagrass habitats, essential for the early life stages of many reef fish, further exacerbates the situation (R. Ahmed & Tamim, 2025; Qiang et al., 2022; Uribe et al., 2022). In addition, the use of destructive fishing gear such as mosquito net trawls alters marine biodiversity by capturing mainly juvenile fish (Behivoke et al., 2021; Jaonalison et al., 2022; Ranaivomanana et al., 2023).

To meet growing demand and reduce pressure on wild fish stocks, aquaculture has emerged as a vital alternative. It is currently the fastest-growing food production sector globally, contributing more than 50% of the fish consumed by humans in 2020 (FAO, 2020). Despite this growth, aquaculture faces a complex array of environmental, social, and economic challenges. These include habitat alteration (notably in mangroves and coastal wetland areas), pollution, introduction of non-native species, and dependence on wild-caught juveniles or fishmeal and fish oil from marine sources (Froehlich et al., 2023). Addressing these challenges while increasing aquaculture production is one of the central tasks of the coming decades.

In Madagascar, aquaculture began in 1914 and has since experienced cycles of development, decline, and revival (Andrianaivojaona et al., 1992). It remains mostly artisanal and focused on freshwater species such as tilapia and carp (Andreas Kunzmann et al., 2023; Angermayr et al., 2023). In the marine sector, activities are dominated by industrial shrimp farming in the north west coast (Gezon, 1999; Onihary et al., 2021; Toubiana et al., 2004). In Toliara, sea cucumber farming already gain into industrial exploitation (Eeckhaut et al., 2009; Lavitra et al., 2010; Rasolofonirina et al., 2021) when coral farming emerged more recently and stayed in research stage (Todinanahary et al., 2017). Marine fish farming is nearly non-existent, despite Madagascar's vast marine area comprising 5,603 km of coastline and an Exclusive Economic Zone (EEZ) of 1,140,000 km² (Giudicelli, 1984), which represents an enormous potential for development. Recognizing this potential, several studies have explored the viability of marine fish aquaculture. An initial study identified the diversity of fish post-larvae and evaluated their potential for aquaculture and ornamental use (Mahafina, 2011). In 2017, we conducted pioneer experimental grow-out trials of whitespotted rabbitfish *Siganus sutor* juveniles, a research that achieved with a 100% survival rate, indicating promising prospects for domestication.

Among the various forms of aquaculture, capture-based aquaculture (CBA) represents a hybrid approach that combines the collection of juvenile fish from the wild with on-growing in captivity until a desired size. This technique is particularly widespread in regions with limited access to hatchery technology or in the early stages of aquaculture development (Ottolenghi, 2004; Lovatelli et al., 2008). However, CBA raises important concerns about sustainability, as it may place additional pressure on wild juvenile populations and disrupt recruitment dynamics if not carefully managed. In some cases, the practice is carried out without adequate monitoring of the ecological impact or the reproductive biology of target species, increasing the risk of local overexploitation (Pettersen et al., 2023; Abdel-Hady et al., 2024).

In response to these challenges, there has been growing interest in developing sustainable aquaculture systems by using more responsible methods like recirculating aquaculture systems, polyculture, careful site selection, low-density stocking, and community-based or co-managed aquaculture systems, the use of local food sources… (Bush et al., 2013; Frankic & Hershner, 2003; Qiang et al., 2022; Shah et al., 2018; Wurts, 2000). A major barrier to fish farming is the high cost of food, which is the most expensive component of aquaculture production (Fao, 2016). This may partly explain the limited development of marine fish farming in Madagascar. To address these issues, conducting sustainable marine fish farming experiments using local resources, especially through the development of safe, affordable, and locally sourced food is essential.

Fish farmers have long been producing local food using ingredients available at local markets. These food are affordable, easy to produce, and accessible year-round. This practice is already gaining traction in freshwater aquaculture, particularly for species such as tilapia. Applying this approach to marine fish farming presents a significant opportunity to lower barriers to the development of this still underexploited sector in Madagascar. A less common practice is the formulation of pellets using beach wrack. Beach wrack or sea wrack refers to the accumulation of organic material, primarily seaweeds, seagrasses, and other marine detritus, washed ashore by tides and waves (Hyndes et al., 2022; Michaud et al., 2019; Ruiz-Delgado et al., 2016). Beyond its ecological rules, beach wrack holds significant nutritional value, particularly when composed of nutrient-rich macroalgae. These seaweeds are naturally high in minerals such as iodine, calcium, magnesium, and iron, as well as vitamins, amino acids, and bioactive compounds like polysaccharides and antioxidants (Dugan et al., 2011; Quintanilla-Ahumada et al., 2023; Sousa et al., 2022). This rich nutrient profile makes beach wrack a valuable resource for use in animal food, where it can improve livestock health and productivity. Beach wrack, has historically been used in coastal regions as animal food due to its high mineral content, including iodine, calcium, and magnesium (Rudovica et al., 2021). The possibility of using beach wrack as a main component of fish food is a strategic approach to producing local, low-cost food with a high nutritional value.

The fish family of Siganidae have long attracted interest in aquaculture due to their ease of adaptation to rearing. These species are commonly cultured in brackishwater ponds, cages, or integrated systems, and are often considered environmentally sustainable due to their low trophic level and compatibility with seaweed or bivalve farming (Chong et al., 1990; Jaikumar et al., 2011). The culture of rabbitfishes began in the 1970s, especially in Southeast Asia, where several species such as *Siganus canaliculatus*, *S. guttatus*, and *S. lineatus* were explored for aquaculture due to their herbivorous diet, fast growth rates, resistance to diseases, and good market acceptance (Ben-Tuvia et al., 1972; Darsono, 1993; Duray & Southeast Asian Fisheries Development Center, 1998b). *Siganus canaliculatus* in particular has become one of the most commonly farmed species, especially in the Philippines and Vietnam, where hatchery technologies and farming protocols have been relatively well developed (Jaikumar et al., 2011; Prihadi et al., 2020, 2020).

In the Western Indian Ocean (WIO) region, rabbitfish aquaculture is still emerging and remains primarily based on capture-based aquaculture (CBA), where juveniles are collected from the wild and reared in cages or ponds (Rajaprabhu et al., 2021; Seale & Ellis, 2019; Syah et al., 2020). Among the species found in the region, *Siganus sutor* is of special interest due to its abundance in coastal seagrass habitats, herbivorous diet, and its socio-economic importance to small-scale fisheries. However, culture of *S. sutor* remains poorly studied and it is essentially in an experimental stage in Kenya (Minyonga, 2022) or Oman (Fourooghifard et al., 2019; Shirinabadi et al., 2013).

*Siganus sutor* is a key target in fisheries in the Bay of Toliara (Behivoke et al., 2021; Jaonalison et al., 2022; Ranaivomanana et al., 2023). Through its omnivorous and herbivorous diet and local market value, *S. sutor* is an attractive candidate for cultivation. However, like many tropical marine fishes, *S. sutor* presents challenges for hatchery production due to limited knowledge of its reproductive biology and larval rearing protocols. As a result, most local aquaculture efforts rely on CBA methods, where juvenile fish are collected from seagrass beds or shallow lagoons and reared in captivity for several months before being harvested.

A better understanding of the biology, feeding ecology, and habitat use of *S. sutor* is crucial to optimize aquaculture protocols and minimize ecological risks. Integrating traditional ecological knowledge from local communities with scientific research offers a powerful strategy to achieve this goal. The general objective of the present study is to evaluate the possibilities of developing controlled rearing of juvenile *S. sutor* caught with mosquito nets in Toliara Bay. The specific objectives are to optimize and control the growth and survival rate in the captive rearing of *S. sutor* and to compare the performance of locally produced food compared to industrial food.

## 2. Material and methods

### 2.1. Study site and fish sampling

Study was carried out at the Marine Biology station “BELAZA”, a research center localized at 22 km south to Toliara. Individuals of *Siganus sutor* used for the experimentations came from the seagrass meadows in Toliara lagoon in front of the village of Sarodrano. Fish were collected in collaboration with local fishers using mosquito nets. Sampling period has been set based on the recruitment period of post-larvae and juvenile *S. sutor* (in January, see Results from the first chapter). The catches were immediately placed into tanks filled with seawater and equipped with a battery-powered aeration system. The captured fish were then sorted on site. Individuals within the desired size range were retained, while those of other sizes were released immediately. The selected fish were then transported to BELAZA. Upon arrival, they were counted and transferred into acclimatization tanks for monitoring. After the acclimatization period, the fish were measured, weighed, and allocated either to nursery tanks for pre-growing or to grow-out tanks for further rearing.

### 2.2. Rearing of *Siganus sutor*

In order to optimise growth and survival of reared *S. sutor*, two differents rearing units were used the experiment. A plastic tank of 200L filled with 150L of sea water was used for the pre-grow-out of *S. sutor* post-larvae. Then a concrete pond of a capacity of 16 $m^3$ (8m x 4m x 0.5m) were used for grow-out of juveniles *S. sutor*. All rearing units were located outdoor with ambient light and temperature. A shading system was installed to limit proliferation of phytoplankton (Fig. 6.1). Each rearing unit was equipped with an aeration system. This system was composed by an air compressor that pumped air through a network of pipes and some sugar-type diffusers that released fine bubbles, ensuring efficient oxygenation. Seawater was drawn from a collector positioned in the sea and conveyed to the rearing units via piping, using a water pump. The rearing water was siphoned off after the last feeding to remove food scraps and fish excrement. The tanks in pre-grow-out experiment were cleaned once a day by changing 50% of the water. For grow-out phases, up to 30% rearing water ware changed every two days. In addition, ponds were cleaned every two weeks by changing 80% of the water. The physicochemical parameters of the rearing water were monitored three times a day using a multiparameter of the HANNA HI 9829 brand. Parameters were taken at fixed locations three times a day (6h, 13h and 18h). The parameter considered for the monitoring are: water temperature, dissolved oxygen (DO), salinity, turbidity and pH. A daily inspection was carried out to observe the behaviour of the farmed fish and to note any dead fish, if any. After each experiment, the reared *S. sutor* individuals were released into their natural habitat.

**Figure 6. 1**. Positioning of rearing tanks with shading and aeration system

### 2.2.1. Phase 1: Pre-grow-out

The pre-grow-out phase concerned the rearing of post-larvae of initial mean length (SL) and weight of 3.06 ± 0.17 cm and 0.75 ± 0.16 g, respectively. This phase was conducted during two months, from February to April 2022. A study conducted by Parazo (1990) focusing on a two months pre-grow-out of *Siganus guttatus* with an average initial body weight of 0.93 ± 0.3 g used a stocking density of 320 individuals/m$^3$. Therefore, for the present study, three stocking densities were tested: D1 = 120 individuals/m$^3$, D2 = 320 individuals/m$^3$ and D3 = 520 individuals/m$^3$. So, the tanks were stocked with the following number of individuals: D1 = 20 individuals/tank, D2 = 50 individuals/tank and D3 = 80 individuals/tank. In addition, the performance of two different food pellets were tested (Tab. 6.1, Tab. 6.2): F1 = industrial fish food (produced in Madagascar especially for in land fish aquaculture) and F2 = artisanal fish food. The F2 is a local food generally used on culture of Tilapia but it remains in experimental and familial use. Both types of food were distributed to the fish at a rate of 12% of the biomass (Nelson, 1992). This rate was distributed to the livestock divided into 5 feedings per day, i.e. one feeding every 2 hours from 8h to 16h. To test the three stocking densities and the two food types, twelve tanks were used with six tests and six others that served for replicas (Fig. 6.1).

Post-larval growth monitoring was carried out every two weeks by weighing (total weight) and measuring (standard length (SL)) the post-larvae. All individuals in tank D1 (20 individuals) were considered for survey. For the two other densities, a sub-sample of 50% of reared post-larvae in D2 (25 individuals) and 40% of reared post-larvae in D3 (32 individuals) ware taken randomly. Before manipulation sample were anesthetized using clove oil with a concentration of 0.3 to 0.4 ml / 10l of sea water (Chanseau et al., 2002). As the fish spines are venomous, all handling was done using cut-resistant gloves.

**Table 6. 1**. Composition of the two tested fish of food od in pre-grow-out, with F1: industrial food and F2: artisanal food. For F1: no proportion was available from the producer.

| F1 | F2 | |
|---|---|---|
| **Composition** | **Composition** | **Rate (%)** |
| Fish meal | Fish meal | 30 |
| Shell | Soya meal | 25 |
| Rice bran | Rice bran | 15 |
| Corn bran | Corn meal | 15 |
| Wheat bran | Peanut meal | 10 |
| Meals (soya, cassava, peanut, sunflower, cottonseed) | Cassava flour | 5 |
| Surfactants, organic acids, molasses, oil, water | | |

Table 6. 2. Nutritional value of the two tested fish food, with F1: industrial food and F2: artisanal food

| F1 | | F2 | |
|---|---|---|---|
| **Nutrient** | **Rate (%)** | **Nutritient** | **Rate (%)** |
| Protein | 30% | Protein | 37% |
| Lipid | 9% | Lipid | 27% |
| Fiber | 5.5% | Carbohydrate | 7% |

### 2.2.2. Phase 2: Grow-out

For the grow-out phase, two experiments were performed. The first one was carried out from April to September 2022 (6 months) and the second one was conducted from April to August 2024 (5 months).

#### 2.2.2.1. Experiment A

The first experiment of grow-out was performed successively after the pre-grow-out phase. The stocking density was 8 individuals/m$^3$ following the setup of (Yousif et al., 2005) with *Siganus canaliculatus*. Therefore, we started with 128 individuals/pond. Juveniles had an initial length and weight of 6.24 ± 0.87 cm and 6.07 ± 2.37 g respectively. The performance of two fish food were tested: F1 = industrial fish pellet (the same that those used for pre-growing) at 8 % (dry weight) of the biomass and F3 = cooked rice at 25 % (wet weight) of the biomass (Tab. 6.3). This ratio was distributed five times a day as in pre-grow-out phase.

Four rearing ponds were used to test the two fish food (F1 and F3) with a replicate of each treatment (F1:pond_1, F1:pond_2, F3:pond_1 and F3:pond_2). The monitoring of fish growth was conducted monthly by weighting and measuring 50 % of reared juveniles after being anesthetized with cloves.

**Table 6. 3.** Nutritional value of the rice from OECD (2011), modified

| Nutrient | Rate (%) |
|---|---|
| Protein | 8 |
| Lipid | 1 |
| Carbohydrate | 32 |
| Amidon | 28 |
| Dietary fiber | 2 |
| Phosphor | 35 |
| Potassium | 16 |
| Vitamins (B1, B2, B3, B5, B6, B9, B12, C, E, K1) | 2 |
| Energy | 145Kcal |

#### 2.2.2.2. Experiment B

We used the same rearing conditions (stocking density, feeding frequency,…) than in the first experiment of grow-out. Juveniles had an initial length and weight of 11.9 ± 2.02 cm and 45.12 ± 22.6 g respectively. Here, we aimed to test an experimental fish pellets composed with 50% of beach wrack (F4) (Tab. 6.4) and compared the performance with the industrial fish pellets (F1) (nutritional value of both food in Tab. 6.5). Fish were fed with an initial ratio of 4% of biomass in both treatments. In addition to the aeration system, a submersible circulation pumps with a Venturi system were added for the experiment B to create circulation currents in each pond. These currents served to circulate aerated water throughout the pond. Before manipulation, sample were anesthetized using MS222 of a concentration of 0.1g.L$^{-1}$ to limit stress in animals.

**Table 6. 4.** Composition of the experimental fish pellet (F4)

| Composition | Rate (%) |
|---|---|
| Beach wrack | 50 |
| Fish meal | 15 |
| Soya meal | 12 |
| Corn meal | 7 |
| Rice bran | 7 |
| peanut meal | 5 |
| Cassava meal | 2 |
| Vegetal oil | 1 |

**Table 6. 5.** Nutritional value of F1 and F4

| Food | Protein rate (%) | Fat rate (%) |
|---|---|---|
| F1 | 36.06 | 0.07 |
| F4 | 13.39 | 0.06 |

### 2.3. Data analysis

In order to assess the survey of reared fish, several parameters were determined.

The Average Daily Weight Gain (ADWG) is a common metric used in aquaculture and animal production to measure how much weight an individual gains per day over a given period.

$$\text{ADWG} = \frac{\text{Final weight (g)} - \text{Initial weight (g)}}{\text{Duration (days)}}$$

The survival rate (SR) is the number of fish alive after a specified time interval, divided by their initial number. The formula to calculate survival rate is:

$$\text{SR (\%)} = \left( \frac{\text{Number of fish at the end}}{\text{Number of fish at the beginning}} \right) \text{X } 100$$

The Feed Conversion Ratio (FCR) indicates the conversion rate of the integrated feed into fish biomass. It is obtained from the ratio between the feed distributed (dry weight) and the weight gain obtained using the following equation:

$$\text{FCR} = \frac{\text{Feed given (g)}}{\text{Weight gain of fish (g)}}$$

The body condition of a fish is typically estimated using a Condition Factor (K), which gives an indication of the overall health of the fish in relation to its length.

$$\text{K} = \left( \frac{\text{Weight (g)}}{\text{Length}^3\text{ (cm)}} \right) \text{X } 100$$

Data analyses were performed with R software (version 4.4.2). We first tested whether the assumptions of parametric analysis were met. The normality of data was evaluated using the Shapiro-Wilk test and the homogeneity of variances was assessed with Levene's test. First, in pre-grow-out experiment, we aimed to test whether To assess temporal variation in water parameters throughout the rearing tank, the measurement time (7h, 13h, and 18h) and date as well as their interactions, we used a non-parametric ART ANOVA test using the art() function with the package (ARTool) (Kay & Wobbrock, 2021). In case of significant difference, a Tukey post-hoc test was used to compare means across factor categories, while controlling for multiple comparison errors. After that, to test the variation of growth (length and weight) over rearing period and over food type a ART ANOVA test was performed. Then the effect of diet and density on fish survival rate was tested using a ART ANOVA. A three-way ANOVA was then used to compare the difference in survival rate across diet, density and week.

For grow-out experiments, the variation of water parameters across the measuring time and rearing date was tested using ART ANOVA. Then, fish growth variation across the tested food was tested with the ART ANOVA test. Then, the variation of fish survival rate across rearing month and food type was tested using a two-way ANOVA test.

## 3. Results

### 3.1. Pre-grow-out

#### 3.1.1. Physicochemical parameters of rearing water

The values of water parameters did not differ significantly mong the twelve rearing tanks (ART ANOVA, all $p > 0.05$). However difference according to measuring time and rearing date as detailed below.

Temperature of rearing water ranged from 22.33 to 32.5 °C with an average of 32.44 ± 2.11°C (Fig. 6.2). Water temperature varied significantly in function of measuring time ($p < 2.22 \times 10^{-16}$) and rearing date ($p = 0.006$) with no interaction between them ($p= 0.19$). The results of the post-hoc test showed a significant increase in water temperature throughout the day. On average, the temperature at 13h was 2.65 °C higher than at 06h, and 3.99 °C higher at 18h ($p < 0.001$). Daily variation analysis showed that temperatures in February and March were approximately 1 °C higher than in April ($p < 0.05$), with no significant difference between February and March.

Values of DO varied between 2.16 and 6 mg/L with an average of 3.79 ± 0.44 mg/L. There was a significant variation of DO depending on measuring time ($p = 5.93 \times 10^{-13}$) and rearing date ($5.16 \times 10^{-16}$). Post-hoc test showed that DO levels were significantly lower at 18h compared to 06:00 (−0.44 mg/L) and 13h (−0.46 mg/L) ($p < 0.001$). DO values in April were approximately 2 mg/L higher than in the previous months.

Concerning the salinity of water in each rearing tank, it varied between 20.18 and 35.61 ‰ with a mean value of 29.95 ± 3.08 ‰. There was no significant variation of the salinity according to measuring time ($p = 0.68$), but the significant variation depended to the rearing week ($p = 1.56 \times 10^{-14}$). For example, Salinity in April was significantly higher than in February (by 4.91‰, $p < 0.001$) and March (by 1.79‰, $p = 0.01$). Salinity in February was 3.11‰ lower than in March ($p < 0.001$).

Turbidity of water had a high fluctuation as its values oscillated between 1.15 FNU in tanks with clearer water and 25.2 FNU in turbid tanks with a mean value of 7.84 ± 4.41 FNU. Turbidity varied significantly over hour ($p = 7.91 \times 10^{-06}$). It was represented by a lower turbidity at 06h than at 13h and 18h (- 3 FNU each) ($p < 0.001$). No significant monthly variation in turbidity was observed ($p = 0.27$).

Finally, the pH represent the lowest variation as it varied between 7.99 and 8.59 with an average of 8.35 ± 0.09. There was a significant variation of pH depending on measuring time (p = 0.01). The pH was significantly lower at 06h (by approximately 0.4 units) compared to 13h and 18h. However, pH did not vary significantly across weeks (ANOVA, p = 0.13).

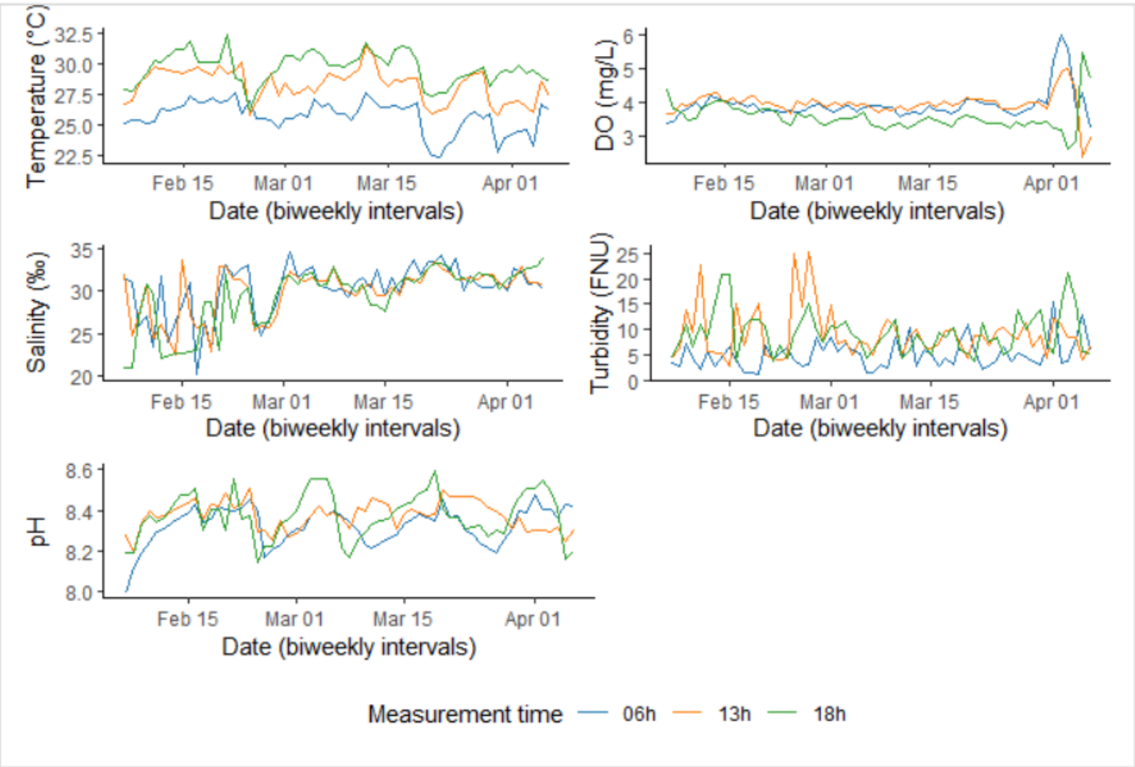


**Figure 6. 2.** Daily variation of mean values of physicochemical parameters of rearing water of all pre-grow-out tanks, DO refers to dissolved oxygen

### 3.2.2. Growth

Post-larvae of *S. sutor* fed with F1 during the pre-grow-out phase had an initial mean weight and length of 0.85 ± 0.28 g and 3.2 ± 0.3 cm, respectively, and reached a final mean weight and length of 4 ± 1.44 g and 5.28 ± 0.7 cm. In contrast, those fed with F2 grew from 0.67 ± 0.27 g and 2.93 ± 0.3 cm to 1.49 ± 0.5 g and 3.78 ± 0.59 cm (Fig. 6.3).

ART ANOVA revealed that both diet type and monitoring week had significant effects on fish growth in terms of length and weight with strong interactions between these factors (all $p < 2.22 \times 10^{-16}$). Post hoc comparisons revealed that fish fed with the industrial food on latest weeks (April 6th) had significantly greater lengths and weight than those in almost all other treatment groups. Significant differences were also found compared to artisanal food groups from the beginning of the experiment till March 22nd (all $p < 0.0001$). No significant difference were found between the two latest monitoring weeks (p=0.18). For weight of this group, the difference was seen between the three latest weeks compared to the the weitgh at the starting weeks (p= 0.001).

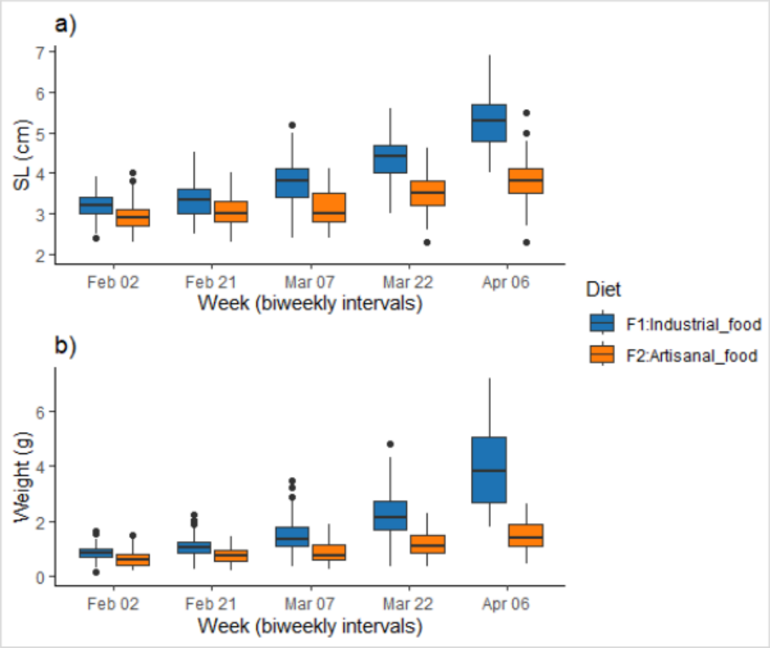


**Figure 6. 3.** Variation of a) length and b) weight of reared *Siganus sutor* post-larvae every two weeks according to the food type

At the end of the two months of pre-grow-out, juveniles had a weight gain of 2 g, 1.97 g and 0.81 g for the respective density D1, D2 and D3 (Fig. 6.4). Tha ART ANOVA revealed a significant effects of stocking density ($p = 1.86 \times 10^{-12}$) and monitoring week ($p < 2.22 \times 10^{-16}$) on fish length with an interaction between the two factors ($p = 9.06 \times 10^{-06}$). Fish weight also varied significantly over stocking density and week ($p < 2.22 \times 10^{-16}$) was observed (ART ANOVA, $p < 0.01$), with significant interactions indicating that the effects of density varied across weeks. Post-hoc pairwise comparisons test revealed that fish at density D3 were significantly smaller than those at D1 ($p = 0.0147$) and D2 ($p = 0.00022$), while the difference between D1 and D2 was not significant ($p = 0.303$).

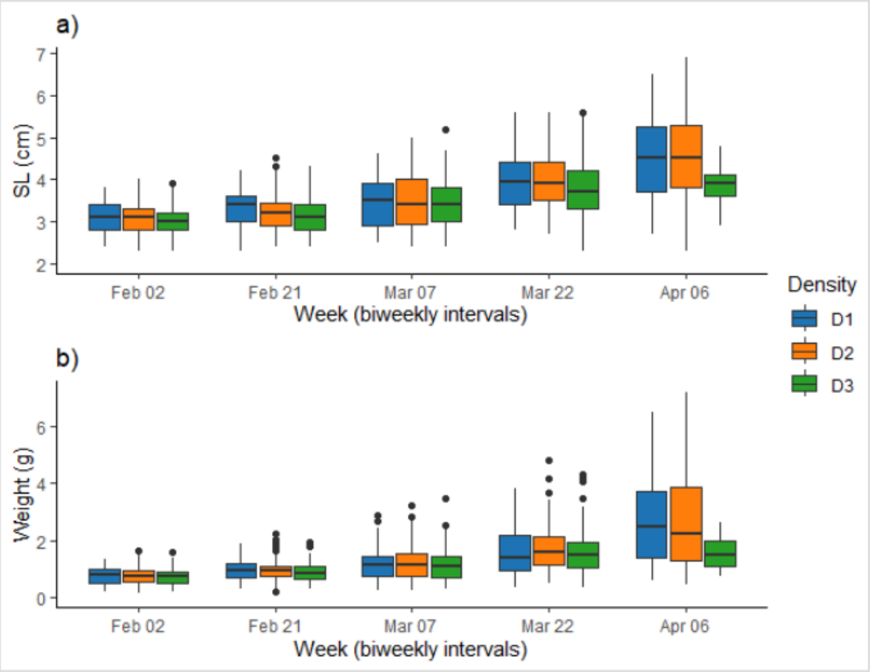


**Figure 6. 4.** Variation of a) length and b) weight of reared *Siganus sutor* post-larvae every two weeks according to the stocking density

### 3.1.3.Survival

Final survival rate was 57.5 and 50 % for D1, 72 and 88 % for D2 and 50% for the two tanks with the third density (D3) (Fig. 6.5). The two-way ANOVA revealed no significant difference of the survival rate according to the density ($p = 0.068$) or diet ($p = 0.092$). However, a significant temporal variation was observed according to monitoring week ($p = 0.001$).

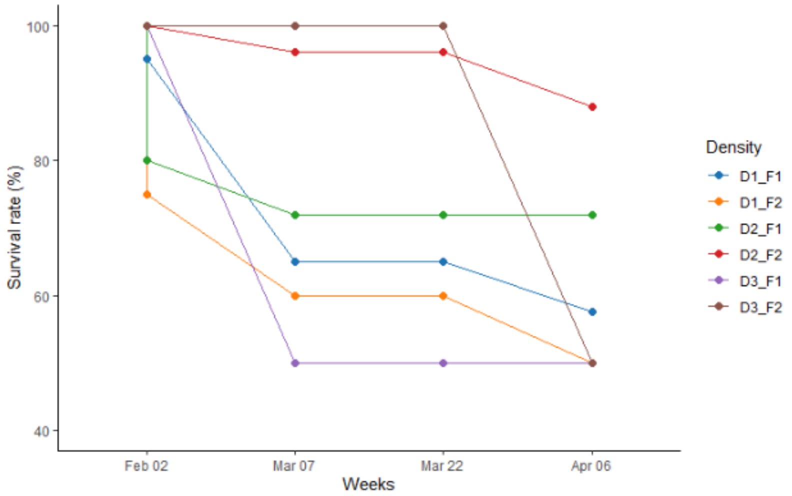


**Figure 6. 5.** Temporal evolution of survival rate by stocking density during pre-grow-out of *Siganus sutor*

## 3.2. Grow-out: first experiment

### 3.2.1. Physicochemical parameters of rearing water

The ART ANOVA revealed no significant differences in water parameters were observed between the four rearing ponds ($p > 0.05$). However, significant daily and monthly variations was detected for all parameters (all $p < 0.05$). During the first experiment of the grow-out phase, water temperature ranged from 19.08 to 28.76 °C with an average of 24.33 ± 1.98 °C. The lower temperature (< 24°C) was measured especially in the morning and the rest of the day only during the cold season (June and July). On average, water temperature at 13h was 1.9°C higher than at 06h ($p < 0.001$). Temperature increased significantly from May to September, with notably lower values in June (-3.2°C) and July (-2.2°C) compared to April ($p < 0.001$). Conversely, the highest temperatures were recorded in August and September, with significantly higher values than in the previous months ($p < 0.001$).

Dissolved oxygen (DO) concentrations varied between 3.03 and 5.16 mg/L, with an average of 4.20 ± 0.46 mg/L. The lower DO values (<3.5 mg/L) were observed in the morning when values usually increased up to 4.5 mg/L for the rest of the day. Dissolved oxygen (DO) levels at 06:00 were significantly lower (by about -0.75 mg/L) than at 13:00 and 18:00 (+0.75 mg/L, $p < 0.001$). DO concentrations increased significantly from June to August compared to April ($p < 0.001$). The lowest DO levels were observed in May, while the highest values were recorded in June and July ($p < 0.001$).

Salinity values ranged from 26.15 to 34.57 ‰, averaging 29.82 ± 1.59 ‰. Salinity was higher at 13:00 than at 06:00 (+0.50 ‰; $p = 0.012$). Regarding monthly variation, salinity was significantly lower in June ($p = 0.036$).

Turbidity exhibited considerable variability, with values spanning from 1.91 to 25.94 FNU and a mean of 9.53 ± 5.46 FNU. Turbidity at 18:00 was 2.57 units higher than at 06:00 ($p < 0.001$). In April, turbidity was significantly lower than in July (difference = -4.51; $p < 0.001$) and May (difference = -2.81; $p = 0.033$). Additionally, turbidity in July was significantly higher than in August (difference = +2.94; $p = 0.002$).

The pH showed the least variation, ranging from 8.47 to 8.76, with an average of 8.52 ± 0.12. The pH was significantly higher at 18:00 compared to both 13:00 (+0.057, $p < 0.001$) and 06:00 (+0.083, $p < 0.001$). There was a clear increase in pH from April to September, reaching the highest value in September (+0.233, $p < 0.001$).

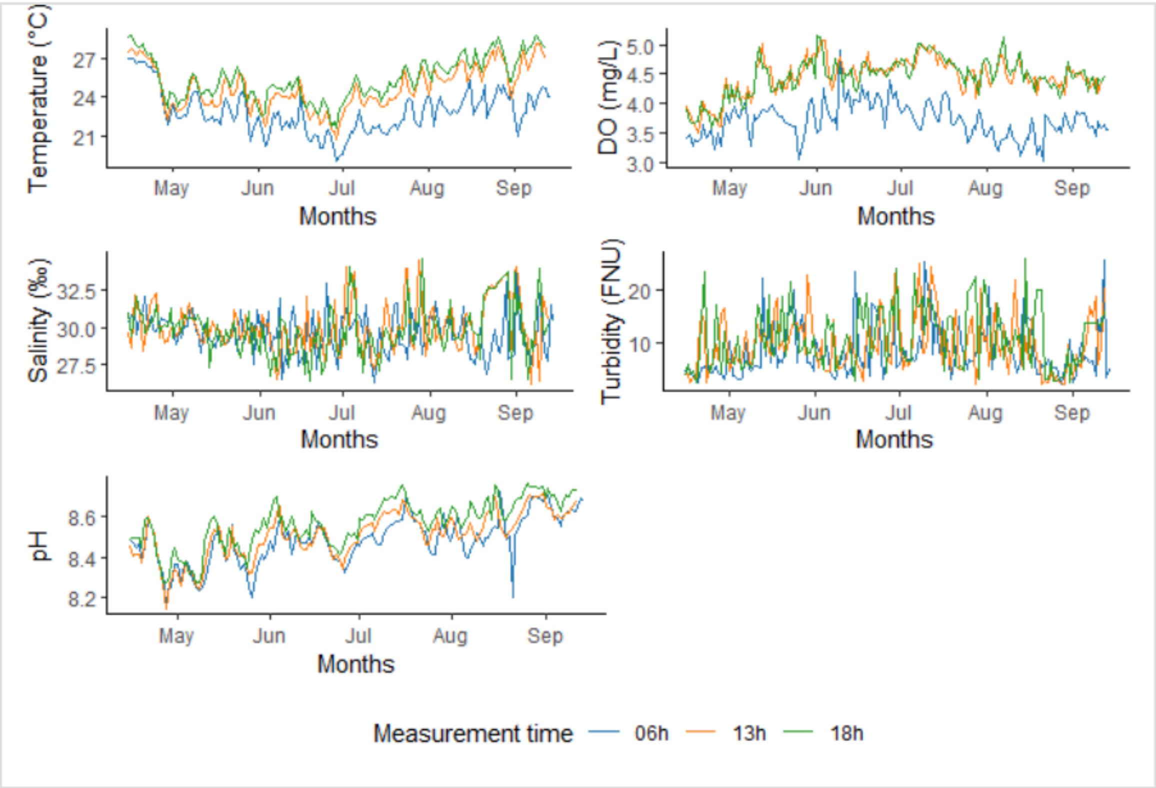


**Figure 6. 6.** Daily variation of mean values of physicochemical parameters of rearing water of all ponds in the first experiment of grow-out phase of juvenile *Siganus sutor*, DO refers to dissolved oxygen

### 3.2.2. Growth

At the end of the experiment, fish fed with F1 reached final average length and weight of 13.91 ± 1.72 cm and 68.11 ± 27.86 g, respectively. Those fed with F3 had final length and weight of 11.15 ± 1.62 cm and 34.81 ± 15.89 g, respectively (Fig. 6.7). The ART ANOVA indicated that both fish length and weight were significantly influenced by fish food, month, and their interaction ($p < 0.001$ for all factors), suggesting that growth increased over time depending on the food. The post-hoc test showed significant month-to-month differences in length was observed between diets from June and from July for fish weight (all $p < 0.05$). For the variation between diet, individuals fed with F1 exhibited significantly higher growth compare to those fed with F3 ($p < 0.05$). Difference in diet performance was found from July.

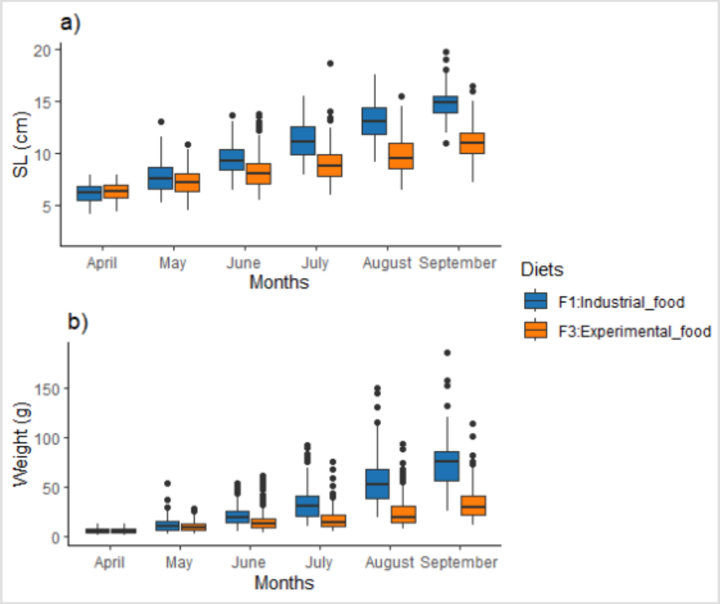


**Figure 6. 7.** Monthly variation of a) length and b) weight of reared *Siganus sutor* juvenile according to the diet for the first grow-out phase

### 3.2.3. Survival rate

Survival rate was relatively constant along the rearing period except a drastic decrease at the fourth months when we lost all livestock in one of the two pond (F1:pond_1) with the F1treatment (Fig. 6.8). The second pond within this treatment reached a survival rate of 84.38 % at the end of the experiment. On the other hand, ponds with the F3 treatment achieved a relatively higher survival rate (95.31 % and 96.09 %) by the end of the rearing period. The two-way ANOVA test revealed that diet type, month, and their interaction all contributed significantly to the variation in fish length (all $p < 0.05$).

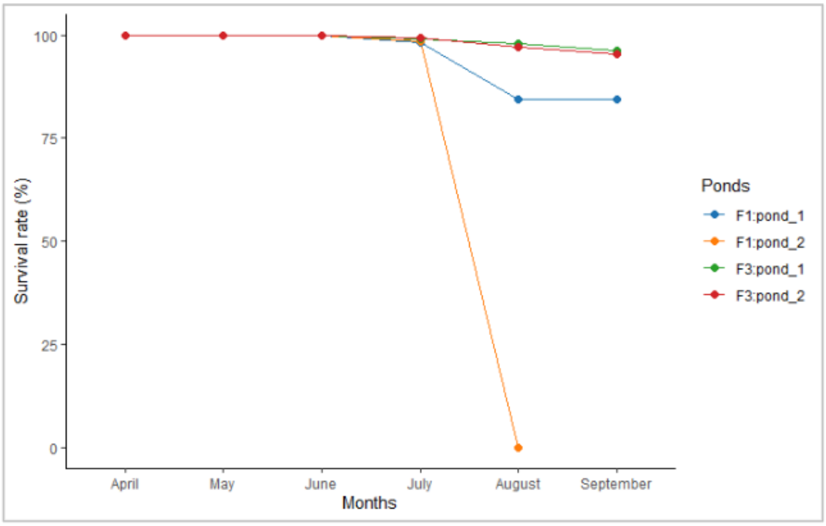
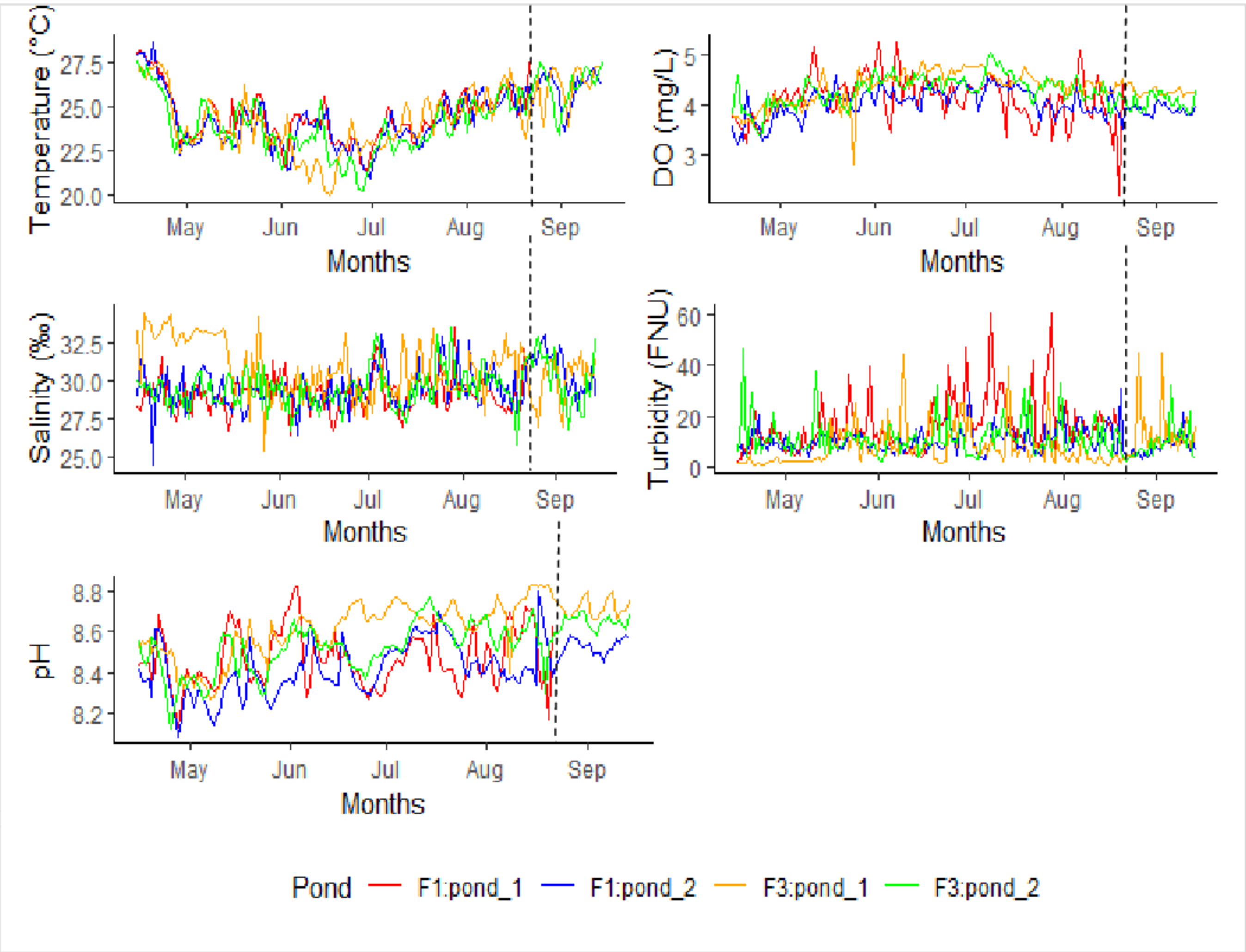


**Figure 6. 8.** Temporal variation of survival rate by diet during first grow-out phase of *Siganus sutor*

In response of this loss of 100% of livestock in F1:pond_1, physicochemical parameters of rearing water in each pond was closely analysed (Fig.6.9) according to the extinction date even if no significant variation was observed. Indeed, during the rearing period, water parameters remained fairly stables across ponds and no significant difference were found. However, F1:pond_1 represented the extreme minimal or maximal values that was measured some days before the decline of all livestock. For example, the lowest DO value (2.23 mg/L) was found in F1:pond_1 Turbidity showed the most striking difference. Results revealed the highest mean turbidity of 16.05 FNU was recorded in F1:pond_1 recorded, with a wide range from 2.54 to 60.30 FNU. In contrast, the three other ponds exhibited lower and less variable turbidity values, with ranges from 3.04 to 30.78 FNU (F1:pond_2), 0.59 to 45.02 FNU (F3:pond_1), and 2.06 to 46.5 FNU (F3:pond_2). Their means were 10.04, 8.06, and 11.25 FNU, respectively.



## 3.3. Grow-out: second experiment

### 3.3.1. Physicochemical parameters of rearing water

The Art ANOVA revealed no significant difference in water parameters between ponds (p=0.37). The variation vas significant both by time of day and by month ($p < 0.001$ for both factors). The details of significant variations are detailed by the post-hoc results below.

Firstly, water temperature ranged from 18.96°C to 28.2°C, with a mean of 22.8 ± 2.0°C (Fig. 6.10). Temperature values demonstrated a clear diurnal increase (F = 293.03), with daily fluctuations. Indeed, compared to water temperature at 06h, a significant increase of +0.37 °C was observed at 13h and a further rise of +1.04 °C by 18h. Overall, temperatures were significantly higher in the afternoon, with mean values at 18h exceeding those at 06h by 1.04 °C ($p < 0.001$) and those at 13h by 0.68 °C ($p < 0.001$). Temperature at 13h was also significantly higher than at 06h (+0.36 °C, p = 0.0004). In terms of seasonal variation, the highest temperatures were recorded in April, with significantly lower values observed in May (-1.99 °C), June (-2.96 °C), July (-4.38 °C), and August (-4.62 °C) ($p < 0.001$). Although temperatures generally increased from May to August.

The DO levels fluctuated between 3.1 and 6.4 mg/L, with an average of 4.4 ± 0.75 mg/L. DO was significantly lower in the early morning (6h) compared to midday (13h) and late afternoon (18h), with average differences of +0.39 mg/L and +0.34 mg/L, respectively ($p < 0.001$). Regarding monthly variation, DO concentrations were significantly higher in April compared to subsequent months, with differences ranging from -0.33 mg/L in May to -1.73 mg/L in August ($p < 0.001$ for all comparisons). Among the cooler months, DO levels were significantly higher in May than in June, July, and August.

The survey of salinity showed that a value ranging from 30.3 to 35.1‰ and a mean of 31.5 ± 0.85‰. Salinity increased progressively throughout the day, with significantly higher values at 13h and 18h compared to 06h, and a modest but significant difference between 13h and 18h (+0.14 ‰, p = 0.011). Seasonally, salinity was highest in August, showing significant increases of up to +1.89 ‰ compared to April, while July and May showed slightly lower values than April ($p < 0.05$). The lowest salinity values were observed in May and July, both significantly lower than August and June.

There was more variation in turbidity with values ranging from 0.95 to 6.43 FNU, averaging 2.74 ± 1.05 FNU. Turbidity was significantly higher at 13h and 18h compared to 06h. Among months, June showed a significantly higher turbidity than April and July (p = 0.016 and p = 0.034, respectively).

Finally, pH values ranged between 7.75 and 8.44, and an average of 8.07 ± 0.13. The pH was significantly higher in the afternoon and evening compared to the early morning, with values increasing from 06h to 18h ($p<0.001$). Monthly comparisons revealed that April consistently had the highest pH, with significantly lower values observed in August, July, and June. The largest differences were between April and August (−0.21 units) and April and July (−0.18 units).

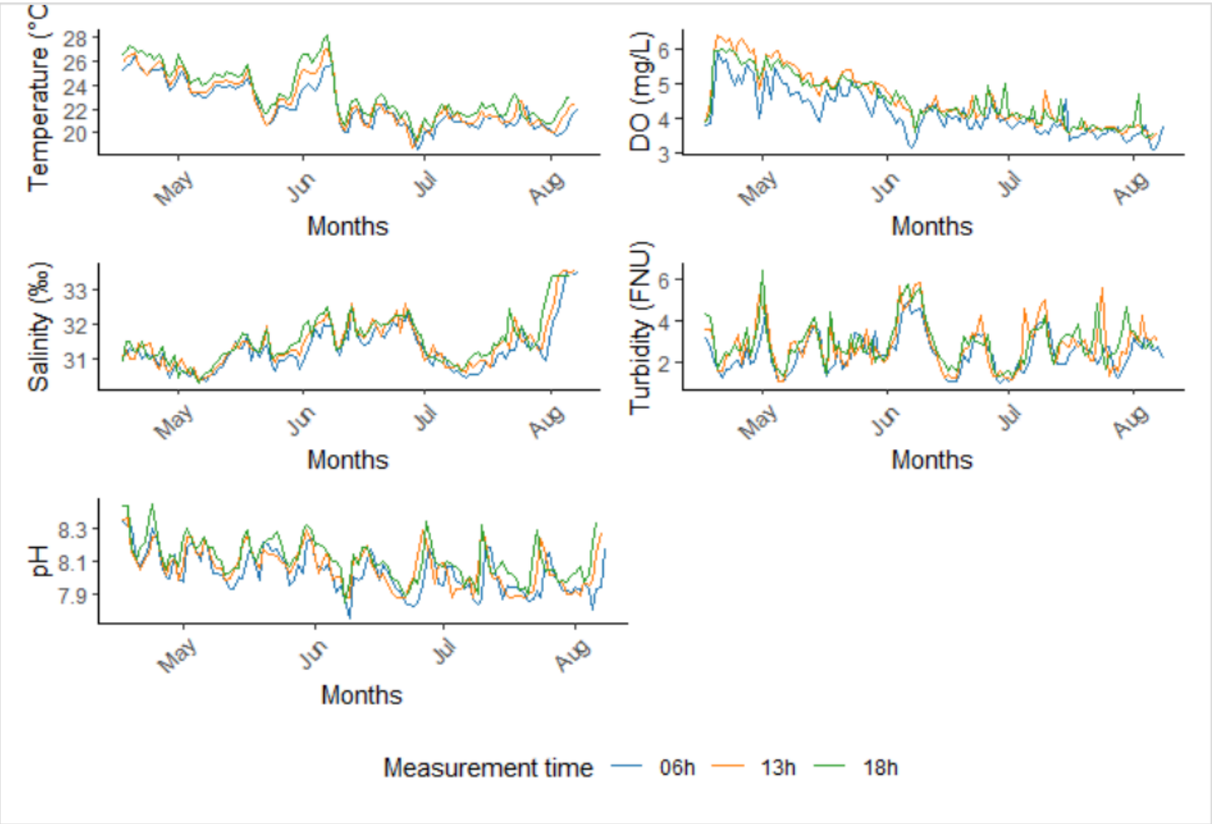


**Figure 6. 10.** Temporal variation of mean values of physicochemical parameters of water in all rearing tank on the second grow-out phase of juvenile *Siganus sutor*

### 3.3.2.Growth

Weight of fish fed with F1 had grew from 60.31 ± 31.77 g to 161.39 ± 52.47 g with biggest individuals reach over 200 g weight (Fig. 6.11). In term of linear growth, these fish started with mean length of 13.32 ± 2.28 cm (SL) and finished with a mean length of 19.37 ± 2.11 cm, when biggest individuals reached 25 cm. For F3 treatment, fish size were smaller but more homogenous with an initial mean weight of 31.58 ± 14.10 g and a final mean weight of 56.18 ± 23.48 g. These fish grew from 10.71 ± 1.44 cm to 13.26 ± 1.6 cm.

Fish growth, assessed through both length and weight, showed significant differences between dietary treatments throughout the production cycle (ART ANOVA, $p < 0.05$). Post-hoc tests revealed that fish fed with the industrial diet (F1) exhibited consistently greater size and mass than those in the F2 group (all $p < 0.001$). In general, mean length difference increased from 2.84 cm in April (95% CI: 2.56–3.12; effect size = 0.80) to at 6.43 cm in August (95% CI: 5.82–7.04; effect size = 0.99). A similar trend was observed for weight, with trimmed mean differences of 29.55 g in April (95% CI: 25.91–33.20; effect size = 0.78) and reaching 107.14 g in August (95% CI: 91.85–122.42; effect size = 0.98).

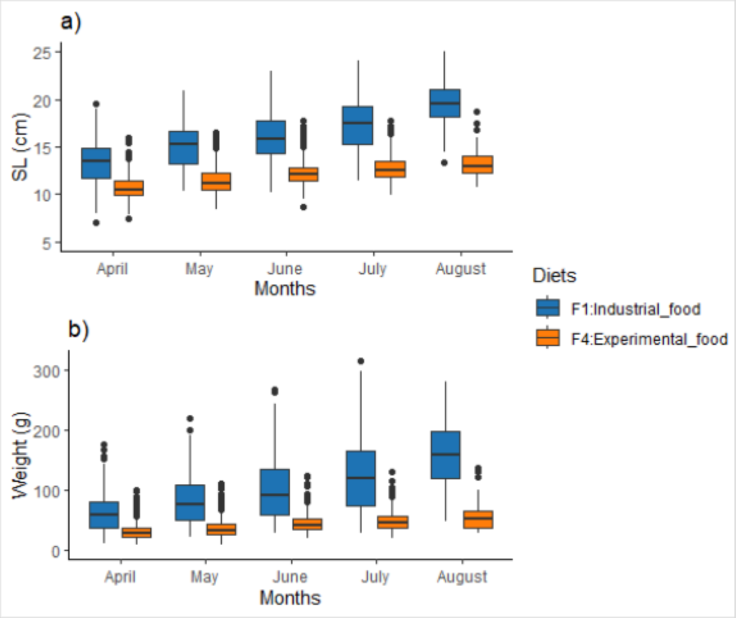


**Figure 6. 11.** Monthly variation of a) length and b) weight of reared *Siganus sutor* juvenile according to the diet for the second grow-out phase

### 3.3.3.Survival rate

The two-way ANOVA showed a significant decrease of survival rate of reared *S. sutor* across the rearing period ($p = 0.001$) (Fig.6.12). Furthermore, diet also contributed into the variation of fish survival rate ($p = 0.007$). The combination of the two factors contribute significantly on the variation of survival rate ($p = 0.005$). Fish fed with F1 ended with a lower survival rate of 68.3 % (pond _1) and 76.76 % (pond_2). In contrast, fish fed with F4 had higher final survival rate that reached up to 83.09 % (pond _1) and 85.21 % (pond_2).

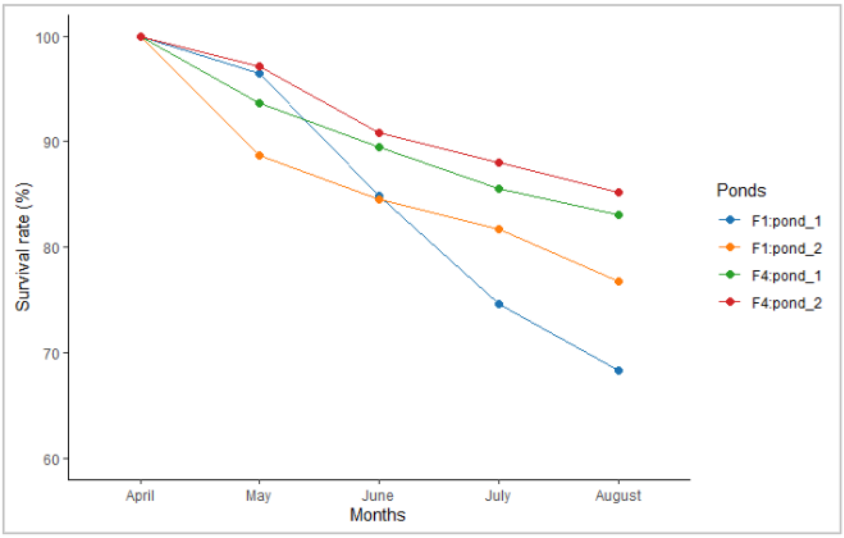


**Figure 6. 12.** Temporal variation of survival rate by diet during second grow-out phase of *Siganus sutor*

### 3.4. Food performance

The performance of the tested foods was compared using several criteria that vary depending on food type. Firstly, the Average Daily Weight Gain (ADWG) presented a moderate variation. The lowest ADWG (0.13 g/day) was observed during the first grow-out phase in fish fed with artisanal pellet (Tab. 6.5). The higher values, were therefore recorded in fish fed with industrial pellet across all experiments using this food with a maximum value reaching up to 0.76 g/day in the second grow-out phase. Feed Conversion Ratio (FCR), a key indicator of feed efficiency, presented a wide variation between the tested feeds. The lowest FCR (1.8), indicating better efficiency, was found in fish fed with industrial food. The highest FCR was observed in those fed with cooked rice (10.89) but this may be reduce while considering the dry weight of the distributed cooked rice, according to the FCR formula. The next indicator is the Fulton's condition factor (K) reflected the fish's response to rearing conditions, especially the type of food. Across all experiments, the K factor remained relatively stable, with values around 2, suggesting consistent body condition. Finally, the survival rate at the end of the experiment provided another indicator of food performance. The highest survival rate (95.7 ± 0.55%) was recorded in fish fed with rice, while the lowest was found in fish fed with industrial pellet (44 %) where only one pond with the two tested arrived until the end of the experiment.

**Table 6. 6.** Comparison of food performance based on growth and condition metrics. P, G1 and G2 refer to pre-grow-out, first grow-out and second grow-out

| Parameters | Industrial food (F1: fish pellet) | Artisanal food (F2: artisanal fish pellet) | Experimental food 1 (F3: Rice) | Experimental food 2 (F4: Wrack-based pellet) |
|---|---|---|---|---|
| **Average Daily Weight Gain (ADWG)** | P: 0.22 g/day<br>G1: 0.59 g/ day<br>G2: 0.91 g/day | 0.13 g/day | 0.19 ± 0.13 g/day | 0.32 g/day |
| **Feed Conversion Ratio (FCR)** | P: 3.21<br>G1: 2.99<br>G2: 1.8 | 5.54 | 10.89 | 2.5 |
| **Fulton' condition factor (K)** | P1: 2.62 ± 0.37<br>G1: 2.44 ± 0.32<br>G2: 2.29 ± 0.29 | 2.65 ± 0.68 | 2.55 ± 0.19 | 2.37 ± 0.23 |
| **Final survival rate (SR)** | P: 59.83 ± 11.18 %<br>G1: 42.19 ± 59.66 %<br>G2: 72.53 ± 4.22 % | 62.66 ± 21.93 % | 95.7 ± 0.55 % | 84.15 1.49 % |

## 4. Discussion

The present study showed the feasibility of rearing *S. sutor* using capture-based techniques. Post-larvae and juveniles of *S. sutor* were successfully caught and maintained alive during transport. Monitoring of water parameters allowed to know the presence of variation of physicochemical parameters of rearing water. In general, water temperature, DO, salinity and turbidity presented a significant increase during the day. The pH values were slightly alkaline, with narrow variation which is within optimal conditions for most aquaculture species. Growth survey revealed that fish fed with industrial food (F1) reached a significantly higher average weight, in the three different experiments. The densities of 120 individuals/m$^3$ (D1) and 320 individuals/m$^3$ (D2) were the most in fish growth in pre-grow-out treatment when no significant effect of density on survival rate was observed. On one hand, F1 remains the most efficient food for both phases in term of fish growth for the grow-out experiments. On the other hand, fish fed with F1 had a significant lower survival rate compared to those fed with locally formulated food.

### 4.1. Physicochemical parameters of rearing water

Many studies confirmed that water parameters such as temperature, DO, salinity, turbidity, pH and water depth are responsible for variations in fish growth and survival (Ball, 2002; Verma et al., 2022). The key to successful *S. sutor* farming lies in effective water quality management to reduce stress. For example, water temperature is a key environmental factor for aquatic life, controlling growth and survival of livestock (Falconer et al., 2020; Islam et al., 2022). During the study, temperature ranged from 22.3 to 32.5 °C (pre-grow-out), from 19.1 to 28.8°C (first grow-out) and from 19.0 to 28.2 °C (second grow-out). These values remained within the tolerance threshold of Siganidae in general, i.e. between 19°C and 38°C (Gundermann et al., 1983). However, temperatures were generally below the growth optimum values, which is comprised between 28°C to 32°C (Duray & Southeast Asian Fisheries Development Center, 1998b). The geographical position of Toliara (right on the Tropic of Capricorn) makes it a high-temperature city with average annual temperatures of 25.3 °C (Randriatsitohaina et al., 2018). The lower water temperature in this study may be due to the rearing period that occurred around and during the cool season in Madagascar. The use of shadow was decided to limit algal proliferation that may reduce considerably the DO especially during the night. This was proven by the higher water temperature during the pre-grow-out, which took place from February to April. During this experiment, a slight drop in temperature was observed from the beginning of the experiment and as long as we approached the cool season.

The DO constitutes one of the fundamental parameters in aquaculture (Culberson & Piedrahita, 1996; Boyd et al., 2018). In this study, dissolved oxygen concentration varied daily, with a minimum in the morning before sunrise and a maximum in the late afternoon. According to Verma et al. (2022), dissolved oxygen concentration varies daily and seasonally depending on several factors such as atmospheric oxygen partial pressure, water temperature, light penetration, water agitation, and nutrient availability. Referring to previous studies, Siganidae do not tolerate a concentration below 2 mg/L (Duray & Southeast Asian Fisheries Development Center, 1998b; Lavina & Alcala, 1974). For this study, although the DO value was relatively low, it remained above the tolerance threshold. In fact, DO values varied from 2.16 - 6 mg/L (pre-grow-out), 3.03 -5.16 m/L (first grow-outs) and 3.1 – 6.4 mg/L (second grow-out). This reflects the high tolerance of *S. sutor* for the varied conditions of oxygen concentrations.

Next, water salinity is essential in the study of seawater species since its variation can affect the growth and survival of the farmed population. During the experiments, the salinity of the rearing water was, most of the time, under the average salinity of seawater in the natural environment (35‰) with a lowest measured value reaching 20.18 ‰. The observed low salinity values may be due to the localisation of the study area that is located near a mangrove ecosystem characterized by a brackish environment. This type of environment results in relatively low salinities due to the mixing of fresh resurgence and salt water (Ahmed et al., 2022; Ball, 2002; Kodikara et al., 2017). The results show that salinity in the four basins varies slightly depending on the time of day, with peak values reached in the evening, likely due to evaporation. Again, this demonstrates the tolerance of *S. sutor* to variation of water parameters. Furthermore, several species belonging to the Siganidae family exhibit strong salinity tolerance. For example, post-larvae of *Siganus guttatus* is capable of surviving in conditions between 14 and 37 ‰ (Young & Dueñas, 1993). Similarly, *Siganus vermiculatus* has demonstrated the ability to withstand extreme salinity variations, from 2 to 55 ‰, which enables it to thrive in mangrove swamp environments (Gundermann et al., 1983). However, a study conducted by Fourooghifard et al. (2019) demonstrated a higher survival rate of *S. sutor* larvae at a salinity of 30 ‰ compared to 25 ‰ and 37 ‰.

Turbidity reflects slight to moderate suspended particle load in the water, likely due to feeding, pond management, or algal growth. Daily increase of water turbidity may due to water agitation by fish activity (Rodrigues et al., 2023). In addition, the activation of circulation pumps during the day results in the resuspension of bottom sediments that increase the water turbidity. This process has been observed in other aquaculture studies, where intensified pumping systems have a direct impact on water quality, particularly on turbidity (Lindholm-Lehto, 2023). The maximum values (at 18h) observed could also be influenced by meteorological events such as the frequency of wind passage in the region. Turbidity, if moderate, can be beneficial in some culture systems. Slight turbidity in fish culture water has been shown to be effective in improving fish comfort by limiting stress and promoting natural productivity (Bristow et al., 1996; De Robertis et al., 2003). However, it must be regularly monitored and adjusted according to the needs of the species being cultured.

Marine fish species tolerate a slightly alkaline water with pH ranging from 7.5 to 8.5. In our case, the pH presented a lower variation in water quality with value ranging from 7.45 to 8.76 with minimum values recorded in the morning and maximum values reached in the afternoon or evening. These diurnal pH fluctuations are typically attributed to aquatic organism photosynthesis and respiration. During the day, photosynthesis consumes carbon dioxide ($CO_2$), reducing water acidity and increasing pH, while organism respiration, which produces $CO_2$, dominates at night, leading to a lower pH (Axelsson, 1988; Long et al., 2017; Yang et al., 2009). However, pH variation remains optimal and constant despite the presence of fish excrement and leftover food.

## 4.2. Performance of food types on *Siganus sutor* farming

Based on the omnivorous potential of juvenile siganids (Chapitre 2), it is important to look for economical formulated food for reducing aquaculture cost. A comparative study have highlighted the capacity of adaptation of reared *Siganus canaliculatus* on a wide variety of food, such as chicken pellets, dried shrimp, fish scraps and even cooked rice (Darsono, 1993). In the present study, among the four tested food, the industrial food (F1) is well know food in Madagascar and is widely used for the culture of freshwater species. The artisanal fish food (F2) used in pre-grow-out have already been tested in local experimental and familial culture of tilapia or carp. The use of the two other food (F3 & F4) were completely new and innovative.

Results showed a significant effect of food type on growth of *S. sutor*. Fish fed with industrial food (F1) consistently achieved higher growth performance compared to those fed with locally produced food (F2, F3 and F4). These results are also consistent with the fact that diets rich in protein, often used in industrial food, are associated with a significant increase in fish weight growth (Tacon et al., 1990). At the end of the rearing period, some individuals fed with F1 have reached a commercial size of 150g (Basyari & Tanaka, 1988).

Our first grow-out experiment (F1 treatment) with an initial mean weight of 6.07 ± 2.37 g ended with a final mean weight of 68.11 ± 27.86 g after five rearing months. For our second grow-out experiment, juveniles weight grew from 60.31 ± 31.77 g to 161.39 ± 52.47 g in four months. These results remain lower compared to similar studies made with another siganids. For example, a culture of *Siganus canaliculatus* in Abu Dhabi ended with an average weight of 180g over 7 months of rearing. Juveniles had an initial average weight of approximately 3.38g and they used the same stocking density as our experiment (8 individuals/$m_3$) (Yousif et al., 2005). Another study showed that *S. vermiculatus* fry reached an average weight of 240g after 9 months of rearing (Gundermann et al., 1983).

Additionally, results of pre-grow-out showed that the stoking density also affect growth of *S. sutor* post-larvae. Lower stocking densities (D1 and D2) were associated with better weight gain, particularly when combined with industrial food. These findings suggest that optimal growth was achieved with industrial food at lower densities, and that combining poor food quality with high density leads to significantly reduced growth. Therefore, improving food quality and managing stocking densities are both critical for maximizing aquaculture performance in this species.

All the three experiments showed a significant lower survival rates in fish fed with F1. Indeed, higher survival rate in local food treatment means a greater number of fish at the end of rearing, which partially compensates for the lower biomass yield of the experimental food. Survival was high, with a rate of over 95% for those fed rice. As for those receiving F1, mean survival rate ranged from 42.19 ± 59.66 % to 72 ± 4.22 %. A total mortality occurred after the fourth month of rearing in the first grow-out phase. This may be due to the interaction of the drop in dissolved oxygen (2.16 mg/L) on the day of the incident. In fact, the day before the incident, excessive precipitation occurred, causing a drop in salinity. This, combined with the decrease in dissolved oxygen levels, caused total fish mortality in the pond when this pond had the highest biomass at the moment. For the three other food, final survival rate was higher with F3 (95.7 ± 0.55 %), followed by F4 (84.15 ± 1.49 %) when the lower survival rate among them was observed in F2 (62.66 ± 21.93 %).

Although less efficient in terms of individual growth, locally-produced food improved overall survival rates. In terms of profitability, although industrial food offers accumulated weight gain per individual, its higher cost may limit its accessibility, particularly for small-scale producers. The lower fabrication cost improve the profitability potential for fish farmers seeking to optimize their margins while minimizing their dependence on the inputs considered. Indeed, F1 performed better in terms of fish growth when F2, F3 and F4 proved advantages in terms of cost and survival rates. These qualities make the locally food an affordable and more sustainable food production in marine fish aquaculture. Most of all, when the F1 was bought from the capital of Madagascar (Antananarivo) localised at about 1 000 km from Toliara, the three experimental foods were made with local ingredients, available year-round and cheaper.

In particular, the food made with 50 % of beach wrack (F4) was the cheapest of all the tested food. This food is an economical and good alternative fish food. In addition, moderate beach wrack removing can be favourable as it may be as cleaning action very favourable for human and tourism activity (Stenis et al., 2020). The beach wrack, composed of marine algae and plant debris washed ashore, is attracting growing interest as a resource for animal food and agriculture. Studies have explored the integration of seaweed, a major component of seaweed, into the diets of ruminants, pigs, and fish. It is valued for its richness in essential minerals, such as iodine, calcium, and dietary fiber, helping to improve digestibility and intestinal health in animals. In aquaculture, algae are also being tested as a partial alternative to fishmeal, providing essential proteins and fatty acids while strengthening the fish's immune system (Stenis et al., 2020). Furthermore, in agriculture, beach wrack has been used as a natural fertilizer, rich in nitrogen, phosphorus, and potassium, nutrients essential for plant growth. As it decomposes, algae enrich soils with organic matter and trace elements, improving water retention and the structure of poor soils (Rudovica et al., 2021).

However, for use of beach wrack-based food, precautions are necessary to avoid potential contaminants, such as heavy metals or microplastics, present in seaweed. Despite these challenges, seaweed is emerging as a promising resource for sustainable use in the agricultural and animal food sectors. In addition, it is important to increase protein values of the food for a better growth of livestock. Protein rate can be increased by adding more protein source ingredient such as fishery sous-product (mollusc and crustacean shell).

The success of capture-based aquaculture of *S. sutor*, the most abundant juvenile in mosquito sein net, is an effective conservation system of this species. This method could improve the species' adult stock by promoting sea ranching. In addition, the promotion of this practise as an alternative activity for local community could reduce considerably the decline of fish stock. As in the second grow-out experiment, the bigger fish reached commercial length after four rearing months. The culture of *S. sutor* could be an effective approach in response to fish conservation and sustainable food intake in Madagascar.

# Chapitre 7 : Discussion générale

Cette thèse s'inscrit dans une dynamique de recherche appliquée en faveur de la conservation et de gestion des ressources halieutiques, en particulier celle du Sigan cordonnier (*Siganus sutor*) à Toliara (Sud-Ouest de Madagascar). Elle vise à développer une exploitation rationnelle des stocks de poissons marins, dans une optique de sécurité alimentaire et de développement durable, bénéfique tant pour l'espèce que pour les communautés locales. Adoptant une approche pluridisciplinaire, ce travail combine la biologie marine, l'écologie marine, l'aquaculture expérimentale et la collaboration étroite avec les petits pêcheurs de la baie de Toliara. Cette thèse avait pour objectifs d'approfondir les connaissances sur la bio-écologie de *S. sutor* et d'étudier les potentialités d'élevage de cette espèce. Cette présente étude a donc permis de i) connaitre la distribution spatio-temporelle de *S. sutor* sur le Grand Récif de Toliara ; ii) déterminer la variation du régime alimentaire de cette espèce au cours de sa croissance ; iii) identifier sa biologie reproductive et iv) de tester un élevage en milieu contrôlé.

## *1.* Caractéristiques générales de la bio-écologie de *Siganus sutor*

L'écologie de *S. sutor* suit des variations spatio-temporelles et ontogénétiques (Fig. 7.1). L'utilisation de l'habitat et le régime alimentaire chez *S. sutor* suit une trajectoire ontogénétique bien définie. Tout d'abord, les œufs de *S. sutor* adhésifs et fixés au substrat éclosent en larves planctoniques dérivantes. En grandissant, les larves rejoignent les zones côtières coloniser les récifs coralliens (Ben-Tuvia, 1966; De Souza, 1988). Après avoir passé plusieurs jours en pleine mer, les larves entament ensuite une migration vers des eaux moins profondes pour s'installer sur les récifs coralliens (Bell et al., 2009; Berenshtein, 2016; Lecaillon, 2004; Malpot et al., 2008). A Toliara, les post-larves de *S. sutor* sont connues pour s'installer sur le Grand Récif de Toliara (GRT) avec un gros pic de recrutement de novembre à décembre en saison chaude (Jaonalison et al., 2022).

Le présent travail a montré qu'après le franchissement de la grande barrière de corail, les post-larves pénètrent dans le lagon de Toliara pour coloniser les zones des herbiers marins. Les individus y resteront jusqu'au stade juvénile. Bien que certaines espèces de poissons marins sont connues pour passer leur stade de juvénile dans ou à proximité des mangroves (Abu El-Regal & Ibrahim, 2014; Kimirei et al., 2013; Sasekumar & Leh, 1992), très peu de juvéniles de *S. sutor* y ont été observés. Sachant que à Toliara, la marée est de type avec un fort marnage atteignant 3,6 durant les marées des vives-eaux (Chevalier et al., 2015). Cette forte exposition des mangroves pourrait expliquer l'absence des juvéniles de S. sutor dans les mangroves de Toliara. Les plus jeunes *S. sutor* ont été trouvés en abondance dans les zones des herbiers, notamment en face du village d'Ankilibe. Les dynamiques de recrutement des juvéniles révèlent une saisonnalité marquée, avec deux périodes distinctes de forte arrivée dans le lagon en janvier et en août (Ravelohasina, et al., (under review)). La zone des herbiers d'Ankilibe serait une zone de nourricerie des juvéniles de *S. sutor* qu'il serait souhaitable de protéger de manière saisonnière.

En grandissant, les juvéniles de *S. sutor* changent progressivement d'habitat, passant des herbiers vers des zones intermédiaires caractérisées par un mélange de patates de coraux et de d'herbiers marins. Ces habitats, présentant une profondeur moyenne assez faible (1,5 m de profondeur), accueillent des juvéniles mesurant entre 3 et 5 cm. Au cours de la croissance, les sub-adultes (10 à 20 cm) colonisent des zones plus profondes, jusqu'à 4,5 m, ainsi que la pente interne du récif barrière caractérisée par des fonds à herbiers et coraux.

Les juvéniles de *S. sutor* ont une alimentation mixte, se nourrissant essentiellement de macroalgues, de phanérogames avec une proportion importante de petits invertébrés benthiques. Les Siganidae regroupent des espèces essentiellement herbivores à l'âge adulte (Horn, 1989; Woodland, 1983) mais l'ingestion de proies animales semble essentiel pour la croissance des jeunes (Dunic & Baum, 2017; Pilati & Vanni, 2007). Les individus adultes consomment les mêmes types de proies mais avec une réduction de la proportion de proies animales, marquant une transition vers un régime essentiellement herbivore comme chez les autres Siganidae (Pillans et al., 2004; Zarco-Perello et al., 2024). A cette optique, l'ajout de source de protéine animale à la confection des aliments utilisés en aquaculture (comme le cas de l'aliment à base de laisse de mer) pourrait augmenter la performance de l'aliment en répondant aux besoins de l'espèce.

Au même titre que le dynamisme spatial de la distribution des juvéniles *S. sutor* dans le lagon de Toliara, leur régime alimentaire connait également une variation spatio-temporelle. En effet, la proportion des principaux types d'aliments comme les macroalgues diffèrent suivant les saisons. De plus, les individus habitant sur le récif ont montré une valeur isotopique différente de ceux dans les autres habitats. Cette variation est observée aussi bien chez les juvéniles que chez les adultes. Chez ces derniers, la quantité des macroalgues, phanérogames et invertébrés marins connait des variation inter et intra-saison.

La taille à la première maturité sexuelle de *S. sutor* a été déterminée à 20,84 cm (Longueur Totale) pour les femelles et 21,38 cm pour les mâles. Les individus adultes (22 à 46,7 cm) se rencontrent essentiellement sur le récif et sa pente externe, dans des zones plus profondes (jusqu'à environ 14 m), parfois jusqu'à une distance à plus de 100 m du récif. Cependant, nos captures ne nous permettent pas d'identifier si les adultes se nourrissent principalement dans le lagon ou sur la pente externe. Des travaux supplémentaires sont nécessaires pour identifier de potentiels déplacements journaliers dédiés à la recherche de nourriture. Des regroupements d'individus matures dans des habitats bien définis suggèrent également l'existence de sites potentiels de reproduction à proximité du GRT.

L'étude complémentaire de suivis des individus et de leur maturité sexuelle a permis de connaitre davantage sur la biologie reproductive de *S. sutor*. Cette espèce a un cycle de reproduction biannuelle avec des pics se produisant en saison fraiche (juillet) et en saison chaude (décembre à mars). Cette saisonnalité de reproduction s'aligne avec le recrutement des juvéniles de *S. sutor* avec un décalage d'environ un mois. Ce décalage correspondrait à la durée de vie larvaire, sachant que celle-ci serait comprise entre 30 et 35 jours selon Woodland (1990). Il est triste de constater que les juvéniles sont cibles de la pêche au chalut à moustiquaire dès leur arrivée sur la zone des herbiers (Behivoke et al., 2021; Jaonalison et al., 2022; Ranaivomanana et al., 2023).

Très peu d'études ont été faites sur la reproduction des poissons marins à Madagascar. Dans cette optique, ces résultats sur le cycle de reproduction et la taille à la maturité sexuelle du *S. sutor* serviront de base pour la gestion de cette espèce et pour les futures études sur d'autres espèces. De plus, l'étude portant sur le régime alimentaire des poissons marins basée sur la combinaison de l'analyse des contenus stomacaux et des isotopes stables pourra servir de référence.

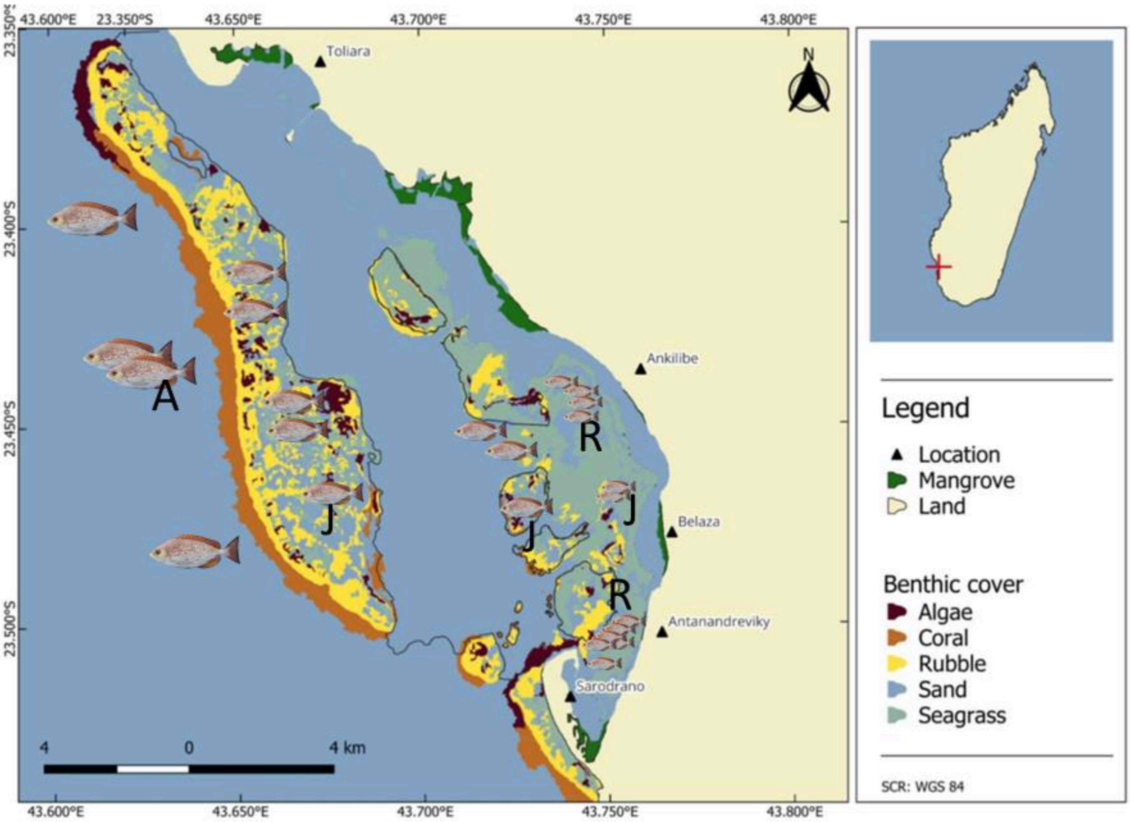


**Figure 7.1 :** Schéma synthétique de l'évolution écologique du *Siganus sutor*. *A : adultes, J : Juvéniles et R : recrutement*

## 2. Vers une aquaculture locale durable du *Siganus sutor* à Toliara

Les Siganidae sont appréciés comme source d'alimentation dans la région Indo-pacifique, y compris à Madagascar. Cependant, peu d'études ont été réalisée sur l'élevage de *S. sutor*, notamment en Afrique de l'Est. Cette étude est pionnière à Madagascar pour avoir expérimenté l'élevage de poisson de bouche marin. Une approche qui pourra aboutir à la promotion de l'élevage de *S. sutor*, dans le but de soutenir les populations naturelles de cette espèce par le biais de production commerciale ou de rempoissonnement (Fig. 7.2).

Toutes les informations recueillies sur le mode de vie des *S. sutor* pourront servir de base pour l'élaboration d'une pratique d'élevage efficace répondant aux besoins spécifiques de cette espèce. L'abondance des juvéniles de *S. sutor* capturés par le chalut à moustiquaire des pêcheurs a donné cette idée de lancement d'une aquaculture basée sur la capture. Durant les premiers essais d'aquaculture, il semble que *S. sutor* soit une espèce résistante vis-à-vis des conditions d'élevage par sa capacité à tolérer des variations des paramètres de l'eau d'élevage parfois en dessous des valeurs optimales de croissance et par sa facilité à s'adapter à différents types d'aliments. Cet aspect en fait de lui une espèce facilement domesticable.

Le régime omnivore des juvéniles *S. sutor* offre plusieurs possibilités en termes d'alimentation dans l'élevage de cette espèce. Cela a permis l'expérimentation sur quatre différents types d'aliments dont trois produits basés sur des ressources locales. L'aspect le plus remarquable réside dans l'utilisation de la laisse de mer, un matériau généralement négligé, abondant et peu coûteux pour constituer jusqu'à la moitié de la formulation de la provende. Cette valorisation ingénieuse de la laisse de mer, souvent considérée comme un déchet, devrait stimuler une véritable innovation circulaire. Elle offre une solution locale, économique et écologiquement responsable à la dépendance aux ingrédients importés ou onéreux. En plus de réduire les coûts de production, cette démarche pourrait contribuer à stimuler des filières locales autour de la collecte raisonnable, du traitement et de l'incorporation de la biomasse marine dans les aliments pour poissons. Cela ouvre la voie à une aquaculture plus résiliente, fondée sur les ressources locales et accessible aux petits producteurs. Cela implique l'optimisation de la formulation de l'aliments à base de laisse de mer (moins cher) par l'ajout de l'apport en protéine par l'élevage d'insecte par exemple.

Bien que ces trois types d'aliments présentent des résultats inférieurs à la provende industrielle en terme de croissance des cheptels, ils offrent un avantage particulier sur le taux de survie. Cela confirme encore la plasticité du régime alimentaire du *S. sutor* qui s'adapte très facilement au type de nourriture disponible comme reflété sur sa capacité d'adapter sa consommation en ses principales types nourriture au grès des saisons.

Ces travaux démontrent la faisabilité de la capture, du transport et de l'élevage en captivité des juvéniles jusqu'à une taille commercialisable (> 160 g) en cinq mois d'élevage. Dans ce contexte, cette thèse apporte des éléments concrets pour initier un modèle de production aquacole adapté aux réalités locales. La croissance acceptable observée, ainsi que la résilience de l'espèce aux conditions de captivité, confirment le potentiel de *S. sutor* pour l'aquaculture à petite échelle, notamment dans les zones côtières où l'espèce est déjà bien connue des communautés de pêcheurs. D'autant plus que des produits de l'élevage pourraient se vendre à un prix plus compétitif par rapport aux juvéniles vendus à moindre coût.

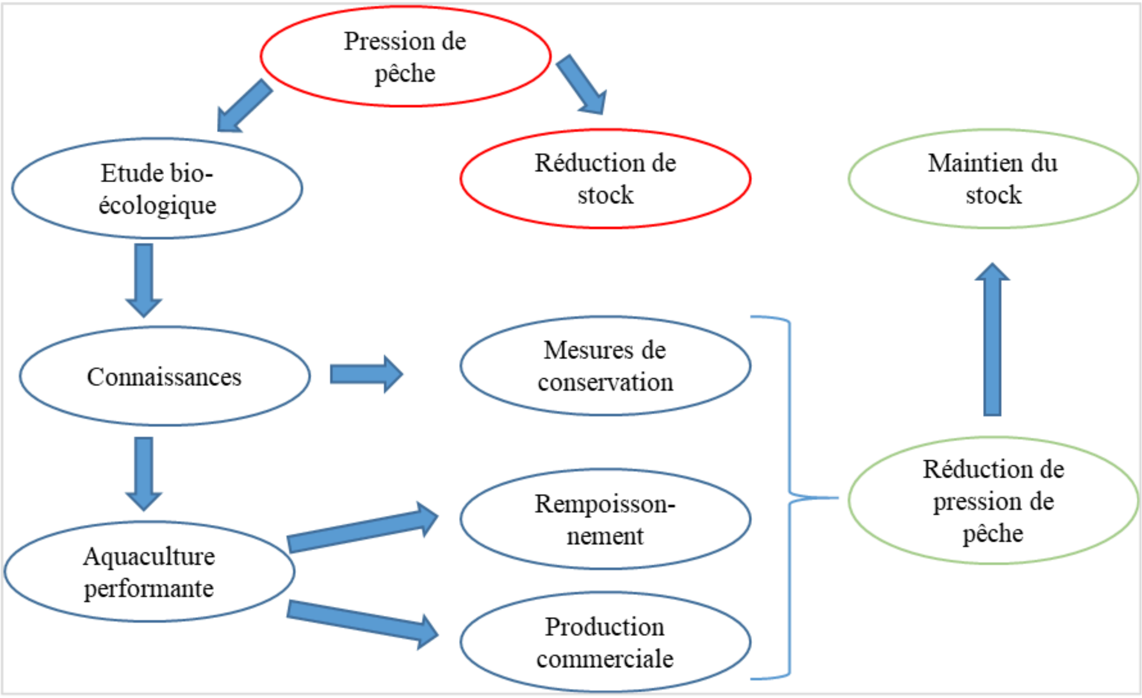


**Figure 7.2 :** Schéma récapitulatif des interactions entre bio-écologie, aquaculture et conservation

## 3. Implications pour la gestion durable des ressources halieutiques

Les résultats de cette thèse apportent des éléments concrets pour appuyer une gestion plus durable des ressources halieutiques, en particulier dans les zones côtières du sud-ouest de Madagascar. Les connaissances apprises sont essentielles pour mettre en place des mesures de gestion ciblées. En étudiant en profondeur la biologie et les dynamiques écologiques de *S. sutor*, ce travail offre des bases scientifiques solides pour mieux comprendre les périodes et les zones sensibles de l'espèce. Par exemple, les zones des herbiers sont essentielles à la croissance des juvéniles. Les périodes de recrutement représentent les moments avec la présence des individus de plus petite taille dans ces zones. Cela procure des données pour la conservation de cette espèce comme la délimitation d'aire marine protégé et ou de réserve temporaire qui serait fermée à la pêche durant les périodes pics de recrutement des juvéniles. En plus de cela, les données sur la reproduction de cette pourraient s'allier à cette prise de décision en limitant voire restreindre la pêche de cette espèce durant la période de reproduction. En complément, les résultats apportent des indications utiles pour déterminer la taille minimale de capture. Ces mesures de protection pourraient avoir des impacts notables sur le maintien du stock de *S. sutor* et bien d'autres espèces affiliées. Un complément en étude du stock naturel de cette espèce s'avère crucial afin de connaitre la production maximale équilibrée.

L'intégration de l'aquaculture raisonnée, telle qu'explorée dans cette thèse à travers des essais d'élevage fondés sur la capture de juvéniles, ouvre de réelles perspectives pour une gestion intégrée des ressources. Cette approche permettrait de réduire la pression sur les stocks sauvages tout en offrant des revenus complémentaires aux petits pêcheurs. En valorisant une espèce locale bien connue et acceptée par les communautés, elle représente une alternative réaliste et adaptée au contexte socio-économique de Toliara. Elle montre qu'il est possible de concilier conservation des ressources marines et développement économique, à condition de mettre en place un encadrement adéquat, un suivi écologique régulier et un accompagnement actif des acteurs locaux. Ainsi, cette étude constitue une base solide pour le développement de pratiques aquacoles responsables, en cohérence avec les dynamiques socio-écologiques des zones côtières du sud-ouest de Madagascar.

L'élevage sur la capture des juvéniles est une technique efficace déjà appliqué dans certaines régions du globe. Elle est plus facile à appliquer car n'a pas besoin de passer par un stade d'écloserie, une des parties les plus difficile à maitriser en aquaculture. Un exemple concret est l'élevage de Siganidae basé sur la capture dans des îles du Pacifique, cas du *Siganus argenteus*. Dans cet exemple, les juvéniles sont capturés sur la zone des herbiers et puis élevés sur des cages flottantes où les poissons sont élevés jusqu'à l'obtention d'une taille commercialisable.

Cette recherche rappelle également l'importance de croiser les savoirs : les connaissances scientifiques, lorsqu'elles sont partagées et discutées avec les pêcheurs, les techniciens et les gestionnaires, peuvent renforcer les stratégies de co-gestion des pêches. Elle montre que les pratiques traditionnelles et les observations locales sont précieuses, notamment pour identifier les zones de reproduction ou les périodes de forte présence d'individus adultes. La mise en place de mesures de gestion ne peut être efficace que si elle s'appuie sur une approche participative et sur la reconnaissance des réalités locales.

## 4. Limites de la thèse

Comme tout travail de recherche, cette thèse présente certaines limites qu'il est important de reconnaître, non pas comme des faiblesses, mais comme des points de vigilance et des opportunités pour de futurs approfondissements. Tout d'abord, les contraintes logistiques et financières ont limité la couverture spatiale et temporelle des échantillonnages. Les données sur les juvéniles et les adultes de *S. sutor* ont été collectés dans des zones précises de la baie de Toliara, ce qui ne permet pas d'extrapoler l'ensemble des résultats à d'autres régions côtières de Madagascar, où les conditions environnementales, les pressions de pêche ou les habitats peuvent différer. L'estimation de l'abondance des poissons a été faite en se basant sur les captures des pêcheurs. Une approche comme le comptage direct des poissons en apnée ou en plongée pourrait être un complément utile à l'étude de la distribution des espèces. Cette méthode pourrait apporter des informations sur la densité réelle des populations dans les habitats naturels, leur distribution spatiale, ainsi que sur les comportements d'évitement face aux engins de pêche, souvent invisibles dans les données de capture.

Par ailleurs, les études sur l'alimentation et l'habitat reposent principalement sur des méthodes de terrain (observations directes, prélèvements, analyses de contenus stomacaux et isotopiques), qui, bien qu'efficaces, restent ponctuelles et parfois sensibles à des biais saisonniers. Une surveillance à plus long terme, combinée à des techniques plus fines (comme la télémétrie ou les suivis automatiques), permettrait de mieux cerner les mouvements et les comportements de cette espèce au cours de son cycle de vie.

Concernant les essais en aquaculture, bien que les résultats soient prometteurs, ils ont été menés à petite échelle, et dans des conditions semi-contrôlées. Ces expériences ne reflètent pas encore les défis d'un élevage en circuit fermé ou à plus grande échelle, notamment en ce qui concerne la maîtrise de la reproduction, ou encore le risque de maladies. De plus, le contexte social, économique et culturel autour de l'aquaculture reste complexe, et nécessite des études complémentaires en sciences humaines pour garantir l'appropriation locale des innovations proposées.

Enfin, si la thèse a intégré des savoirs traditionnels et engagé un dialogue avec les communautés locales, le temps imparti n'a pas permis d'approfondir davantage cette approche participative. Or, un travail plus collaboratif et transdisciplinaire pourrait renforcer l'impact concret de la recherche sur le terrain.

Ces limites n'enlèvent rien à la valeur des résultats obtenus, mais rappellent que la compréhension d'un socio-écosystème aussi riche que celui de Toliara exige une approche patiente, continue et ouverte à la diversité des regards scientifiques et locaux.

## 5. Conclusion générale

Cette thèse s'est attachée à mieux comprendre la biologie, l'écologie et le potentiel aquacole du poisson *S. sutor*, une espèce clé des récifs coralliens de la région de Toliara. Nous avons pu mettre en lumière les dynamiques spatiales, temporelles et ontogénétiques qui caractérisent cette espèce, tout en explorant des solutions durables pour sa valorisation.

Nos résultats ont révélé des trajectoires écologiques bien définies chez *S. sutor*, avec des préférences d'habitats changeant avec les stades de développement, depuis les herbiers du lagon jusqu'aux zones plus profondes du récif barrière. De plus, *S. sutor* présente une reproduction prolongée, marquée par deux pics principaux dans l'année. Cette connaissance des périodes de ponte pourrait orienter la mise en place de mesures de protection saisonnières adaptées, contribuant ainsi à une gestion durable de l'espèce. Parallèlement, les essais d'aquaculture ont montré que des pratiques basées sur de capture raisonnée et d'élevage à faible coût sont possibles. Ces travaux soulignent que l'aquaculture, si elle est bien pensée et intégrée dans son environnement socio-écologique, peut devenir un levier concret pour atténuer la pression sur les stocks naturels tout en soutenant les moyens de subsistance des communautés locales. Au-delà des résultats scientifiques, ce travail propose une réflexion plus large sur la manière dont la recherche peut accompagner les transitions vers une gestion durable des ressources marines, en réunissant connaissances scientifiques, savoirs traditionnels et innovation locale.

Cette étude a soulevé plusieurs questions, ouvrant ainsi la voie à de nombreuses perspectives. Il serait utile d'approfondir les recherches sur la reproduction en captivité de *S. sutor* afin de poser les bases d'un élevage en circuit fermé. D'autres études pourraient explorer la formulation d'alimentation locale à meilleur performance pour réduire les coûts et les dépendances aux aliments industriels. Par ailleurs, une approche plus intégrée entre aquaculture, conservation et éducation à l'environnement permettrait de renforcer l'acceptation sociale et la durabilité des projets mis en place. Enfin, les résultats de cette thèse pourraient servir de base à des programmes de formation et de sensibilisation à destination des communautés locales, des jeunes et des professionnels de la région, pour faire de l'aquaculture une véritable opportunité de développement durable à Toliara et ailleurs. Ainsi, en raison de son importance écologique et socio-économique, *S. sutor* pourrait non seulement devenir un pilier de la conservation des poissons marins à Madagascar, mais aussi ouvrir la voie au développement d'une aquaculture de poisson marin durable.

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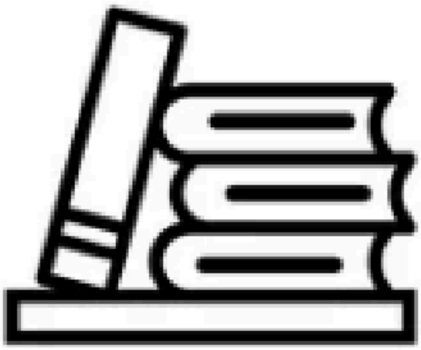

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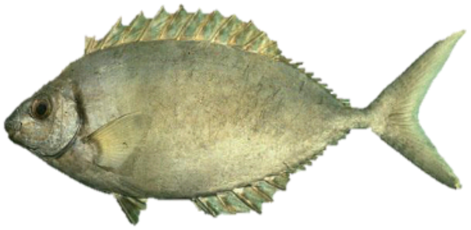
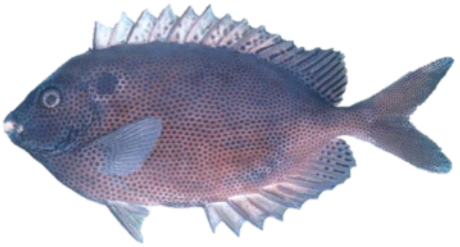
# Annexes

**Annexe 1 :** Photos des quatre espèces de Siganidae présentes à Toliara avec leurs noms vernavulaires malagasy. Source (Froese & Pauly, 2000)



*Siganus argenteus* (Amboramasaky)



*Siganus laqueus*
(Amboramasaky am-bohony)

*Siganus luridus* (Kely teraky)

*Siganus sutor* (Amboramasaky)

**Annexe 2 :** Abondance et taille des juveniles *Siganus sutor* capturés par mois et par habitat pour l'étude de la distribution

| Année | Mois | Habitat | Nombre | Longueur moyenne (LS en cm) | Ecart-type |
|---|---|---|---|---|---|
| 2021 | Juillet | Mangrove | 3 | 0.56 | 0.96 |
| 2021 | Juillet | Herbier | 88 | 2.99 | 1.52 |
| 2021 | Juillet | Zone intermédiaire | 3 | 3.80 | 3.41 |
| 2021 | Juillet | Platier récifal | 4 | 5.23 | 3.83 |
| 2021 | Août | Mangrove | 3 | 0.56 | 0.97 |
| 2021 | Août | Herbier | 2601 | 1.81 | 0.33 |
| 2021 | Août | Zone intermédiaire | 18 | 2.17 | 1.02 |
| 2021 | Août | Platier récifal | 5 | 2.25 | 1.92 |
| 2021 | Septembre | Mangrove | 0 | 0.00 | 0.00 |
| 2021 | Septembre | Herbier | 242 | 3.75 | 0.43 |
| 2021 | Septembre | Zone intermédiaire | 90 | 4.59 | 0.90 |
| 2021 | Septembre | Platier récifal | 57 | 4.59 | 0.46 |
| 2021 | Octobre | Mangrove | 5 | 1.15 | 1.05 |
| 2021 | Octobre | Herbier | 160 | 3.26 | 1.16 |
| 2021 | Octobre | Zone intermédiaire | 8 | 5.71 | 1.46 |
| 2021 | Octobre | Platier récifal | 47 | 6.70 | 1.41 |
| 2021 | Novembre | Mangrove | 3 | 1.06 | 1.84 |
| 2021 | Novembre | Herbier | 174 | 3.23 | 0.90 |
| 2021 | Novembre | Zone intermédiaire | 54 | 4.18 | 1.96 |
| 2021 | Novembre | Platier récifal | 42 | 4.33 | 2.05 |
| 2021 | Decembre | Mangrove | 3 | 1.75 | 1.55 |
| 2021 | Decembre | Herbier | 127 | 3.44 | 1.32 |
| 2021 | Decembre | Zone intermédiaire | 43 | 3.93 | 1.22 |
| 2021 | Decembre | Platier récifal | 31 | 4.86 | 1.96 |
| 2022 | Janvier | Mangrove | 0 | 0.00 | 0.00 |
| 2022 | Janvier | Herbier | 533 | 2.13 | 0.45 |
| 2022 | Janvier | Zone intermédiaire | 39 | 3.74 | 1.99 |
| 2022 | Janvier | Platier récifal | 26 | 7.41 | 2.54 |
| 2022 | Février | Mangrove | 39 | 2.36 | 0.48 |
| 2022 | Février | Herbier | 83 | 3.32 | 1.20 |
| 2022 | Février | Zone intermédiaire | 32 | 4.47 | 1.22 |
| 2022 | Février | Platier récifal | 4 | 3.93 | 3.06 |
| 2022 | Mars | Mangrove | 0 | 0.00 | 0.00 |
| 2022 | Mars | Herbier | 9 | 3.59 | 2.32 |
| 2022 | Mars | Zone intermédiaire | 38 | 4.44 | 1.35 |
| 2022 | Mars | Platier récifal | 61 | 6.03 | 1.98 |
| 2022 | Avril | Mangrove | 0 | 0.00 | 0.00 |
| 2022 | Avril | Herbier | 7 | 3.94 | 1.72 |
| 2022 | Avril | Zone intermédiaire | 32 | 5.74 | 1.48 |
| 2022 | Avril | Platier récifal | 6 | 6.23 | 1.48 |
| 2022 | Mai | Mangrove | 3 | 0.00 | 0.00 |

| | | | | | |
|---|---|---|---|---|---|
| 2022 | Mai | Herbier | 6 | 5.86 | 3.35 |
| 2022 | Mai | Zone intermédiaire | 3 | 0.00 | 0.00 |
| 2022 | Mai | Platier récifal | 6 | 5.01 | 3.94 |
| 2022 | Juin | Mangrove | 18 | 2.40 | 0.92 |
| 2022 | Juin | Herbier | 42 | 3.37 | 0.63 |
| 2022 | Juin | Zone intermédiaire | 9 | 3.50 | 0.38 |
| 2022 | Juin | Platier récifal | 49 | 3.57 | 0.64 |

**Annexe 3 :** Abondance et taille des adultes *Siganus sutor* capturés par mois pour l'étude de la distribution

| **Habitat** | **Site** | **Nombre** | **Longueur moyenne (LS en cm)** | **Ecart-type** |
|---|---|---|---|---|
| Patate récifale | Tandeolava | 2 | 11.95 | 2.05 |
| Patate récifale | Nosimboro | 15 | 17.48 | 3.65 |
| Patate récifale | Nosy tsena | 11 | 13.935 | 4.19 |
| Patate récifale | Beambitse | 4 | 15 | 4.19 |
| Patate récifale | Sakatelo | 25 | 15 | 2.45 |
| Patate récifale | Kely nosy | 26 | 17.28 | 0.35 |
| Pente externe | Noropasy | 2 | 36 | 2.04 |
| Pente externe | Fasindava | 5 | 36 | 2.06 |
| Pente externe | Norondriake | 3 | 30.5 | 1.91 |
| Pente externe | Ankororoaky | 4 | 33.33 | 1.52 |
| Pente externe | Befy | 7 | 29.95 | 4.35 |
| Pente externe | Lazizy | 12 | 22.15 | 2.00 |
| Pente externe | Fay | 8 | 32.33 | 4.24 |
| Pente externe | Tsakata | 5 | 34.5 | 2.12 |
| Pente externe | Ambanevera | 6 | 28.75 | 3.74 |
| Pente externe | Nanavina | 8 | 31 | 6.86 |

**Annexe 4 :** Différents aliments testés durant l'élevage de *Siganus sutor* et procédure de fabrication

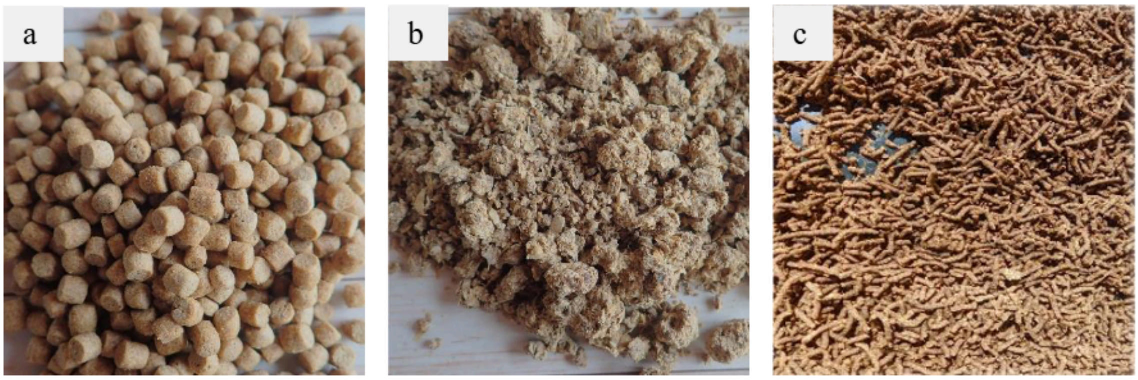


**Figure a1 :** Les différents aliments testés durant l'élevage de *Siganus sutor*. a : F1, b : F2, c : F4

La provende F1, produite par une entreprise privée, et acheté à la capitale (Antananarivo). Le riz a été cuite au laboratoire chaque jour. La provende F2 a été préparé en mélangeant différentes farines, détaillées dans le tableau 6.1, et agglomérées à l'aide d'un liant (farine de manioc). Le processus de préparation de l'aliment F4 s'est déroulé en plusieurs étapes (Fig. 6.9). D'abord, les ingrédients tels que la farine de soja, de maïs, de manioc, de poisson, d'arachide et huile de tournesol ont été mélangés au selon les proportions indiquées dans le tableau 6.3. Puis, de la laisse de mer a été collectée sur les plages aux alentours de la station de Belaza, puis transportées à la station pour la préparation. Une fois à la station, la laisse de mer a été triée pour éliminer les matière indésirables (plastic, morceau de bois, …). Ensuite elle a été rincée à l'eau de mer, égouttées et broyées. Le broyat a été dilué avec 0,5 litre d'eau de mer et cuit dans une casserole jusqu'à ébullition pour faciliter sa digestibilité. Après la cuisson, le produit a été étalé et séché pendant une journée au soleil. Le produit séché a ensuite été mélangé avec le mélange de farine et d'huile à une proportion de 50% chacun. Enfin, ce mélange a été extrudé avec une filière de 2.5 mm de diamètre pour avoir des granulés. Les granulés ainsi produits sont ensuite séchés au soleil pendant une journée et stockés dans une salle aérée et à l'abri du soleil avant d'être distribués au cheptel.

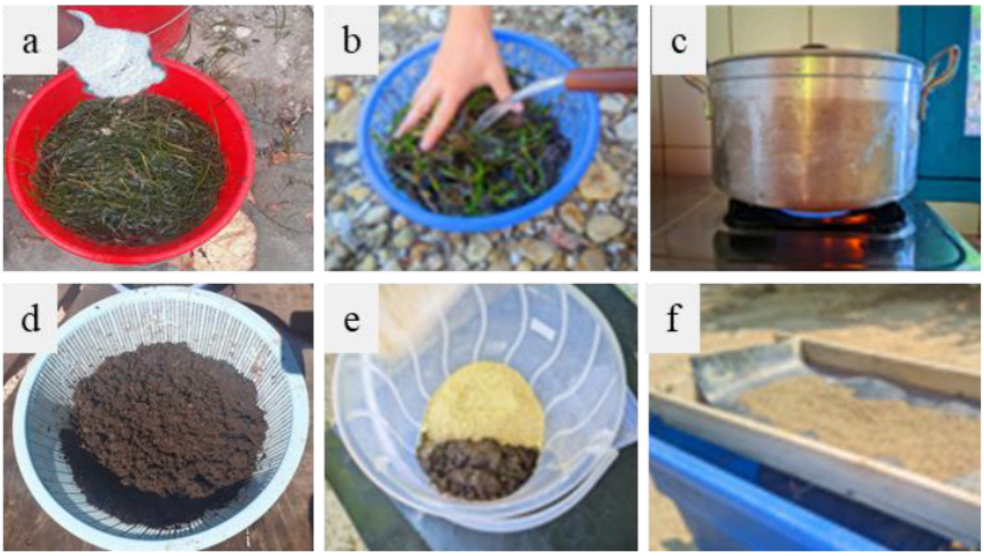


**Figure a2 :** Processus de fabrication de la provende à base de laisse de mer (F4)

**Annexe 5 :** Evolution du nombre, longueur moyenne et poids moyen des individus élevé en pré-grossissement

| Semaine | Aliment | Densité | Bac | Nombre | LS moyen (cm) | Poids moyen (g) |
|---|---|---|---|---|---|---|
| 07/02/2022 | F1 | D1 | Test | 20 | 3.28 | 0.92 |
| 07/02/2022 | F1 | D2 | Test | 50 | 3.26 | 0.82 |
| 07/02/2022 | F1 | D3 | Test | 80 | 3.1 | 0.8 |
| 07/02/2022 | F2 | D1 | Test | 20 | 2.99 | 0.59 |
| 07/02/2022 | F2 | D2 | Test | 50 | 2.91 | 0.64 |
| 07/02/2022 | F2 | D3 | Test | 80 | 3.09 | 0.72 |
| 21/02/2022 | F1 | D1 | Test | 18 | 3.54 | 1.14 |
| 21/02/2022 | F1 | D2 | Test | 50 | 3.46 | 1.15 |
| 21/02/2022 | F1 | D3 | Test | 80 | 3.21 | 1.06 |
| 21/02/2022 | F2 | D1 | Test | 15 | 3.06 | 0.73 |
| 21/02/2022 | F2 | D2 | Test | 50 | 3.28 | 0.78 |
| 21/02/2022 | F2 | D3 | Test | 80 | 3.33 | 0.88 |
| 07/03/2022 | F1 | D1 | Test | 17 | 3.95 | 1.61 |
| 07/03/2022 | F1 | D2 | Test | 50 | 3.81 | 1.71 |
| 07/03/2022 | F1 | D3 | Test | 80 | 3.56 | 1.43 |
| 07/03/2022 | F2 | D1 | Test | 12 | 3.15 | 0.85 |
| 07/03/2022 | F2 | D2 | Test | 50 | 2.85 | 0.72 |
| 07/03/2022 | F2 | D3 | Test | 80 | 3.2 | 0.88 |
| 22/03/2022 | F1 | D1 | Test | 15 | 3.5 | 2.12 |
| 22/03/2022 | F1 | D2 | Test | 50 | 4.43 | 6.41 |
| 22/03/2022 | F1 | D3 | Test | 0 | - | - |
| 22/03/2022 | F2 | D1 | Test | 11 | 3.6 | 1.21 |
| 22/03/2022 | F2 | D2 | Test | 50 | 3.43 | 1.09 |
| 22/03/2022 | F2 | D3 | Test | 80 | 3.7 | 1.35 |
| 06/04/2022 | F1 | D1 | Test | 13 | 5.44 | 4.19 |
| 06/04/2022 | F1 | D2 | Test | 50 | 5.18 | 3.68 |
| 06/04/2022 | F1 | D3 | Test | 0 | - | - |
| 06/04/2022 | F2 | D1 | Test | 11 | 3.9 | 1.66 |
| 06/04/2022 | F2 | D2 | Test | 50 | 3.74 | 1.33 |
| 06/04/2022 | F2 | D3 | Test | 0 | - | - |
| 07/02/2022 | F1 | D1 | Réplicat | 20 | 3.35 | 0.96 |
| 07/02/2022 | F1 | D2 | Réplicat | 50 | 3.12 | 1.02 |
| 07/02/2022 | F1 | D3 | Réplicat | 80 | 3 | 0.7 |
| 07/02/2022 | F2 | D1 | Réplicat | 20 | 2.79 | 0.53 |
| 07/02/2022 | F2 | D2 | Réplicat | 50 | 2.92 | 0.62 |
| 07/02/2022 | F2 | D3 | Réplicat | 80 | 2.89 | 0.68 |
| 21/02/2022 | F1 | D1 | Réplicat | 20 | 3.47 | 1.13 |
| 21/02/2022 | F1 | D2 | Réplicat | 30 | 3.41 | 1.17 |
| 21/02/2022 | F1 | D3 | Réplicat | 80 | 3.07 | 0.85 |
| 21/02/2022 | F2 | D1 | Réplicat | 15 | 2.9 | 0.71 |
| 21/02/2022 | F2 | D2 | Réplicat | 50 | 2.98 | 0.8 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 21/02/2022 | F2 | D3 | Réplicat | 80 | 2.92 | 0.69 |
| 07/03/2022 | F1 | D1 | Réplicat | 15 | 3.79 | 1.48 |
| 07/03/2022 | F1 | D2 | Réplicat | 24 | 3.85 | 1.5 |
| 07/03/2022 | F1 | D3 | Réplicat | 80 | 3.52 | 1.3 |
| 07/03/2022 | F2 | D1 | Réplicat | 14 | 2.9 | 0.76 |
| 07/03/2022 | F2 | D2 | Réplicat | 50 | 3.11 | 0.96 |
| 07/03/2022 | F2 | D3 | Réplicat | 80 | 3.25 | 0.89 |
| 22/03/2022 | F1 | D1 | Réplicat | 11 | 4.58 | 2.22 |
| 22/03/2022 | F1 | D2 | Réplicat | 22 | 4.28 | 1.88 |
| 22/03/2022 | F1 | D3 | Réplicat | 80 | 4.38 | 2.29 |
| 22/03/2022 | F2 | D1 | Réplicat | 13 | 3.33 | 0.92 |
| 22/03/2022 | F2 | D2 | Réplicat | 46 | 3.58 | 1.24 |
| 22/03/2022 | F2 | D3 | Réplicat | 80 | 3.21 | 1.16 |
| 06/04/2022 | F1 | D1 | Réplicat | 10 | 5.02 | 3.56 |
| 06/04/2022 | F1 | D2 | Réplicat | 22 | 5.38 | 4.32 |
| 06/04/2022 | F1 | D3 | Réplicat | 80 | 3.89 | 1.59 |
| 06/04/2022 | F2 | D1 | Réplicat | 9 | 3.44 | 1.27 |
| 06/04/2022 | F2 | D2 | Réplicat | 38 | 3.83 | 1.49 |
| 06/04/2022 | F2 | D3 | Réplicat | 80 | 3.87 | 1.53 |

**Annexe 6 :** Evolution du nombre, longueur moyenne et poids moyen des individus élevé en grossissement A

| Mois | Aliment | Bac | Nombre | LS moyen (cm) | Poids moyen (g) |
|---|---|---|---|---|---|
| Avril | F1 | Test | 128 | 6.42 | 7.09 |
| Avril | F3 | Test | 128 | 6.26 | 5.86 |
| Mai | F1 | Test | 128 | 7.93 | 14.44 |
| Mai | F3 | Test | 128 | 7.07 | 9.86 |
| Juin | F1 | Test | 128 | 9.22 | 20.26 |
| Juin | F3 | Test | 128 | 7.92 | 13.46 |
| Juillet | F1 | Test | 126 | 11.18 | 34.44 |
| Juillet | F3 | Test | 127 | 8.6 | 14.46 |
| Août | F1 | Test | 108 | 13.2 | 55.09 |
| Août | F3 | Test | 125 | 8.92 | 16.79 |
| Septembre | F1 | Test | 108 | 14.85 | 77.94 |
| Septembre | F3 | Test | 123 | 12.68 | 53.22 |
| Avril | F1 | Réplicat | 128 | 5.95 | 5.06 |
| Avril | F3 | Réplicat | 128 | 6.32 | 6.26 |
| Mai | F1 | Réplicat | 128 | 7.62 | 11.13 |
| Mai | F3 | Réplicat | 128 | 7.51 | 11.18 |
| Juin | F1 | Réplicat | 128 | 9.63 | 23.19 |
| Juin | F3 | Réplicat | 128 | 8.68 | 18.74 |
| Juillet | F1 | Réplicat | 126 | 11.33 | 35.6 |
| Juillet | F3 | Réplicat | 127 | 9.52 | 22.3 |
| Août | F1 | Réplicat | 0 | - | - |
| Août | F3 | Réplicat | 124 | 10.86 | 34.82 |
| Septembre | F1 | Réplicat | 0 | - | - |
| Septembre | F3 | Réplicat | 121 | 11.78 | 41.11 |

**Annexe 7 :** Evolution du nombre, longueur moyenne et poids moyen des individus élevé en grossissement A

| **Mois** | **Aliment** | **Bac** | **Nombre** | **LS moyen (cm)** | **Poids moyen (g)** |
|---|---|---|---|---|---|
| Avril | F1 | Test | 128 | 12.22 | 47.32 |
| Avril | F4 | Test | 128 | 10.28 | 27.6 |
| Mai | F1 | Test | 123 | 14.17 | 69.18 |
| Mai | F4 | Test | 120 | 10.88 | 32.87 |
| Juin | F1 | Test | 108 | 15.05 | 80.25 |
| Juin | F4 | Test | 114 | 11.86 | 43.29 |
| Juillet | F1 | Test | 95 | 15.93 | 96.2 |
| Juillet | F4 | Test | 110 | 12.54 | 48.43 |
| Août | F1 | Test | 87 | 16.79 | 111.58 |
| Août | F4 | Test | 106 | 13.26 | 56.18 |
| Avril | F1 | Réplicat | 128 | 12.89 | 56.1 |
| Avril | F4 | Réplicat | 128 | 10.85 | 29.62 |
| Mai | F1 | Réplicat | 113 | 14.84 | 80.88 |
| Mai | F4 | Réplicat | 124 | 11.21 | 33.78 |
| Juin | F1 | Réplicat | 108 | 15.81 | 102.3 |
| Juin | F4 | Réplicat | 116 | 11.82 | 40.82 |
| Juillet | F1 | Réplicat | 104 | 17.88 | 138.75 |
| Juillet | F4 | Réplicat | 112 | 12.27 | 44.33 |
| Août | F1 | Réplicat | 98 | 19.37 | 161.4 |
| Août | F4 | Réplicat | 109 | 13.29 | 50 |