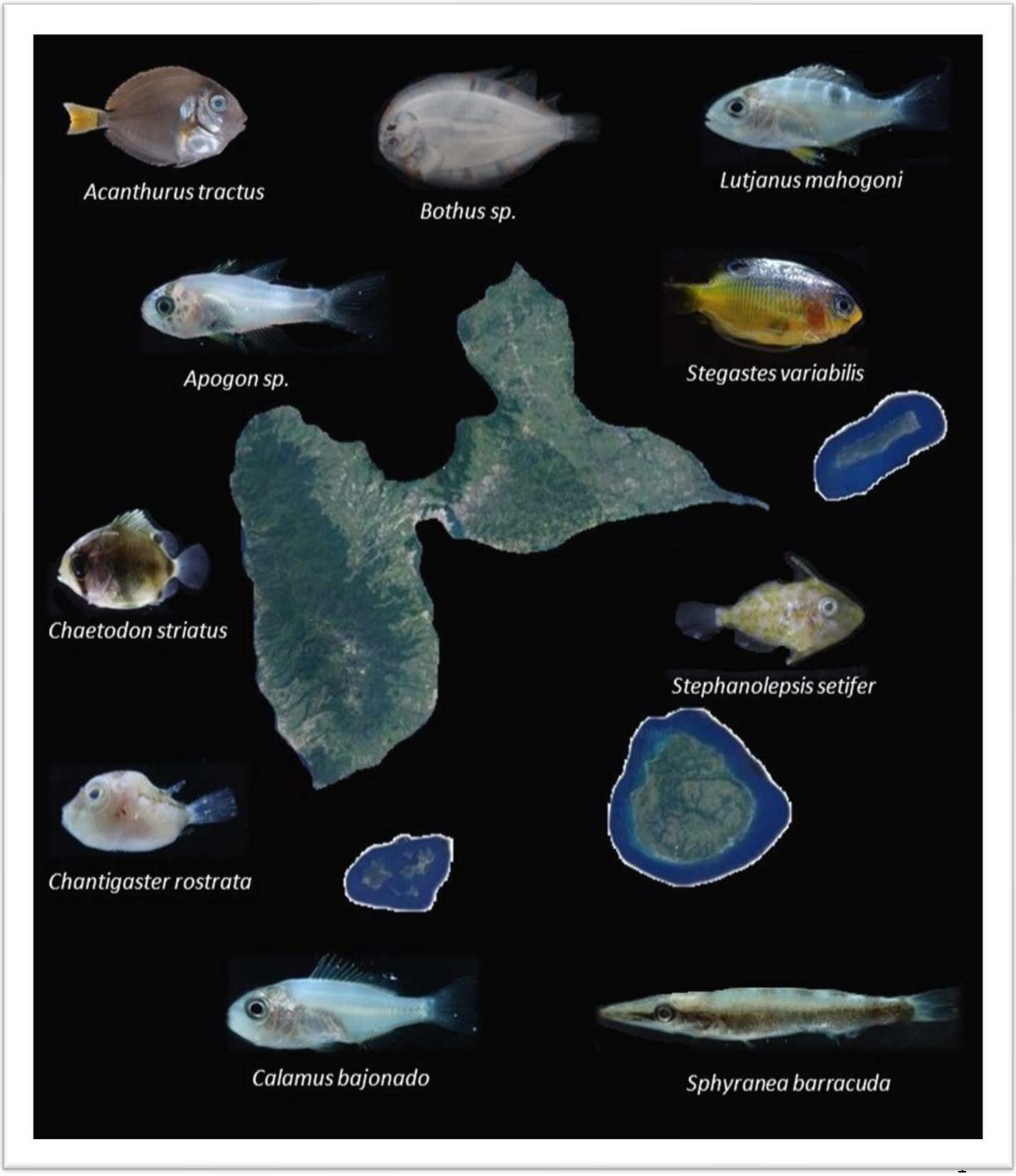
RECRUTEMENT ET MÉTAMORPHOSE DES POISSONS DE RÉCIFS DE LA GUADELOUPE.



Recrutement et métamorphose des poissons de récifs de la Guadeloupe.

Thèse de doctorat en physiologie et biologie des organismes – populations - interactions
présentée par VIGNAUD Léa, le 02 février 2024

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Résumé

Les poissons de récifs sont des organismes au cycle de vie complexe, du fait des nombreux processus et divers habitats utilisés. Ils fournissent de nombreux services écosystémiques et représentent une source importante de revenus pour les populations des îles à travers la pêche et le tourisme. Cependant, de nombreuses menaces pèsent sur les poissons de récifs comme la surpêche, la dégradation et la disparition de leurs habitats avec le changement climatique et les pressions d'origine anthropique.

L'objectif de cette thèse est d'apporter des nouvelles informations concernant le cycle de vie des poissons de récifs autour de l'île de la Guadeloupe, pour permettre une meilleure gestion et protection de ces organismes. Je commencerai par décrire la dynamique du recrutement (intégration des nouveaux individus dans la population adulte) autour de l'île ainsi que son influence sur le renouvellement des populations adultes. Ensuite seront abordés les changements d'habitats au cours de l'ontogénie chez plusieurs espèces, en utilisant une nouvelle méthode d'isotopie appliquée aux cristallins des yeux des poissons. Enfin, j'aborderai les changements morphologiques et alimentaires nécessaires à l'adaptation des poissons de récifs aux différents habitats occupés au cours de leur vie.

Les poissons de récifs de Guadeloupe recrutent tout autour de l'île, généralement pendant la saison humide. Cependant, un plus grand nombre d'individus juvéniles a été observé dans la Baie du Grand Cul-de-Sac Marin et sur la côte sud-ouest de la Basse Terre, où l'on trouve les récifs de type barrière et de type non-bioconstruits. En fonction des espèces et des sites étudiés, les variations et l'abondance des juvéniles peuvent permettre de prévoir celles des adultes de mêmes espèces, notamment pour des espèces commerciales comme *Sparisoma viride*. Au cours de l'ontogénie, certaines espèces de poissons de récifs peuvent utiliser des habitats appelés « zones de nourriceries » avant de rejoindre le récif une fois devenus adultes. Cependant, ces habitats n'étant pas présents uniformément autour de l'île, des changements d'histoire de vie peuvent être observés pour une même espèce entre différents sites d'étude. Parallèlement à ces changements d'habitats, les poissons de récifs changent aussi de morphologie et d'alimentation au cours de leur cycle de vie, et ces modifications sont propres à chaque espèce.

Mots clés : poissons de récifs – recrutement – changements ontogénétiques

Abstract

Reef fish are organisms with a complex life cycle, involving numerous processes and different habitats, leading to the renewal of adult populations. They provide many ecosystem services in coral reefs and are an important source of income for island populations through fishing and tourism. However, reef fish face several threats, including overfishing, habitat degradation and loss because of climate change and anthropogenic pressures.

The aim of this thesis is to provide new information on the life cycle of reef fish around the island of Guadeloupe, to enable better management and protection of these organisms. I will begin by describing the dynamics of recruitment (integration of new individuals into the adult population) around the island and its influence on adult populations. Then I'll look at habitat changes during ontogeny in several species, using a new method called isotopy applied to the crystalline lens of adult fish. Finally, I'll look at the morphological and dietary changes required to adapt to different habitats during the life of reef fish.

Reef fish on the island of Guadeloupe recruit all around the island, generally during the wet season. However, greater numbers of juveniles have been observed in the Baie du Grand Cul de Sac Marin and on the south-western coast of Basse Terre, where barrier and patch reefs are found. Depending on the species and sites studied, the variations and abundance of juveniles can be used to predict those of adults of the same species, particularly for commercial species such as Sparisoma viride. During ontogeny, certain species of reef fish may use habitats known as nursery areas before returning to the reef as adults. However, as these habitats are not present all around the island, changes in life history are observed for the same species between different sites. Associated with these changes in habitat, reef fish also change morphology and diet during their life cycle, and this is specific to each species.

Key words: reef fish - recruitment - ontogenetic changes

Avant-propos

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Articles en cours de préparation

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Communications orales et posters

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Boudault, M., Vignaud, L., Cordonnier, S., Frédérich, B., Dromard, C.R., Lecchini, D. (2022). Morphological variability of Ocyurus chrysurus in coral reefs of Guadeloupe (Lesser Antilles). Gulf and Caribbean Fisheries Institute (présentation de poster, distanciel).

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Introduction générale

Parmi les organismes associés aux récifs coralliens, il existe plus de 4000 espèces de poissons Téléostéens appelés communément « poissons de récifs », « poissons récifaux » ou « poissons coralliens » (Lieske & Myers, 1994 ; Allen, 2007). Les poissons de récifs sont dépendants de la présence des récifs coralliens qui se développent dans les zones chaudes de la bande intertropicale. Les récifs coralliens sont caractérisés par leur structure tridimensionnelle, principalement construite par des coraux Scléractiniaires, qui synthétisent leurs squelettes par accrétion de carbonate de calcium. D'autres Anthozoaires (par exemple, les alcyonaires et les gorgones) ainsi que les Hydrozoaires (par exemple *Millepora spp.*) contribuent également à former l'architecture complexe des récifs (Stoddart, 1969 ; Bellwood *et al.*, 2004). Les récifs coralliens de la Caraïbe peuvent être divisés en trois grand types : *i)* les récifs frangeants, qui se développent dans des eaux peu profondes et bordent étroitement la côte, ou en sont séparés par une étroite étendue d'eau, *ii)* les récifs-barrières qui se situent également parallèles à la côte mais en sont éloignés et séparés par la formation d'un lagon, et qui s'étendent sur de plus grandes distances et enfin, *iii)* les récifs dits « non-bioconstruits » qui sont des fonds rocheux, généralement issus d'une activité volcanique, supportant des communautés coralliennes (Goreau *et al.*, 1979 ; Bouchon *et al.*, 2008, DEAL, 2012). La biologie unique des coraux joue un rôle vital dans le cycle des nutriments au sein de la communauté récifale. En effet, bien que les eaux tropicales soient oligotrophes, et donc caractérisées par de faibles concentrations en sels nutritifs (nitrates, nitrites, ammoniaque et phosphates), les récifs coralliens ont des taux de fixation photosynthétique du carbone, de fixation de l'azote et d'accrétion calcaire parmi les plus élevés de tous les écosystèmes du monde. Cette grande productivité et les nombreux habitats disponibles au sein des structures coralliennes font des récifs coralliens un des écosystèmes les plus diversifiés au monde (Goreau *et al.*, 1979 ; Bellwood *et al.*, 2004).

En Guadeloupe, les formations coralliennes représentent une superficie de 158 km², avec plus de cinquante espèces de coraux dont des espèces emblématiques tels que les *Acropora cervicornis*, *Acorpora palmata*, *Orbicella annularis* ou encore *Mycetophyllia lamarckiana* (Bouchon & Laborel, 1990 ; Andréfouët, 2008 ; Magnin, 2018). Dans le Grand Cul-de-Sac Marin, les formations coralliennes forment une barrière récifale de 29 km de long ainsi que de larges récifs frangeants bordant la côte à l'est de la baie. Les fonds sous-marins des côtes ouest et sud de la Basse-Terre, en revanche, abritent des récifs non-bioconstruits, dont la biodiversité est la plus élevée de l'île. Enfin, la côte sud de la Grande Terre est représentée par une ligne discontinue de récifs frangeants (Bouchon *et al.*, 2008 ; Magnin, 2018). Dans la caraïbe, les poissons de récifs regroupent environ 600 espèces dont 450 recensées sur les côtes de la Guadeloupe. Ces communautés ichtyologiques sont caractérisées par des stratégies reproductives, des comportements, des morphologies et des stratégies alimentaires extrêmement diversifiés (Blanchet *et al.*, 2015 ; Ghilardi *et al.*, 2021 ; Ifrecor, 2021).

Les poissons de récifs ont un cycle de vie complexe, divisé en différents stades ontogénétiques et se déroulant dans différents environnements : le milieu pélagique océanique et le milieu benthique dans les récifs ou les écosystèmes associés (Leis *et al.*, 1996; Hixon, 1998). La majorité des espèces se reproduisent et libèrent leurs gamètes dans la colonne d'eau, généralement lors d'événements agrégatifs de reproduction. Dans certains cas en revanche, les pontes peuvent être benthiques et les œufs sont alors protégés par un parent, comme pour certaines espèces de Pomacentridae par exemple. Dans les deux cas, l'embryon se développe dans l'œuf jusqu'à l'obtention de traits morphologiques relatifs à une larve, avant d'être libéré dans le milieu lors de l'éclosion (Richard & Lindeman, 1987 ; Bobe & Labbé, 2010). Le stade larvaire est le premier stade de vie après l'éclosion (Pittman *et al.*, 2013) et se déroule dans le domaine pélagique océanique (Richard & Lindeman, 1987). Le terme de « larve » fait référence aux organismes qui présentent des spécificités pour la vie pélagique : contrôle de la flottabilité (modulation de la vessie natatoire), de la capacité de nage (développement de la nageoire caudale) et de l'orientation (en utilisant divers indices tels que les variations de température, la lumière, la pression, la salinité ou la gravité) (Richards & Lindeman, 1987). Les larves ont la capacité de se disperser dans la colonne d'eau grâce aux courants et en utilisant leurs capacités de nage. Dans l'étude de Fisher *et al.* (2000), les larves utiliseraient leur capacité natatoire dès cinq jours après leur éclosion, ce paramètre diffère en fonction des espèces. Les larves peuvent rester de quelques jours à plusieurs mois en pleine mer, période durant laquelle la larve passe par différents stades larvaires et durant laquelle elle contribue à la dispersion de sa population dans le milieu naturel (Victor *et al.*, 2010). Les larves « compétentes » correspondent aux individus qui ont atteint leur dernier stade de développement larvaire (Fisher *et al.*, 2000) et qui se distinguent par le développement d'une plus grande capacité natatoire avec des trajectoires non aléatoires dans la colonne d'eau (Leis, 1997 ; Wolanski *et al.*, 1997 ; Leis & Carson-Eward, 2003). Grâce à ces caractéristiques, elles ont la capacité de se déplacer vers les récifs coralliens ou des zones de « nourricerie » (herbiers, mangroves) dans le but de s'y installer (Stobutski & Bellwood, 1994, 1997) (Figure 1). Les sens olfactif, auditif et visuel sont utilisés par les larves compétentes pour s'installer dans leur premier habitat benthique. Comme décrit dans la synthèse bibliographique de Barth *et al.* (2015), plusieurs études ont déjà démontré quels étaient les repères chimiques principalement utilisés par les larves pour trouver un habitat benthique adéquat (Atema *et al.*, 2002 ; Lecchini & Nakamura, 2013), pour retrouver des congénères (Lecchini *et al.*, 2007) ou pour éviter les prédateurs (Dixson *et al.*, 2012). De même, les résultats de deux études mettent en avant le fait que les larves de poissons de récifs sont attirées par les signaux acoustiques des habitats coralliens au moment de leur retour à la côte (Parmentier *et al.*, 2015a), mais que le gradient sonore du récif ne serait détectable par les larves de poissons qu'à des distances inférieures à quelques kilomètres (Parmentier *et al.*, 2015b). Enfin, la détection visuelle des congénères par les larves pendant la journée et les nuits claires a été décrite par Lecchini *et al.* (2014) sur des larves *d'Acanthurus triostegus*. Lorsqu'elles ont trouvé un habitat propice, les larves compétentes s'installent sur le récif, ou un habitat associé, en passant par-dessus la crête récifale, ce qui correspond au processus de « colonisation ». Cette action n'est pas constante dans le temps : elle se produit généralement de nuit, avec des abondances maximales plus souvent en période de nouvelle lune, mais cette dynamique diffère selon les espèces, les mois de l'année et les sites d'études (Dufour & Galzin, 1993 ; Caley, 1993 ; Lecaillon & Lourié, 2007). La colonisation nocturne permet de diminuer la pression de prédation qui peut être très importante lors de l'arrivée des larves dans les écosystèmes côtiers peu profonds (Dufour & Galzin, 1993 ; Dufour & Lo-Yat, 1996 ; Almany & Webster, 2006). Une fois que les individus ont atteint une taille d'évitement (taille à laquelle ils sont moins vulnérables face à la prédation), ils rejoignent le milieu récifal, contribuant ainsi à l'augmentation de la biomasse ichtyologique à l'échelle d'un récif (Parish, 1989 ; Nagelkerken *et al.*, 2001 ; Adams *et al.*, 2006 ; Nagelkerken *et al.*, 2000 ; Mumby *et al.*, 2004). Cette intégration des nouveaux individus dans la communauté adulte est appelée « recrutement ». Les juvéniles peuvent recruter sur leur lieu de naissance et intégrer la population adulte dont ils sont issus, il s'agit alors « d'auto-recrutement ». En revanche, si les individus intègrent une population adulte différente de celle dont ils sont issus, il s'agit « d'allo-recrutement » (Lecchini & Galzin, 2003 ; Green *et al.*, 2015). Entre l'étape de colonisation larvaire et de recrutement, les individus entament une métamorphose au cours de laquelle ils passent d'individus adaptés à la vie pélagique à d'autres parfaitement adaptés à la vie benthique et récifale. La métamorphose débute ainsi au stade de larve compétente et se termine au stade juvénile, et représente un processus clé du cycle de vie des poissons de récifs (Holzer *et al.*, 2017 ; Roux *et al.*, 2019). Ce processus est associé à des modifications morphologiques telles que des changements dans la coloration, la forme du corps, le changement de position des nageoires et des yeux, la formation d'écailles ou la mise en place d'adaptations osmorégulatrices

(Bishop *et al.*, 2006 ; Braverman *et al.*, 2020). Elle est régulée la plupart du temps par des facteurs internes : le déterminisme génétique ou des signaux chimiques, tels que les hormones thyroïdiennes (Deal & Volkoff, 2020). La métamorphose peut également être influencée par des facteurs environnementaux comme la température de l'eau ou des interactions avec les congénères (McCormick et Molony,1995 ; Vissio *et al.*, 2021). Une fois métamorphosé, le juvénile partage la plupart des traits morphologiques, physiologiques et écologiques d'un adulte, mais n'est cependant pas reproducteur contrairement aux adultes (Osenberg *et al.*, 1992 ; Bishop *et al.*, 2006) (Figure 1).

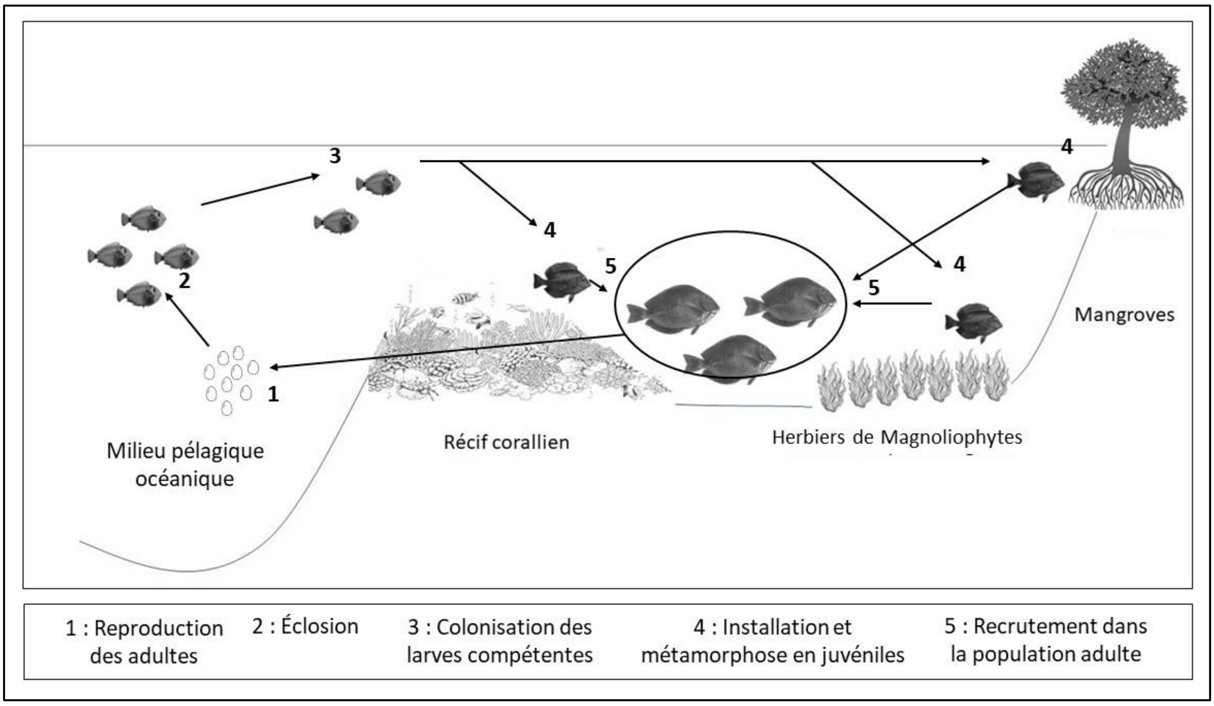


Figure 1 Schéma récapitulatif du cycle de vie des poissons de récifs.

De nombreuses données existent sur le cycle de vie des poissons de récifs dans la Caraïbe, notamment sur les processus de métamorphose et de recrutement. Ces études ont été essentiellement menées au Panama, dans les Iles Vierges américaines, en Jamaïque ou à la Barbade. Parmi les sujets principaux : l'importance du développement et de la survie des individus aux premiers stades dans le renouvellement des populations de poissons (Victor, 1983 ; Kaufman *et al.*, 1992 ; Robertson 1992 ; Sponaugle & Cowen, 1996 ; Bergenius *et al.*, 2002 ; Hamilton, 2008), la menace de prédation et le taux de mortalité au moment de ces deux processus clés (Shulman & Ogden, 1987 ; Beets, 1997 ; Searcy & Sponaugle, 2001), les variabilités temporelles dans l'apparition de la métamorphose (Kaufman *et al.*, 1992 ; Searcy

& Sponaugle, 2000), les dynamiques spatiales et/ou temporelle dans le processus de recrutement (Shulman, 1985 ; Booth & Beretta, 1994 ; Tupper & Hunte, 1994 ; Caselle & Warner, 1996 ; Sponaugle & Cowen, 1997 ; Tolimieri *et al.*, 1998 ; Valles *et al.*, 2008, 2009), et enfin la détermination de la durée de vie larvaire (Robertson *et al.*, 1988 ; Robertson, 1990 ; Robertson *et al.*, 1993).

En Guadeloupe, les poissons des récifs coralliens ont également été le sujet de nombreuses études, cependant peu ont été menées sur les premières étapes de leur cycle de vie comme la métamorphose ou le recrutement. En effet, les études concernant les poissons de récifs ont porté sur le suivi spatio-temporel des communautés adultes ou des études ciblées sur certaines espèces d'intérêt écologique ou économique (Bouchon-Navaro, 1997 ; Bouchon *et al.*, 1994 ; Gobert, 2000 ; Vaslet *et al.*, 2009 ; Kopp *et al.*, 2010b ; Dromard *et al.*, 2016 ; Dromard *et al.*, 2018). Par ailleurs, une seule étude a été menée sur la colonisation des larves de poissons de récifs, ce qui a permis d'apporter des données conséquentes sur la dynamique de colonisation et le lien entre colonisation et les facteurs environnementaux influants (Fréjaville, 2007). Malheureusement, cette étude n'a été réalisée que sur un seul site d'étude (Ilet du Gosier). Les précédentes études renseignent donc sur les poissons de récifs au moment de la colonisation, ou après la métamorphose, c'est-à-dire sur les stades juvéniles et adultes. Aucune étude ne décrit directement la dynamique de renouvellement des populations, en considérant la pluralité des récifs coralliens autour de la Guadeloupe. Dans le premier chapitre de cette thèse, je présenterai ainsi la dynamique spatiale et temporelle du recrutement de plusieurs espèces de poissons de récifs autour de l'île ainsi que l'influence de ce recrutement sur les populations adultes de même espèce, grâce aux données issues d'un suivi sous-marin que j'ai réalisé durant 12 mois.

Après la colonisation, l'installation des larves peut s'effectuer directement sur le récif (généralement sur la partie peu profonde) ou dans des zones de nourricerie, qui serviront de zones de transition au cours du cycle de développement des poissons de récifs. Ces zones de nourricerie sont connues pour favoriser la croissance et la survie des juvéniles de poissons, mais aussi d'autres organismes du récif tel que les invertébrés benthiques. Ces zones apportent des ressources alimentaires ainsi que des abris contre les prédateurs (Odum & Heald, 1972 ; Carr & Adams, 1973 ; Parrish, 1989). Le passage transitionnel des poissons par des zones de nourricerie permet donc de favoriser leur croissance et de réduire la mortalité des juvéniles (Adams *et al.*, 2006). En Guadeloupe, en plus des formations coralliennes, deux écosystèmes côtiers se répartissent autour de l'île et sont connus pour jouer le rôle de zones de nourricerie :

les herbiers de Magnoliophytes marines et les mangroves (Chauvaud *et al.*, 2001). Les herbiers de Magnoliophytes marines forment des prairies marines en eaux peu profondes. Ils sont essentiellement constitués des espèces *Thalassia testudinum* et *Syringodium filiforme* (Mege & Delloue, 2007). Ils constituent l'écosystème marin le plus étendu à l'échelle de l'archipel puisqu'ils couvrent environ deux fois plus de surface que les récifs coralliens. On les trouve notamment dans la baie du Grand Cul-de-Sac Marin (De Battisti *et al.*, 2015). Ces herbiers jouent plusieurs rôles écologiques majeurs. Tout d'abord, ils sont décrits comme zones de nourricerie favorisant le développement et la survie des juvéniles de poissons de récifs (Baelde, 1990 ; Kopp *et al.*, 2010a). Ensuite, ils servent d'habitat et apportent des sources de nourriture pour les peuplements de poissons et de nombreux macro-invertébrés tels que les oursins blancs (*Tripneustes ventricosus*), les lambis (*Aliger gigas*) ou les étoiles de mer (*Oreaster reticulatus*) (Baelde, 1990 ; Mege & Delloue, 2007 ; Kopp *et al.*, 2010a). Parallèlement, les mangroves sont nombreuses en Guadeloupe. En effet, 42% des mangroves de l'arc insulaire des Petites Antilles sont localisées en Guadeloupe (Spalding *et al.*, 1997). Les mangroves sont composées principalement de palétuviers, représentés par plusieurs espèces qui se succèdent du front de mer vers l'intérieur de la formation végétale (Imbert *et al.*, 1988). Il existe quatre types de formation de mangroves en Guadeloupe, dont la mangrove en « ceinture côtière » qui est étroitement liée aux récifs coralliens. Ce type de mangrove, formée presque exclusivement de palétuviers rouges *Rhizophorae mangle,* borde immédiatement le lagon (Roussel, 2007). Les mangroves sont localisées essentiellement dans le fond de baie du Grand Cul-de-Sac Marin, ainsi que dans la baie du Petit Cul-de-Sac Marin (Bouchon *et al.*, 2008). Ces écosystèmes côtiers sont d'une importance capitale en Guadeloupe puisqu'ils abritent une centaine de poissons de récifs (Ifrecor, 2021). Les études précédemment menées sur l'utilisation de ces différents habitats côtiers par les poissons en Guadeloupe, se sont concentrées sur les assemblages de juvéniles et d'adultes (Baelde, 1990 ; Aliaume, 1990 ; Blanc *et al.*, 2001 ; Kopp *et al.*, 2010a ; Kopp *et al.*, 2012), mais aucune n'a été menée sur les premiers stades de vie des poissons, ni leur importance dans le processus de recrutement. Dans le second chapitre de cette thèse, je proposerai de retracer d'histoire de vie des poissons de récifs et l'utilisation qu'ils font des divers habitats côtiers par l'analyse des trajectoires isotopiques de leur cristallin.

Les poissons de récifs présentent une grande diversité morphologique et anatomique, en ce qui concerne la forme de leur corps ou celle de leurs organes (Ghilardi *et al.*, 2021). La morphologie générale est généralement liée au régime alimentaire ainsi qu'à l'éthologie des poissons (par exemple s'ils doivent se déplacer entre les coraux ou s'il restent dans la colonne d'eau). Les poissons herbivores ont généralement le tube digestif plus long que celui des carnivores, la bouche des poissons planctonophages est généralement supère (c'est-à-dire ouverte vers le haut) tandis que celle des invertivores est plutôt infère (ouverte vers le bas) (Boyle & Horn, 2006). La forme des dents et de la cavité buccale sont également de bons indicateurs du régime alimentaire et varient de façon importante chez les poissons récifaux. De même, la forme et la position des nageoires pectorales sont reliées à l'efficacité de nage et la manœuvrabilité des poissons sur le récif (différente entre les poissons occupant les zones les plus proche du récif, et ceux qui dominent la colonne d'eau ou les habitats peu profonds soumis aux courants) (Wainwright *et al.*, 2002). Un autre exemple concerne la forme des yeux, et notamment le diamètre oculaire, qui diffère considérablement entre les espèces diurnes et nocturnes (Goatley & Bellwood, 2009). La diversité morphologique des espèces de poissons de récifs varie également entre les stades de développement. Ainsi, de nombreuses espèces changent de forme et/ou de couleur (ou de livrée) au cours de leur développement. Un bon exemple est la girelle à tête bleue *Thalassoma bifasciatum*, un des poissons les plus communément rencontrés dans les récifs de la Caraïbe (Figure 2). Les individus juvéniles présentent un dos jaune et un ventre blanc divisé par une bande latérale noire. Plus l'individus grandit, plus la bande noire s'éclaircie pour donner lieu à une série de taches rectangulaires. Enfin, l'adulte mâle possède une tête bleue suivie de deux bandes noires verticales, séparées par une étroite bande blanche ou pâle juste derrière les pectorales. La moitié arrière du corps varie en couleur du jaune-vert au bleu (Ehrlich, 1975).

Figure 2 Photographies illustrant les changements de livrées qui apparaissent au cours du développement chez A) *Thalassoma bifasciatum*, B) *Sparisoma aurofrenatum*, C) *Stegastes variabilis*.

La richesse des sources de nourritures présentes sur les récifs a pour conséquence l'occurrence d'une diversité de régimes alimentaires chez les poissons coralliens (Ghilardi *et al.*, 2021) (Figure 3). Les poissons chirurgiens (Acanthuridae), les poissons perroquets (Scaridae), mais aussi de nombreuses espèces de poissons demoiselles (Pomacentridae) et de gobies (Gobiidae) sont des herbivores, c'est-à-dire qu'ils se nourrissent en majeure partie (plus de 50%) de matériel végétal et notamment de gazon algal. D'autres espèces sont classées comme carnivores de premier ordre (C1) ou invertivores. Parmi ces espèces, il est possible de regrouper les consommateurs de zooplancton (espèces zooplanctonophages), comme les poissons soldats ou poissons écureuils (Holocentridae) ainsi que certaines espèces de demoiselles. Les organismes sessiles du récif, comme les éponges ou les vers Annélides, sont consommés par les poissons anges (Pomacanthidae) et poissons papillons (Chaetodontidae), tandis que les Mollusques (bivalves ou gastéropodes), les oursins, les crabes et autres invertébrés représentent des proies privilégiées pour de nombreuses espèces de girelles (Labridae), de diodons (Diodontidae) ou de balistes (Balistidae). Ce régime alimentaire est possible grâce à des adaptations anatomiques des espèces concernées qui sont alors capables d'écraser les carapaces et les coquilles de leurs proies avec leurs puissantes mâchoires ou leurs dents pharyngiennes, ou de projeter leurs proies contre des roches pour en extraire la partie consommable (*cf.* Balistidae). Les poissons nettoyeurs sont également des carnivores de premier ordre, en consommant les ectoparasites installés sur d'autres organismes, comme les juvéniles de girelle *Thalassoma bifasciatum*, *Microspathodon chrysurus*, de *Bodianus rufus*, ou encore certaines espèces de gobies. Les carnivores de deuxième ordre (C2) sont les poissons de récifs qui consomment des invertébrés mais aussi d'autres espèces de poissons. Ces carnivores sont représentés par les familles des Haemulidae, Lutjanidae et Holocentridae par exemple (Randall, 1967). Enfin, les piscivores ou prédateurs sont des poissons ne consommant que d'autres espèces de poissons, tels que les barracudas (Sphyraenidae ou les Aulostomidae, par exemple) (Figure 3). Ces différents niveaux trophiques permettent de classer les poissons de récifs en plusieurs groupes fonctionnels, c'est-à-dire des ensembles d'espèces qui remplissent des fonctions essentielles sur le récif (Steneck & Dethier, 1994 ; Mooney *et al.*, 1996), comme le maintien des équilibres écologiques au sein de l'écosystème récifal (par exemple relations proies-prédateurs ou régulation des algues, Belwood *et al.*, 2004).

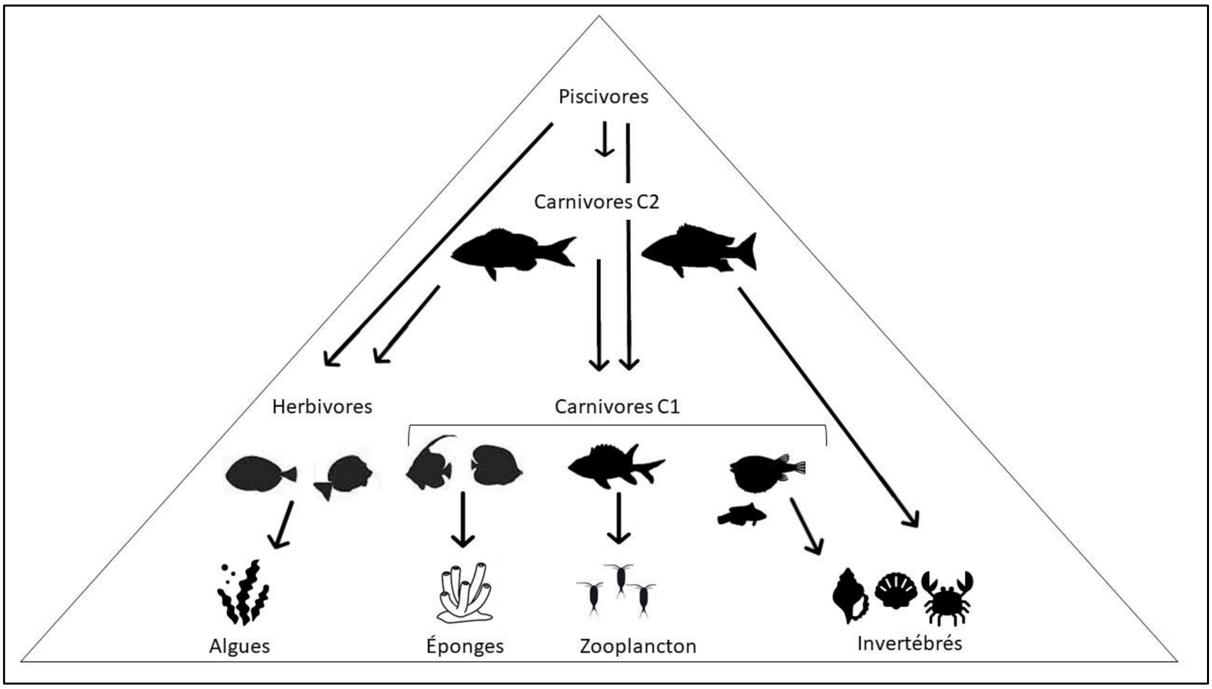


Figure 3 Schéma simplifié de la chaîne alimentaire des poissons de récifs.

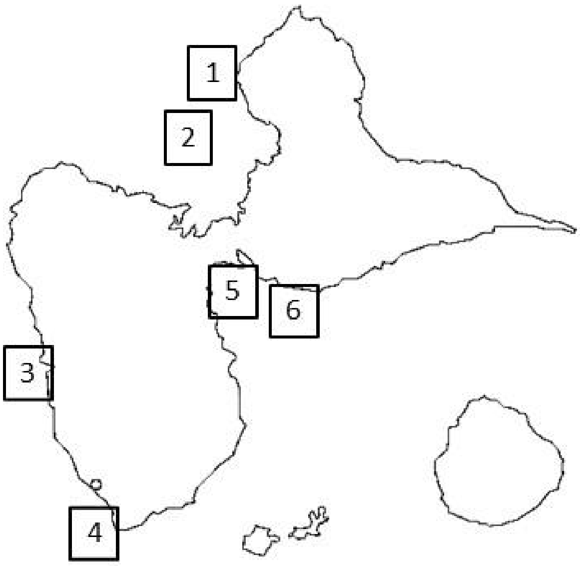
Le régime alimentaire des espèces récifales varie au cours des différentes phases de développement. L'approche isotopique est un outil particulièrement intéressant pour mettre en évidence les changements de niches trophiques chez les poissons, et peu d'étude ont porté jusqu'à présent sur l'étude des niches isotopiques dans le contexte du développement ontogénétique des poissons de récifs. Le dernier chapitre de cette thèse abordera ainsi l'étude des changements de forme du corps, par une approche morphométrique, et du régime alimentaire par une approche isotopique, au cours de l'ontogénie de différentes espèces de poissons de récifs.

Outre leur importance écologique, les poissons de récifs représentent aussi une source de revenus financiers importante pour de nombreuses populations humaines vivant proches des côtes (Allison *et al.*, 2009), par le biais du tourisme par exemple, et apporte surtout une sécurité alimentaire vitale (Moberg & Folke, 1999). Plus d'un milliard de personnes bénéficient directement des ressources des récifs coralliens pour se nourrir et vivre des activités liées à la pêche et au tourisme (Burke e*t al.*, 2011). En Guadeloupe et en Martinique, la pêche sur les récifs procurait déjà au début des années 2000, quelques 3 000 emplois pour la population. Le secteur est resté pendant plusieurs années sur un modèle de pêcherie artisanale au circuit de commercialisation très court (Caillart, 2002).

Malgré leur importance, les poissons de récifs subissent de nombreuses menaces directes ou indirectes, lorsque ces dernières impactent leurs lieux de vie, par exemple tel que les récifs coralliens, les mangroves ou encore les herbiers marins. En effet, les récifs coralliens font partie des écosystèmes les plus menacés, principalement en raison de dégradations d'origine anthropique (Jackson *et al.*, 2001), mais aussi du fait du changement climatique mondial (Hoegh-Guldberg *et al.*, 2007 ; Hughes *et al.*, 2007). En 2011, déjà 60% des récifs coralliens de la planète étaient considérés comme menacés de disparition (Burke *et al.*, 2011). La surpêche menace aussi les poissons des récifs coralliens dans de nombreuses régions du monde, et peut engendrer des déséquilibres écologiques majeurs comme le phénomène de « coral-algal phase-shift » (Bellwood *et al.*, 2004 ; Mumby *et al.*, 2006).

Les poissons de récifs ont une importance écologique et économique majeure. La complexité de leur cycle de vie, se déroulant en plusieurs phases dans divers écosystèmes en font cependant des individus difficiles à protéger face aux menaces grandissantes. L'objectif de cette thèse, intitulée « Recrutement et métamorphose des poissons de récif sur le littoral de la Guadeloupe », est donc d'apporter de nouvelles informations sur les mécanismes du cycle de vie des poissons récifs qui mènent au renouvellement des populations sur l'île de la Guadeloupe. Ces informations pourront aider à la mise en place de mesures de protection et de gestion des poissons de récifs, afin d'allier conservation et utilisation des ressources. Le premier chapitre portera sur le recrutement des poissons de récifs autour de l'île. Il sera divisé en deux parties : la première aura pour but l'étude de la dynamique spatiale et temporelle du recrutement sur l'île, la seconde aura pour but l'étude de l'influence du recrutement des juvéniles sur le renouvellement des adultes. Le deuxième chapitre portera sur le déplacement des poissons entre les différents habitats côtiers au cours de leur développement ontogénétique, en utilisant une nouvelle méthode qui permet d'étudier les trajectoires isotopiques dans le cristallin des yeux des poissons. Ce chapitre aura pour but de décrire l'histoire de vie de plusieurs espèces de poissons de récifs, à partir des mouvements qu'ils réalisent entre les habitats côtiers. Enfin, le troisième chapitre portera sur l'étude des changements de morphologies et de régime alimentaire au cours de l'ontogénie. Il sera aussi divisé en deux parties. La première partie aura pour but de décrire les changements de forme du corps entre différents stades de développement (larve, juvénile et adulte) pour plusieurs espèces de poissons de récifs, tandis que la deuxième partie aura pour but de décrire les changements de régime alimentaire au cours du développement par l'étude des niches isotopiques.

Chapitre 1 Recrutement des poissons de récifs autour de l'île de la Guadeloupe



1.1) Dynamique de recrutement des poissons de récifs autour de l'île de la Guadeloupe.

Article 1 – Vignaud L., Vallès H., Cordonnier S., Chatagnon A., Lecchini D., Dromard C.R. (2023) Spatio-temporal distribution of juvenile fish species in Guadeloupean reefs (Lesser Antilles) Regional Studies in Marine Science (accepté)

Abstract

In the life cycle of coral reef fishes, recruitment is a key process which permit the renewal and the replenishment of adult fish populations. Numerous biotic and abiotic factors can influence recruitment, such as the quality of habitat, fish density and fish predation, and reef fish larvae can disperse over long distances. As a result, the distribution of fish juveniles among different habitats can significantly vary spatially and temporally. Here, we described spatio-temporal variation in juvenile fish distribution at the scale of Guadeloupe Island (Caribbean). Visual surveys of fish juveniles were conducted monthly for one year, on six sites representing three types of reef present in Guadeloupe (barrier reef, fringing reef, and patch reef). Significant differences were found in the abundance and species richness of juvenile reef fish depending on the geographical location, and reef type of the studied site. Significant differences were found in abundance between months of the year, and in species richness between the two seasons of the Caribbean region. Species composition differed between sites function of the month of observation, and it was established that the most abundant species at each site were responsible for the spatio-temporal variation observed in the juvenile fish assemblage. Overall, the distribution of juvenile reef fish in Guadeloupe varies both spatially (depending on geographical position and reef type) and temporally (depending on the season). These variations certainly have a strong influence on the stock of adult fish found all around the island of Guadeloupe.

Key words: coral reef, recruitment, fish survey, Caribbean

1. Introduction

Most coral reef fishes have two distinct phases in their life cycle: a pelagic larval stage and a reef resident stage. After having realized a dispersive phase in the ocean, pelagic larvae return to shore to recruit and metamorphose into juveniles, which will have all the biological characteristics of adults except the size and the sexual maturity (Hixon, 1998). Recruitment is defined as the integration of juveniles into the adult population (Shapiro, 1987). During this process several biotic and abiotic factors can influence the choice of reef habitat such as lunar cycle, larval sensory systems or swimming behavior, presence, or absence of predators (Robertson, 1992; Shenker *et al.*, 1993; Leis *et al.*, 2011; Leis *et al.*, 2015). The recruitment success is recognized as a major ecological factor to ensure the renewal and the recovery of reef fish populations (Richards and Lindeman, 1987; Abesamis and Russ, 2010). Connectivity or exchange between reef fish populations is an important parameter when studying recruitment on an island scale, and for the Caribbean region, larval dispersal distances are of the order of 10 to 100 km (Cowen *et al.*, 2006). Therefore, variation in juvenile fish recruitment often affects the distribution and abundance of fish adult species between different reefs (Tolimieri, 1995, Tupper and Hunte, 1994).

In the Caribbean, many studies concerning recruitment process have been done in Florida, Bahamas, Jamaica, Panama coast, St Croix and Virgin Islands, Barbados, St Lucia, and Curacao islands (*e.g.*, Stimson, 1990; Kaufman *et al.*, 1992; Tupper and Hunte, 1994; Risk, 1998). The introduction of artificial reefs (Alevizon and Gorham, 1989; Beets, 1989; Sherman *et al.*, 2001) or SMURF devices (Vallès *et al.*, 2008) was done to assess variability in recruitment. Other studies focused on the recruitment determinism through the predation pressure (*e.g.*, Forrester, 1995; Beets, 1997; Steele and Forrester, 2002). Then, the influence of the benthic composition (*e.g.*, Tolimieri, 1995; Vallès *et al.*, 2008), the protection status by Marine Protected Areas (Vallès *et al.*, 2001; Watson and Munro, 2004; Sponaugle *et al.*, 2012) and the reef degradation (Booth and Beretta, 2002) was assessed on sites where recruitment occurs. These studies have shown that the composition (*e.g.*, abundance of fish, species richness, coral degradation, degrees of conservation) and complexity (*e.g.*, artificial reefs and SMURFS designs) of a reef can influence the success of recruitment. However, they also shown that what happened at small spatial-scale (on one site) was not necessarily applicable at large spatial-scale (between several sites).

On the island of Guadeloupe, only one study was conducted on the recruitment, and was focused on the butterflyfish (Harmelin-Vivien, 1989). Other studies focused on the colonization phase, and spatio-temporal monitoring of fish juveniles in nursery habitats such as mangroves and seagrass beds (Baelde, 1990; Bouchon *et al.*, 1994; Vaslet *et al.*, 2009; Kopp *et al.*, 2010). Results have shown how the location of nursery habitats relative to the reef can influence the abundance and species richness of juvenile individuals. In addition to nursery areas, Guadeloupe has three types of reefs: fringing reefs (*i.e.*, reefs developing close to the coastline), barrier reefs (*i.e.*, continuous reefs parallel to the coastline, separated by larger lagoons) and patch reefs (*i.e.*, discontinuous coral communities) (Bouchon *et al.*, 2008). To date, no studies have been carried out to test the influence of reef type on the abundance and species richness of juvenile fish.

Thus, in the present study, we investigated the spatio-temporal variability of recruitment on an island-wide scale, by monitoring the juvenile fish assemblage (abundance and species richness). To do this, we asked several questions: 1) Do reefs close to each other have more similar recruitment dynamics than reefs that are further apart, due to the arrival of larval patches (typically several km large), emphasizing the role of hydrodynamics on recruitment? 2) Do reefs belonging to different types (barrier, fringing or patch) have different recruitment dynamics, due to the nature of the cues they would provide for the arrival of fish larvae, underlining the importance of larval behavior in setting recruitment? 3) Do recruitment peaks tend to occur at specific times of the year (*e.g.,* rainy season), as the results of other studies suggest (Sponaugle and Cowen, 1997; Vallès *et al.*, 2009)? 4) Does the composition of species have an influence on spatio-temporal variation in juvenile fish assemblages?

2. Materials and methods

Juvenile fish surveys were carried out between June 2021 and June 2022 (except in December 2021), at six sites on the island of Guadeloupe. The sites represent the island's three reef types: fringing reefs in Port Louis (PL) and Petit Bourg (PB), barriers reefs in Grand Cul-de-Sac Marin (GCSM) and Ilet du Gosier (IG), and patch reefs in Anse Cardonnet (AC) and Anse Dupuy (AD) (Figure 1).

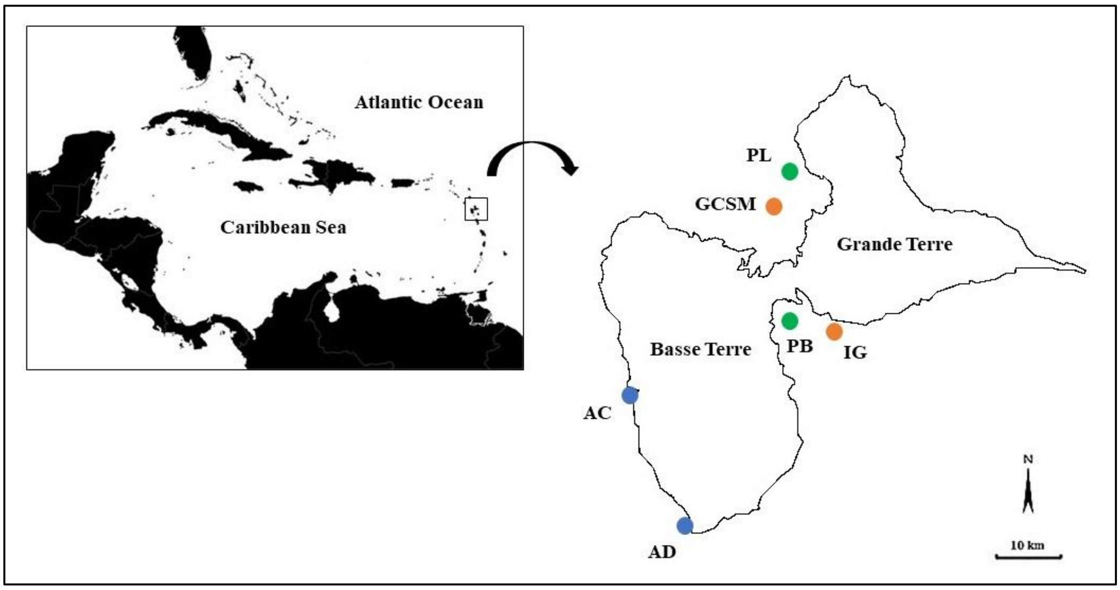


Figure 1 Location of the six study sites in Guadeloupe. Anse Cardonnet (AC) and Anse Dupuy (AD) are patch reefs (blue circles), Grand Cul-de-Sac Marin (GCSM) and Ilet du Gosier (IG) are barrier reef (orange circles), Port Louis (PL) and Petit Bourg (PB) are fringing reefs (green circles).

On each site, diurnal underwater visual censuses (Brock, 1954) of fish juveniles were conducted monthly (one week after new moon) in scuba diving, along three transects (30 m long and 2 m wide). Fish species, abundance and size of juveniles were recorded on each transect. The juvenile stage of fishes was identified, by the color pattern of the individuals (initial phase) and their sizes, when using identification guides (IGRECMer, 2016; Humann and Deloach, 2018) and websites (Froese and Pauly, 2002) as references (detailed for each species in table 1). In addition, on each site, the cover percentages of substrate categories (living coral, dead coral, coral rubble, algal turf, sand, seagrass beds, macroalgae, algal turf, gorgonians, and sponges) were measured on the three transect by the line intersect transect method (one point per meter) (Madsen, 1999) (Figure 2).

Table 1 Size range (cm) of juveniles observed for each species.

Species	Juvenile size ranges (min-max, cm)
Abudefduf saxatilis	4 - 5
Acanthurus coeruleus	2 - 5
Acanthurus tractus	2 - 4
Bodianus rufus	1 - 3
Canthigaster spp.	1 - 4
Chaetodon capistratus	3 - 5
Chromis cyanea	1 - 3
Chromis multilineata	1 - 3
Halichoeres bivittatus	1 - 4
Halichoeres garnoti	1 - 4
Halichoeres maculipinna	3 - 4
Microspathodon chrysurus	1 - 5
Ocyurus chrysurus	4 - 5
Scarus iseri	1 - 5
Serranus tigrinus	3 - 4
Sparisoma viride	1 - 5
Stegastes diencaeus	1 - 3
Stegastes leucostictus	1 - 3
Stegastes partitus	1 - 4
Stegastes planifrons	1 - 3
Thalassoma bifasciatum	1 - 3

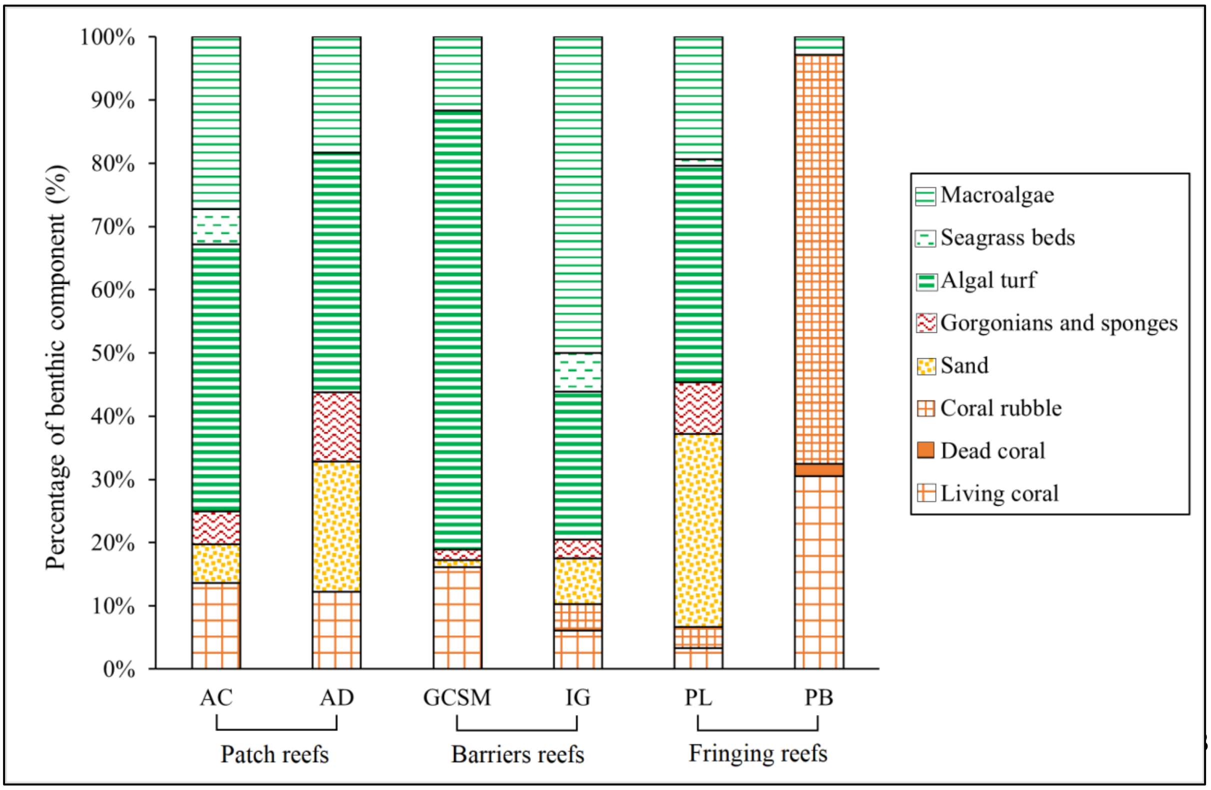


Figure 2 Percentage cover of benthic component at each site Anse Cardonnet (AC), Anse Dupuy (AD), Grand Cul-de-Sac Marin (GCSM), Ilet du Gosier (IG), Port Louis (PL) and Petit Bourg (PB).

Normality of data was tested using Shapiro-Wilk tests. As data were normally distributed, parametric analyses were used for comparisons. Then, the difference in abundance and species richness of juvenile fish assemblage 1) between the sites, 2) between reef types, and 3) between seasons (considering the variability between each month) were evaluated. For the seasons we have chosen the two seasons generally defined in the Caribbean: the dry season (from mid-November to mid-April) and the rainy season (from mid-April to mid-November) (Martinez *et al.*, 2020). Analysis of variance table (one-way ANOVA) was conducted for four linear models. The first linear model was performed on dataset containing the abundance of the juvenile fish assemblage obtained for each transect, each season, each month, and each site. The second linear model was performed on dataset containing the species richness of the juvenile fish assemblage for each transect, each season, each month, and each site. These two first linear models tested the effect of sites and seasons (and their interaction) on abundance or species richness, with months of the year nested in seasons (from January to March for the dry season, and from April to November for the rainy season). Because there was significant impact of several parameters on the abundance and species richness, Tukey post-hoc test was carried out following the one-way ANOVA, to determine which sites showed differences.

Then, the third and fourth linear model were performed on dataset containing the abundance and the species richness of the juvenile fish assemblage for each transect, each season, each month, and each reef type. These two other linear models tested the effect of reef types and seasons (and their interaction) on abundance or species richness, with months of the year nested in seasons. Because there was significant impact of several parameters on the abundance and species richness, Tukey post-hoc test was conducted following the one-way ANOVA, to determine which sites showed differences.

In the second part of the study, a PCA analysis was performed to summarize variability in species assemblage composition in space and time. To do this, transect data of abundance were averaged for each site during each month, yielding a total of twelve-monthly observations per site. Only the most abundant eight species (species with abundance from 10 to 300 individuals) were included in these analyses. A MANOVA test was performed on the effect of months and sites (and their interaction) on species assemblage composition using the transects as replicates. In the same way, only the most abundant species (n=8) were included in these analyses.

3. Results

3.1 Spatio-temporal variation of the juvenile fish assemblage

Variation in fish abundance was observed between study sites, with AC and AD (west coast) having the highest abundance, and IG and PB (to the south) having the lowest one (Figure 3). In fact, the results of statistical analyses showed significant differences in abundance between sites with different geographical positions (west, north, south), while abundance on sites with the same geographical position showed no significant differences (Table 2, Table 4). Variation in abundance was also observed between the reef types studied, with patch reefs having the highest abundance (Figure 3). Indeed, the results of statistical analyses showed significant differences in abundance between the three reef types studied (Table 3, Table 5). Finally, variation in abundance have been observed over time, with peaks in abundance observed in July (AD, IG and PL), August (AC), September (GCSM), November (AC and AD), January (AC and IG) and May (AC, AD and PL) (Figure 3). Although no significant differences were found between the two seasons described in the Caribbean (dry season and rainy season), a significant interaction between seasons and months of the year showed that abundance still varied between months of the year (Table 3).

Variation in species richness was observed between the study sites. The highest species richness was observed at GCSM site (located to the north) and the lowest one at PB site (located to the south) (Figure 4). The results of statistical analyses showed significant differences in species richness between sites with different geographical positions (west, north, south). Species richness was not significantly different between the western and northern sites, but differed from the southern sites, probably due to the low species richness at the PB site (Table 2, Table 4). Variation in species richness was also observed between the reef types studied (Figure 4). In fact, statistical analyses showed significant differences in species richness between patch reefs and fringing reefs (Table 3, Table 5). Finally, variation in species richness was observed over time, with peaks in species richness in September for all sites (except PB), November (PL), or January (GCSM and IG) (Figure 4). A significant difference in species richness was found between the two seasons, as well as a significant interaction between seasons and months of the year (Table 3).

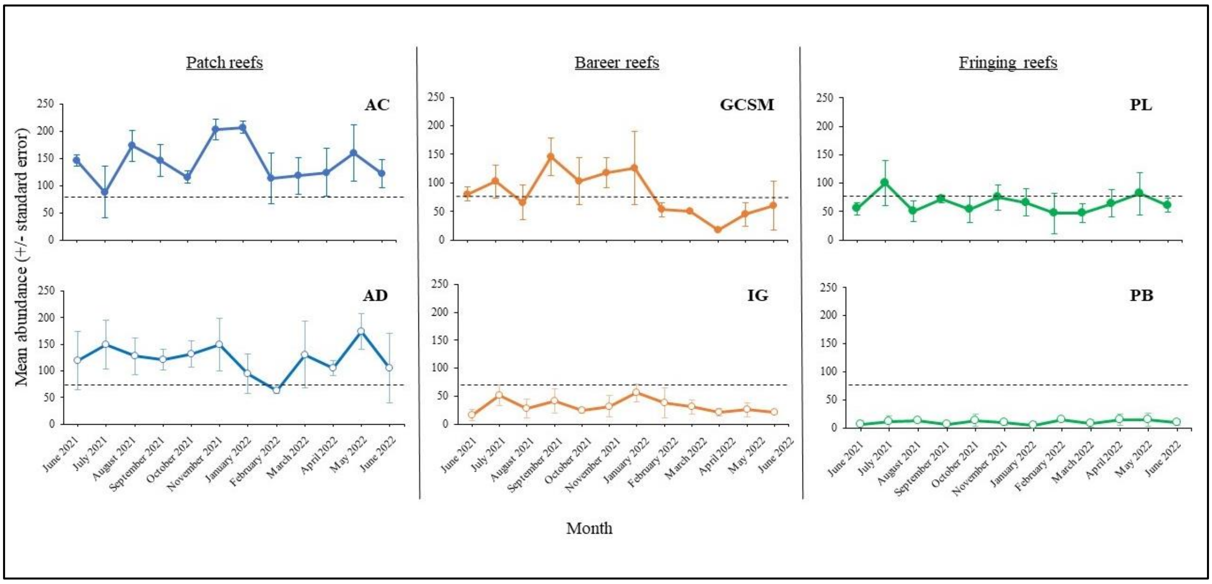


Figure 3 Mean abundances (of the three transects) and standard error of the juvenile fish assemblage observed at each site, Anse Cardonnet (AC), Anse Dupuy (AD), Grand Cul-de-Sac Marin (GCSM), Ilet du Gosier (IG), Port Louis (PL) and Petit Bourg (PB), and over time (month of year). The dot line represents the average abundance per transect for the dataset.

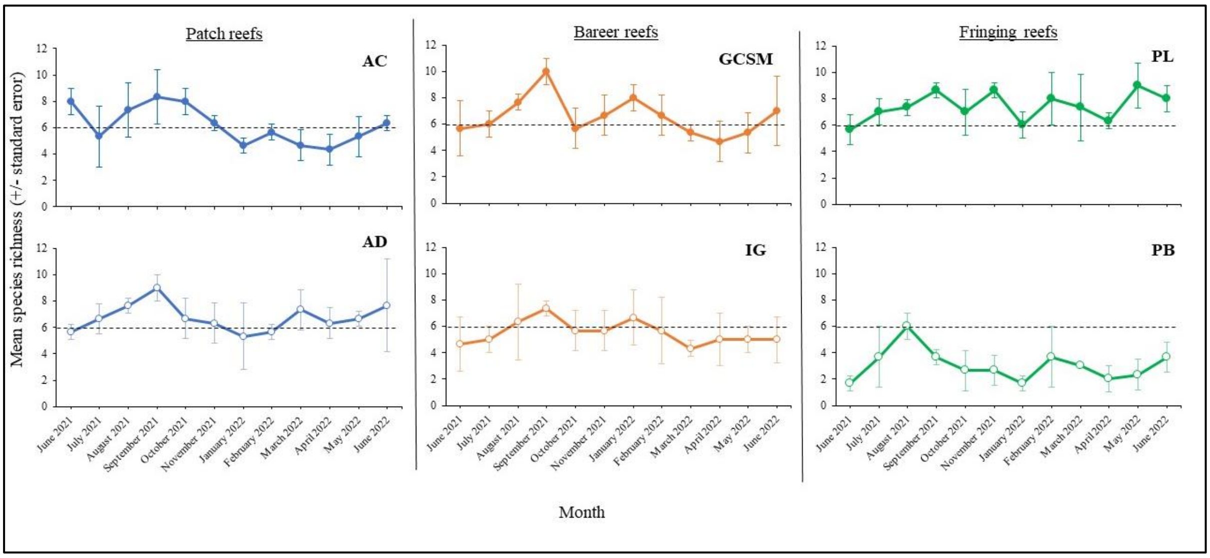


Figure 4 Mean species richness (of the three transects) and Standard Error of juveniles fish observed at each site, Anse Cardonnet (AC), Anse Dupuy (AD), Grand Cul-de-Sac Marin (GCSM), Ilet du Gosier (IG), Port Louis (PL) and Petit Bourg (PB), and over time. The dot line represents the average species richness per transect for the dataset.

Table 2 Results of one-way ANOVA for linear models, testing the effect of sites, seasons (with months nested) and their interaction on the abundance and species richness of juvenile fish assemblage. "ns" refers to a non-significant p-value.

		ANOVA		
		df	F	p-value
Abundance	Sites	5	89.3062	< 0.001
	Seasons	1	1.8329	ns
	Sites : Seasons	5	1.8213	ns
	Seasons : Months	10	3.5464	< 0.001
Species richness	Sites	5	35.4376	< 0.001
	Seasons	1	4.4751	< 0.05
	Sites : Seasons	5	1.1775	ns
	Seasons : Months	10	5.4857	< 0.001

Table 3 Results of one-way ANOVA for linear models, evaluating the effect of reef types, seasons (with months nested) and their interaction on the abundance and species richness of juvenile fish assemblages. "ns" refers to a non-significant p-value.

		ANOVA		
		df	F	p-value
Abundance	Type	2	116.6622	< 0.001
	Seasons	1	1.0503	ns
	Type : Seasons	2	0.8009	ns
	Seasons : Months	10	2.3523	< 0.05
Species richness	Type	2	6.4750	< 0.01
	Seasons	1	2.1538	ns
	Type : Seasons	2	1.5094	ns
	Seasons : Months	10	3.1070	< 0.01

Table 4 Result of Tukey test (p-values obtained), testing the differences between sites, for abundance and species richness (S) of juvenile fish assemblages. P-value obtained for the abundance are shown above the diagonal, and p-value obtained for the species richness are below the diagonal. Anse Cardonnet (AC), Anse Dupuy (AD), Grand Cul-de-Sac Marin (GCSM), Îlet du Gosier (IG), Port Louis (PL) and Petit Bourg (PB). "ns" refers to a non-significant p-value.

		Abundance – Tukey test (p-value)					
	Sites	AC	AD	GCSM	IG	PL	PB
S – Tukey test (p-value)	AC	-	ns	< 0.001	< 0.001	< 0.001	< 0.001
	AD	ns	-	< 0.001	< 0.001	< 0.001	< 0.001
	GCSM	ns	ns	-	< 0.001	ns	< 0.001
	IG	ns	< 0.05	ns	-	< 0.001	ns
	PL	< 0.05	ns	ns	< 0.001	-	< 0.001
	PB	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	-

Table 5 Result of Tukey test (p-value obtained), evaluating the difference between reef types, for abundance and species richness (S) of juvenile fish assemblages. P-value obtained for the abundance are shown above the diagonal, and p-value obtained for the species richness are below the diagonal. "ns" refers to a non-significant p-value.

		Abundance – Tukey test (p-value)		
	Type	Patch	Barrier	Fringing
S – Tukey test (p-value)	Patch	-	< 0.001	< 0.001
	Barrier	ns	-	< 0.05
	Fringing	< 0.01	ns	-

3.2 Spatio-temporal variation of composition of species assemblages

The graphical representation of species composition at each site showed that although the list of species recorded may be similar between sites, the abundance of individuals is not the same from one site to another (Figure 5). For example, between sites AD and GCSM, the species composition was globally the same, but three species (*Chromis multilineata*, *Scarus iseri* and *Stegastes partitus)* exhibited contrasted abundances between the two sites (Figure 5). However, if we look at the geographical position of the sites, we can see that for sites located on the west coast (AC and AD) and on the north coast (GCSM and PL), same species were observed (between one and three species differ), with similar abundances between sites.

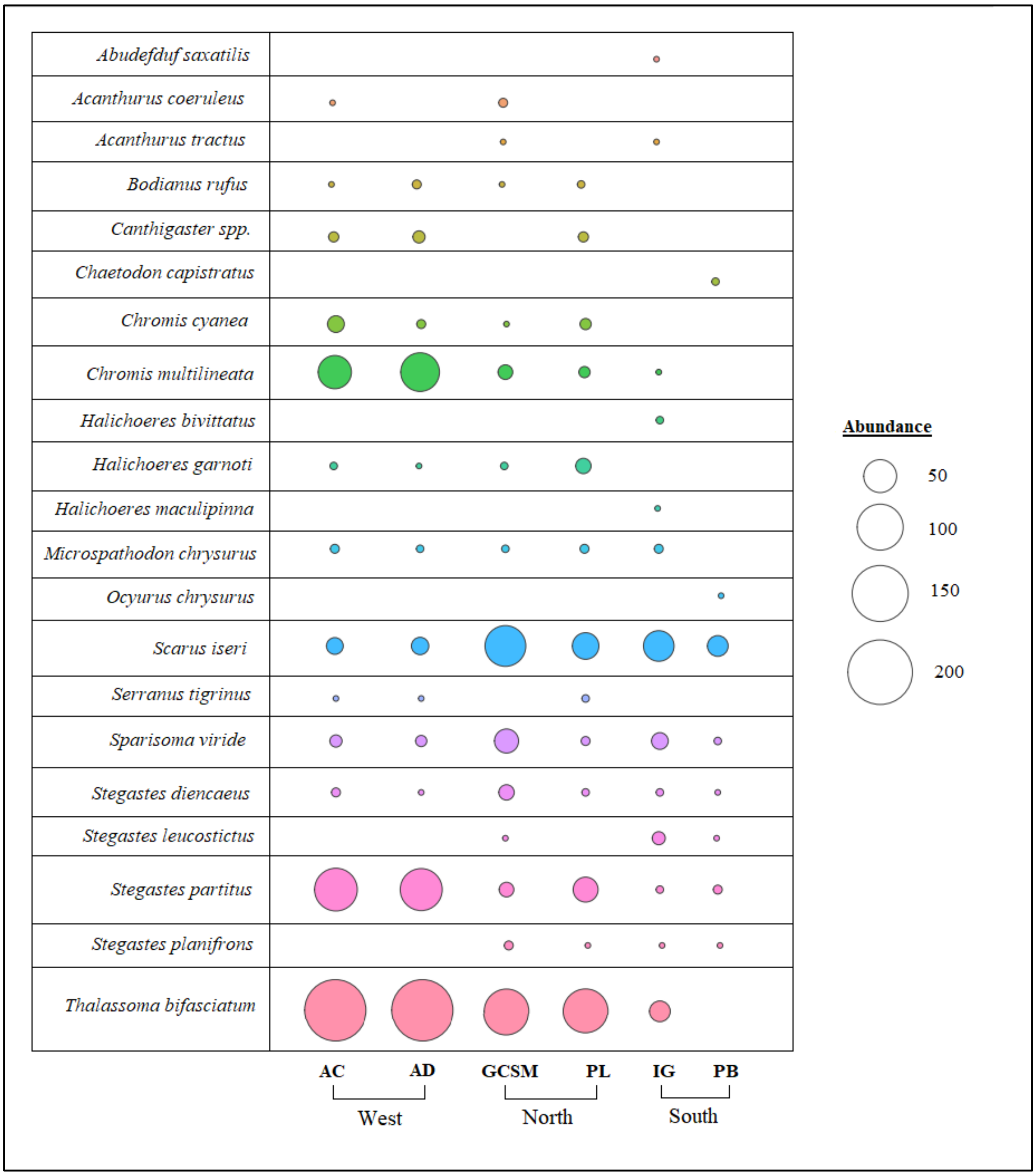


Figure 5 Bubble plot of the juvenile fish abundance for each species (mean of all months) on each site. Anse Cardonnet (AC), Anse Dupuy (AD), Grand Cul-de-Sac Marin (GCSM), Îlet du Gosier (IG), Port Louis (PL) and Petit Bourg (PB).

A PCA analysis with MANOVA test were performed on the species composition for each site every month (Figure 6, Table 6). Panel A of PCA graphical representation showed the polygons of each site, obtained from monthly species composition (twelve points per polygons corresponding to the twelve months of the study). Except for the polygons of sites AC and AD, and sites GCSM and IG, the polygons did not intersect or only slightly. This result reflected that even if the species composition was globally similar between some sites (*e.g.*, sites AC and AD), the abundance of some species differed (Figure 6A). On panel B, all the juvenile fish species observed during the study were represented by arrows proportional to their abundance. The graph showed that *Thalassoma bifasciatum* was the species the most abundant among the assemblage (largest arrow), particularly at sites AC, AD, GCSM, and PL (Figure 6B). This suggest that *T. bifasciatum* dominates the juvenile fish assemblage at these five sites (Figure 5). In contrast, *Stegastes partitus* and *Chromis multilineata* dominate the assemblage in term of abundance at sites AC and AD (Figures 5 and 6B). Similarly, the graph showed that *Sparisoma viride* and *Scarus iseri* were the species the most abundant among the assemblage at sites IG and GCSM (Figure 6B) (Figure 5).

Then, the MANOVA test performed on species composition showed a significative p-value for sites, month and for their interaction. This means that differences in specific composition between the study sites depended on the months of observation (Table 6).

Moreover, among the twenty-five species observed during the study, the five mentioned above accounted for over 90% of all juvenile fish abundance. The abundance of these species has a considerable influence on the variation observed in the juvenile fish assemblages between sites and over time.

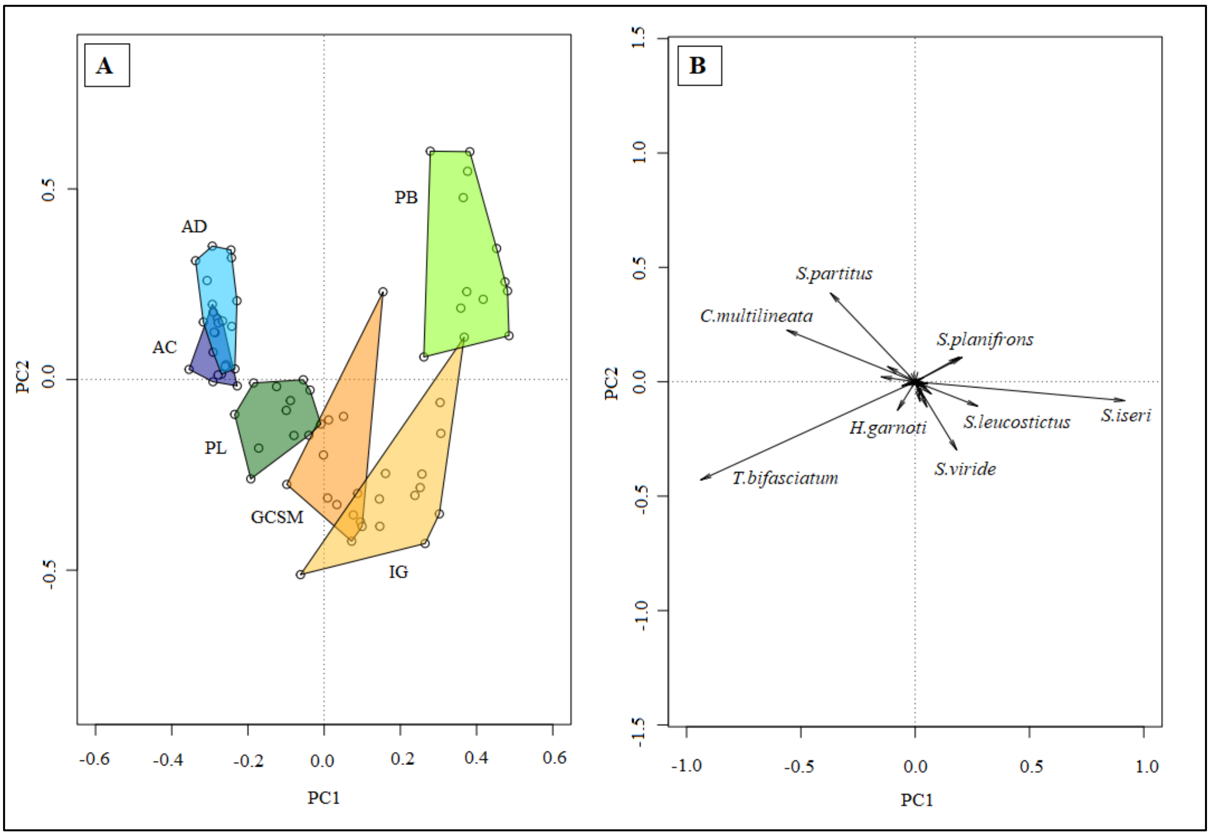


Figure 6 RDA biplot of the distribution of sites, Anse Cardonnet (AC), Anse Dupuy (AD), Grand Cul-de-Sac Marin (GCSM), Ilet du Gosier (IG), Port Louis (PL) and Petit Bourg (PB), and juvenile fish species independently of the temporal parameter. Panel A: distribution of the sites according to the species composition. Panel B: distribution of species in relation to sites, with arrows the representativeness of fish species on the different sites.

Table 6 Results of MANOVA, evaluating the effect of sites and months (and interaction) on the species composition of juvenile fish assemblages.

		MANOVA		
		df	F	p-value
Species composition	Sites	5	39.3936	0.001
	Months	11	2.5636	0.001
	Site * Months	55	1.5548	0.001

4. Discussion

Juvenile fish assemblage varies geographically. Sites geographically close to each other did not showed differences in their abundance. They also did not show differences in the species richness except for IG and PB sites, probably because PB exhibited the lowest species richness of the study. The position of reefs around the island is an important factor to consider the spatial distribution of juvenile fish. Indeed, hydrodynamic (waves, currents), habitat diversity (presence of marine reserves, mangroves) and anthropogenic activities could strongly influence the recruitment processes (Planes *et al.*, 1993; Sale *et al.*, 2005; Arceo *et al.*, 2006; Kimirei *et al.*, 2011; Iotti *et al.*, 2022).

Juvenile fish assemblage varies also with the type of reef studied. The three reef types showed significant differences in their abundance, with patch reef exhibited the highest abundance, followed by barrier reef and fringing reef. The species richness between patch reefs and fringing reefs also showed significant differences.

Similar results have already been shown between several types of reefs: patch reefs and barrier reefs exhibit higher reef fish abundance and diversity than fringing reefs (Nadon *et al.*, 2005). Moreover, in the Caribbean, patch reefs have also been shown as nursery habitat for some reef fish species (Adams *et al.*, 2002), this could potentially explain the highest abundance of juvenile in the present study. Reef type therefore plays a role in the spatial distribution of juvenile individuals. It is known that reef fish larvae settle on reefs they choose by detecting various visual, chemical, and acoustic signals from the reefs (Barth *et al.*, 2015). Each type of reef emits different signals due to the benthic composition and communities (ichthyological for example) that reside here.

Juvenile fish assemblage varies over time around Guadeloupe Island. There were differences in abundance and species richness between the months of the year, depending on the season observed. Most peaks in abundance were observed between May and November, and peaks in species richness were observed between September and January. Thus, in the present study, most peaks in juvenile fish abundance and species richness tend to be observed in months that are part of the wet season (Martinez *et al.*, 2020). Higher recruitment during the rainy season has already been observed in other studies such as in the Philippines, where recruitment is more intense during the monsoon due to the higher wave actions on reefs in this season (Arceo *et al.*, 2006). Similarly, numerous studies on recruitment have been conducted considering the seasonal nature of locations, and the months on the year have been identified as temporal parameters playing a major role in the movements of reef fish during their ontogeny (Green, 1996; Kimirei *et al.,* 2011). In the Caribbean, recruitment studies have shown various species (*e.g., Chaetodon miliaris*, *Thalassoma bifasciatum*, *Stegastes partitus* or *Halichoeres garnoti*) mainly recruit from April to June (Stimson, 1990), or from May to November (Tupper and Hunte, 1994). Thus, seasons influence variation of juvenile fish assemblages.

Finally, composition of species assemblage varies over space around the island of Guadeloupe. The abundance of individuals of each species differed between sites depending on the month observed, and five species accounted for more than 90% of the total abundance of juvenile fishes: the brown chromis *Chromis multilineata,* the bicolor damselfish *Stegastes partitus*, the bluehead wrasse *Thalassoma bifasciatum*, the striped parrotfish *Scarus iseri* and the stoplight parrotfish *Sparisoma viride*. These species have already been described as having the highest abundance (González-Sansón *et al*., 2009) or density (Alemu and Jahson, 2014) in studies of fish assemblages in the Caribbean. When studying an assemblage, the most abundant species are important to determine, since the variation associated with them (*e.g.*, temporal variation) may conceal variation associated with less abundant species. Variation observed at the assemblage level may therefore reflects variation of the most abundant species. Therefore, the similarity in the juvenile fish assemblage abundance between Anse Cardonnet and Anse Dupuy sites, could be due to the high abundance of *Chromis multilineata* and *Stegastes partitus*. The difference between these two sites and to the four other sites can be explained by the presence of these two species which are not found in such abundance elsewhere. Likewise, the highest abundances of *Sparisoma viride* and *Scarus iseri* abundances were found at Ilet du Gosier and Grand Cul-de-Sac Marin, which are both characterized by the same reef type (*i.e.,* barrier reef). Thus, the difference in juvenile fish assemblage abundance between barrier reefs and the other reef types can be explained by the high abundance of these two species on barrier reefs. *Thalassoma bifasciatum* is the most abundant species at all sites, except for the Petit Bourg site where it is absent. The presence of this species in high abundance at the Grand Cul-de-Sac Marin and Port Louis may be the reason for the similarity between these two sites if we consider the abundance of juvenile fishes.

5. Conclusion

The present study showed that reef fish recruitment varied strongly over space and time around Guadeloupe Island. Space through geographical location and reef type influenced the presence of juvenile fishes. The juvenile fish assemblage varied temporally, as a function of the seasons, which explained much of the variability in recruitment. Finally, the spatio-temporal variation in juvenile fishes is species-specific, and therefore the spatio-temporal variation of the species in the assemblage can be masked by the variation of the most abundant species. Thus, it is important to describe recruitment at a species level in addition to descriptions made at juvenile fish assemblage level.

Moreover, results from this study enabled us to identify sites ecologically important for reef fish recruitment at Guadeloupe Island. These sites are located at the south-west of the island and represent the patch reef types, and at the north, in the Grand Cul de Sac Marin reserve and represent both barrier reef and fringing reef types. The periods of the peaks of recruitment (months of the year) were also highlighted. These data could also be used to explain the composition of adult fish stocks. This would require comparison with data on the spatial distribution of adults at the same sites around the island.

Sample Credit author statement

Lea Vignaud: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing, Visualization and Funding acquisition. **Henri Vallès:** Conceptualization, Software, Validation, Formal analysis, Writing and Visualization. **Sébastien Cordonnier:** Methodology, Investigation and Resources. **Amélia Chatagnon:** Investigation and Resources. **David Lecchini:** Conceptualization, Methodology, Validation, Resources, Writing, Visualization, Supervision and Funding acquisition. **Charlotte R. Dromard:** Conceptualization, Methodology, Validation, Resources, Writing, Visualization, Supervision and Funding acquisition.

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1.2) Influence du recrutement sur les populations adultes de même espèce.

Article 2 – Vignaud L., Vallès H., Cordonnier S., Chatagnon A., Lecchini D., Dromard C.R., Can spatial variation in juvenile recruitment explain adult distribution in Caribbean reef fishes ? Gulf and Caribbean Research (en révision)

Abstract

Recruitment (*i.e.*, the integration of juveniles into the adult population) is a key process in the life cycle of reef fishes, allowing for the replenishment of adult fish populations. This process can strongly vary in space and time and can drive the distribution and abundance of adults over a range of scales. Depending on the species, juveniles and adults may differ markedly in terms of vulnerability to mortality, movement, and behavior. As a result, the extent to which juveniles can be used to predict adult abundance is likely to depend on the life history characteristics of the fish species concerned. Here, we examined the extent to which the abundance and distribution of juveniles can be a good predictor for adult abundance and distribution at two spatial scales: between transects of a similar site and between sites, and for species with contrasting life history traits. We conducted monthly visual underwater surveys along three transects at four sites around the island of Guadeloupe, over one year (June 2021 to June 2022). Five species were chosen for their high abundance at both stages and their different behavior: two damselfishes *Stegastes diencaeus* and *Stegastes partitus*, and one wrasse *Thalassoma bifasciatum* as sedentary species, and two parrotfishes *Scarus iseri* and *Sparisoma viride* as highly mobile species. Two types of analyses were carried out for each species: one at the site scale and one at the transect scale. We founded that *S. diencaeus, S. partitus* and *S. iseri* adult abundances were not explained by juvenile abundances at the transect and site scale. On the contrary for the two other species, adult abundances were explained by juvenile abundances at the transect scale (*T. bifasciatum*) and at both transect and site scales (*S. viride*). Thus, classification by life history trait does not adequately help explain our results. Finally, in this study the juvenile abundance can be good predictor of adult abundance for at both scale for *S.*

viride only. This underlines the fact that each species has its own behavior to study, beyond its historical traits.

Keywords: Coral reef fish – Ontogenetic stages – Spatial scales – Population dynamic

1. Introduction

Most reef fish have a complex life cycle: after a pelagic phase, larvae return to the shore to settle and metamorphose into juveniles. Juveniles have all the biological characteristics of adults, except for size and sexual maturity (Hixon, 1998). The integration of juveniles into the adult population corresponds to the "recruitment" process (Shapiro, 1987). This crucial biological process ensures the renewal of individuals within reef fish populations (Richards and Lindeman, 1987; Abesamis and Russ, 2010). Recruitment is influenced by a variety of biotic and abiotic factors that direct larvae toward favorable reef habitats.

Considering abiotic factors, hydrodynamics (*e.g.,* waves, currents) and climatology (e.g., season, water temperature) could influence recruitment processes (Arceo *et al.*, 2006; Cheal *et al.*, 2007; Munday *et al.*, 2008; Kimirei *et al.*, 2011; Wilson *et al.*, 2017; Iotti *et al.*, 2022). For example, Iotti *et al.*, in 2022 showed that juveniles preferentially selected microhabitats with medium to high structural complexity. They also showed that juvenile abundance was mainly temporal, following the seasonal shifts in water temperature, salinity, and chlorophyll *a* concentration. On the other hand, Arceo *et al.,* (2006) and Kimirei *et al.* (2011) putted in light that various juvenile reef fishes' species abundance at different locations or spatial scale (localities and island-scales). Moreover, anthropogenic activities such as artificial light or sounds produced by boats (modification of environmental sounds) could also negatively affect recruitment processes (Ferrari *et al.*, 2018; Schligler *et al.*, 2021). For example, Ferrari *et al.*, in 2018 conducted three experiments to assess the effect of boat noise on the ability of fish to learn to recognize predation threats. Juvenile fish unaccustomed to boat noise did not react to the presence of predators, in contrast to those "accustomed" to such noise since the start of their development. These ambient noises may therefore increase juvenile mortality on the reef, and thus impact recruitment. Similarly, during a field experiment conducted on orange-finned anemonefish (*Amphiprion chrysopterus*), Schligler *et al.,* (2021) showed that environmentally significant underwater illumination (mean: 4.3 lux) reduced juvenile survival and growth to that of juveniles exposed to natural underwater moonlight (mean: 0.03 lux).

For biotic factors, habitat diversity (*e.g.,* presence of marine reserves, mangroves) or interaction with other reef organisms (*e.g.*, predation, or competition with adult's conspecifics) have been identified as factors influencing recruitment process (Shulman, 1985; Forrester, 1990; Caley, 1993; Planes *et al.*, 1993; Tolimieri, 1995; Sale *et al.*, 2005; Iotti *et al.*, 2022). For example, Planes *et al.*, in 1993 showed that, depending on the species studied, juvenile fish were observed in specific habitats: *Acanthurus triostegus* on the fringing reef, while Mugilidae species were only found near the beach and *Stegastes nigricans* was present everywhere except near the beach. This distribution highlights the influence of habitat on the distribution of juveniles on the reef, and therefore on future recruitment. Furthermore, in Shulman's 1985 study, juvenile recruitment of almost all species in the sand and rubble fish assemblage was greater on reefs built away from the main reef than on those built at the edge of the backreef. This is due to the presence of seagrass and algae, which provide shelter for very small juvenile fish. This component is absent in a "halo" zone close to the reef due to the feeding activities of grazers associated with the reef, and juveniles are therefore more exposed to predators. Furthermore, in 1993, Caley showed that predation on juvenile reef fish affected the abundance of populations of the species monitored in subsequent years. These two studies clearly show that predation on juvenile reef fish affects recruitment and therefore the number of individuals in adult populations. Then, Forrester *et al.*, in 1990 showed that the survival of juveniles on a reef could be reduced as a function of the number of adults and the availability of food resources. Indeed, for species with the same diet, competition between juveniles and larger adults can lead to a drop in juvenile survival on the reef.

Combining abiotic and biotic factors, as well as the biological patterns of fish species, recruitment varies both spatially and temporally. Temporal variations in recruitment are partly linked to the seasons, and that recruitment of various reef fish species takes place mainly during the rainy season (Stimson, 1990; Tupper and Hunte, 1994; Sponaugle and Cowen, 1997; Arceo *et al.*, 2006). Recruitment also varies according to the spatial scale at which it is studied. In a study carried out at three spatial scales (between reefs separated by hundreds of km, by tens of km and within the same reef), the recruitment of Pomacentridae does not vary in the same way (Fowler *et al.*, 1992). At the scale of reefs separated by hundreds of kilometers, recruitment was higher in the southern region than in the northern. There was also a difference in recruitment between reefs separated by tens of kilometers, but a homogeneous distribution of recruitment within the same reef (Fowler *et al.*, 1992). Thus, it has already been described that variations in recruitment on a small scale (within a site) are influenced by the choice of micro-habitats during the settlement of individuals, while recruitment on a large scale (between sites) was not influenced by microhabitats but by larval supply other refill processes such as predation or competition (Tolimieri, 1995; Caselle and Warner, 1996). These studies confirm the importance of considering the notion of spatial scale when studying recruitment in reef fish, as well as inter-specific variations in this ecological process.

Dynamic and variations in juvenile recruitment can directly affect the distribution and abundance for adults on coral reefs. Firstly, in a review on the maintenance of diversity in coral reef fish community published in 1977, Sale described that the relative abundance of species in a guild at a given site is largely the result of juvenile recruitment to that site and will therefore change as the site changes. Then, as shown by an experiment conducted on *Pomacentrus amboisis* damselfish, over a three-year period, adult densities were positively correlated with recruitment success at each site (Jones, 1990). Similarly, in another study conducted on *Thalassoma bifasciatum*, adult densities on the reefs directly reflected the densities of recruiting juveniles (Victor, 1986).

Finally, Caribbean coral reef fish assemblages are highly diverse, and species utilize multiple habitat types (*e.g.*, complex coral reefs, shallow patch reefs, seagrass beds and mangroves), through daily movements within the home range (*i.e.,* the area in which an individual spends most of its time of its day-to-day activities, including foraging and resting) and ontogenetic habitat changes (Kramer and Chapman, 1999; Chapman and Kramer, 2000; Pittman *et al.*, 2014). Some species can have very small home ranges of just a few square meters, limited to a single site or habitat. These are generally small fish species, with limited mobility and/or actively defending a territory, like some damselfish. Conversely, some species can occupy large home ranges (up to several kilometers square), such as herbivorous fish (*e.g.*, parrotfish, surgeonfish) or large predators (such as groupers), which move over wide areas to feed or reproduce (Lawson *et al.*, 1999; Welsh *et al.*, 2013). Home range size generally varies according to the species size. In the wrasse family, for example, small to medium-sized species (*e.g., Thalassoma bifasciatum*), have small home ranges a few meters square, while larger species can occupy home ranges several kilometers square (*e.g.*, *Cheilinus undulatus*) (Green *et al.*, 2015). Species with small or restricted home ranges are generally considered sedentary. On the other hand, species with large home ranges that move within them are considered highly mobile. The home range generally increases with ontogeny, and serves three distinct purposes: avoiding predation, finding adequate food, and reproducing. The larger the individual, the lower the predation and the greater the quantity of food, which is why small adult species often have smaller home ranges than larger individuals (Huey, 1991; Jetz *et al.*, 2004; Börger *et al.*, 2008). The home ranges of juveniles at the time of recruitment are often like those of adults, as shown in a study on parrotfish (Welsh *et al.*, 2013). While some larvae recruit directly on the reef, others may transit through nurseries (shallow patch reefs, seagrass beds or mangroves), if these habitats are present, before migrating to coral reefs when their size makes them less vulnerable to predation. These ontogenetic changes in habitat influence the structure of adult fish assemblages on coral reefs and the presence of a nursery area close to the reef increases the adult biomass of fish species found as juveniles in the nursery area (Mumby *et al.*, 2004; Nagelkerken, 2007). Thus, for the same species, the link between juvenile and adult abundance on a reef also depends strongly on the location of the reef and its proximity to nursery sites.

Thus, the extent to which juveniles can be used to predict adult abundance is likely to depend on the life history characteristics of the fish species concerned. In this study, we expect that juvenile abundance will be a good predictor of adult abundance at both small (transects several meters apart) and larger (sites several kms apart) scales for species that are highly sedentary and/or maintain small territories throughout their life cycle such as damselfishes and wrasses. In contrast, we expect that such spatial relationships would break up for species that are highly mobile as adults and/or can use different nursery habitats throughout their life cycle such as the parrotfishes.

2. Material and method

From June 2021 to June 2022 (except in December 2021), underwater fish monitoring was conducted in Guadeloupe Island, on four study sites characterized by the presence of coral reefs: West1 (Anse Cardonnet) and West2 (Anse Dupuy) along the west coast of the island, and North1 (Grand Cul-de-Sac Marin) and North2 (Port-Louis) to the north. The site North1 is a barrier reefs (*i.e.*, continuous barrier parallels the coastline separated by wider lagoons) with 20% living corals for 80% mixed algae (L. Vignaud, unpublished data), and site North2 is a fringing reef (*i.e.*, reefs growing near the coastline) with 5% living coral for 60% mixed algae. Both are located in the bay of Grand Cul-de-Sac Marin, which also features seagrass beds and mangroves. Sites West1 and West2 are patch reefs (*i.e.*, highly diversified non-reef building coral communities) with 10% living coral for 60% mixed algae (L. Vignaud, unpublished data) located close to the coast, and seagrass beds can be seen next to these sites. On each site, diurnal underwater visual censuses of fish were conducted monthly for one year (one week after new moon) in scuba diving, along three fixed transects lines (30 m long and 2 m wide). Fish species, abundance, and size of all individuals (juveniles and adults) crossing the transect were recorded. The difference between the juvenile and adult stages was made using identification guides (Humann and Deloach, 2002; Froese and Pauly, 2002) and by following information on coloration patterns and size of the individuals. Moreover, all observed juvenile and adult sizes given below fall within the size ranges already described for each species in the identification guides (Humann and Deloach, 2002; Froese and Pauly, 2002).

Of the different species observed in both adult and juvenile stages on each site, the five most abundant species have been chosen to carry out the study. For the two damselfish, *Stegastes diencaeus* and *Stegastes partitus* (Pomacentridae), the size of juveniles observed ranged from 1 to 3 cm, and adults from 6 to 10 cm. These species have small home range: from 1 to 3 m², the average home range for Pomacentridae (McDougall and Kramer, 2007; Cowlishaw, 2014). For the wrasse *Thalassoma bifasciatum* (Labridae), the size of juveniles observed ranged from 1 to 3 cm, and adults from 6 to 15 cm. It also has small home range: from 2.6 to 4.8 m² for initial phase adults and 7.8 to 11.3 m² for terminal phase adults (Jones, 2005). For the three species, newly arrived individuals have already been described as attracted by the presence of conspecifics and the habitat quality. They generally position themselves in corals, at the same place than adults or relatively close to them (Booth and Beretta, 1994; White and Warner, 2007; Johnson and Hixon, 2010). Given that individuals of this species have a small home range on a reef, they will be considered as sedentary species in the analyses. Then, for the two parrotfish *Scarus iseri* and *Sparisoma viride* (Scaridae), the size of juveniles observed ranged from 1 to 3 and 1 to 5 cm, and adults from 21 to 25 and 26 to 35 cm, respectively. They have large home ranges: average home ranges of adult *S. iseri* range up to about 100 m² and those of *S. viride* up to about 200 m² (Mumby and Wabnitz, 2002). Like other parrotfish, these two species have been described both using seagrass beds (or mangrove) and coral reefs as nursery area at a juvenile stage but include the adult population, which lives in groups at the end of its development (Jaxion-Harm *et al.*, 2012; Overholtzer and Motta, 2000; Nagelkerken and Van Der Velde, 2003; Nagelkerken, 2007). Given their home range, which covers a large part of the reef, and their mobility, they will be considered as highly mobile species in the analyses.

Two types of analyses were carried out for each species. At the site scale, a one-tailed Pearson correlation test was performed between juvenile and adult abundance across sites after averaging abundance data across months and transects at each site. If the correlation was significant (p-value < 0.05), we concluded that a link between juvenile and adult abundances existed at site level. Then, if the correlation p-values were between 0.05 and 0.1, we conclude that it's rather "inconclusive", probably because of the limited number of sites included in the analyses. Finally, if the p-values are well above 0.1, we conclude that there is no link between juvenile and adult abundances at site level. At the transect scale, we used an AICc linear model framework to model adult abundance on the transects 1) as a function juvenile abundance (on the same transects), 2) as function of site, 3) as function of juvenile abundance on transects and site without interaction term, 4) with interaction term, and 5) as function of increasingly simpler models (null model). We retained the model with the lowest AICc. If the model retained included juvenile abundance, we interpreted this as evidence of a link between juvenile and adults at the transect level. To do these tests transect abundance data were averaged across months to remove temporal variation.

3. Results

Concerning sedentary species, for *S. diencaeus* and *S. partitus* juvenile abundances didn't explain adult abundances, at the scale of the site or the scale of the transect. *S. diencaeus* had low correlation coefficient and correlation p-value above 0.1, signifying that no correlation existed between juvenile and adult abundances at site scale (Table 1). Linear model selected was the null model meaning that site and juvenile factors did not explain adult variation at all (Table 2). *S. partitus* had high correlation coefficient but correlation p-value was between 0.05 and 0.1, signifying that it was not possible to conclude about this correlation (Table 1). On the other hand, linear model selected mean that there are differences between sites in terms of adults, but no links with juveniles at the transect scale (Table 2). Visually there were no evident link for juvenile and adult abundances between transects for each site (except at the North1 site for *S. diencaeus*), and between sites (represented by diamonds) (Figure 1). Then, for *T. bifasciatum*, adult abundances were explained by juvenile abundance at the transect scale, with some evidence that such differences also manifested at the site scale. This species had high correlation coefficient and correlation p-value was between 0.05 and 0.1, signifying that it was not possible to conclude about this correlation (Table 1). However, linear model selected mean that there was link between adult and juvenile abundances at the transect scale, and that this would explain any potential differences between sites (Table 2). There was visual link for North1 and North2 sites adult and juvenile abundances between transects: with decreasing adult abundance, juvenile abundance seems to increase. The same tendency seems to exist between sites (Figure 1).

Concerning highly mobile species for *S. iseri*, juvenile abundances didn't explain adult abundances, at the scale of the site or the scale of the transect. Correlation coefficient was low and correlation p-value was above 0.1, signifying that no correlation existed between juvenile and adult abundances at site scale (Table 1). Linear model selected was the null model meaning that site and juvenile factors did not explain adult variation at all (Table 2). Visually there was no evident link for juvenile and adult abundances between transects for each site and between sites (Figure 1).

For *S. viride*, adult abundance was explained by juvenile abundance at both the transect and site scales. Correlation coefficient was high, and correlation had significant p-value (Table 1), signifying that a link between juvenile and adult abundances existed at site level. Additionally, the linear model selected mean that there was link between adult and juvenile abundances at the transect scale, and that this would explain any potential differences between sites (Table 2). Visually, at the transect scale, the juvenile abundance seems to increase when adult abundance decreases at North2 and West2 sites. On the contrary between sites, the abundance of adult seems to increase with the abundance of juveniles (Figure 1).

Table 1 Results of correlation, testing the significance of the relationship between abundance of adults and, juvenile abundances at each site. Significant p-value are bolded.

Species	Pearson correlation test	
	r	p-value
S. diencaeus	-0.40	0.699
S. partitus	0.82	0.087
T. bifasciatum	0.85	0.076
S. iseri	0.18	0.412
S. viride	0.94	**0.028**

Table 2 Results of AIC framework, comparing the five linear models applied on adult abundance (response variable) and juvenile abundance on transect and site (explanatory variables). Result which permitted to select the best model are bolded.

Linear models	*S. diencaeus*		*S. partitus*		*T. bifasciatum*		*S. iseri*		*S. viride*	
	dAICc	df	dAICc	df	dAICc	df	dAICc	df	dAICc	df
Juvenile	3.4	3	8.1	3	**0**	**3**	3.3	3	**0**	**3**
Site	0.1	5	**0**	**3**	3.4	5	0.1	5	8.1	5
Site + Juvenile	8	6	8.8	6	10.6	6	8.5	6	15.6	6
Site : Juvenile	86.1	9	82.6	9	89.6	9	80.8	9	94.6	9
Intercept only	**0**	**2**	15.2	2	2.5	2	**0**	**2**	3.3	2

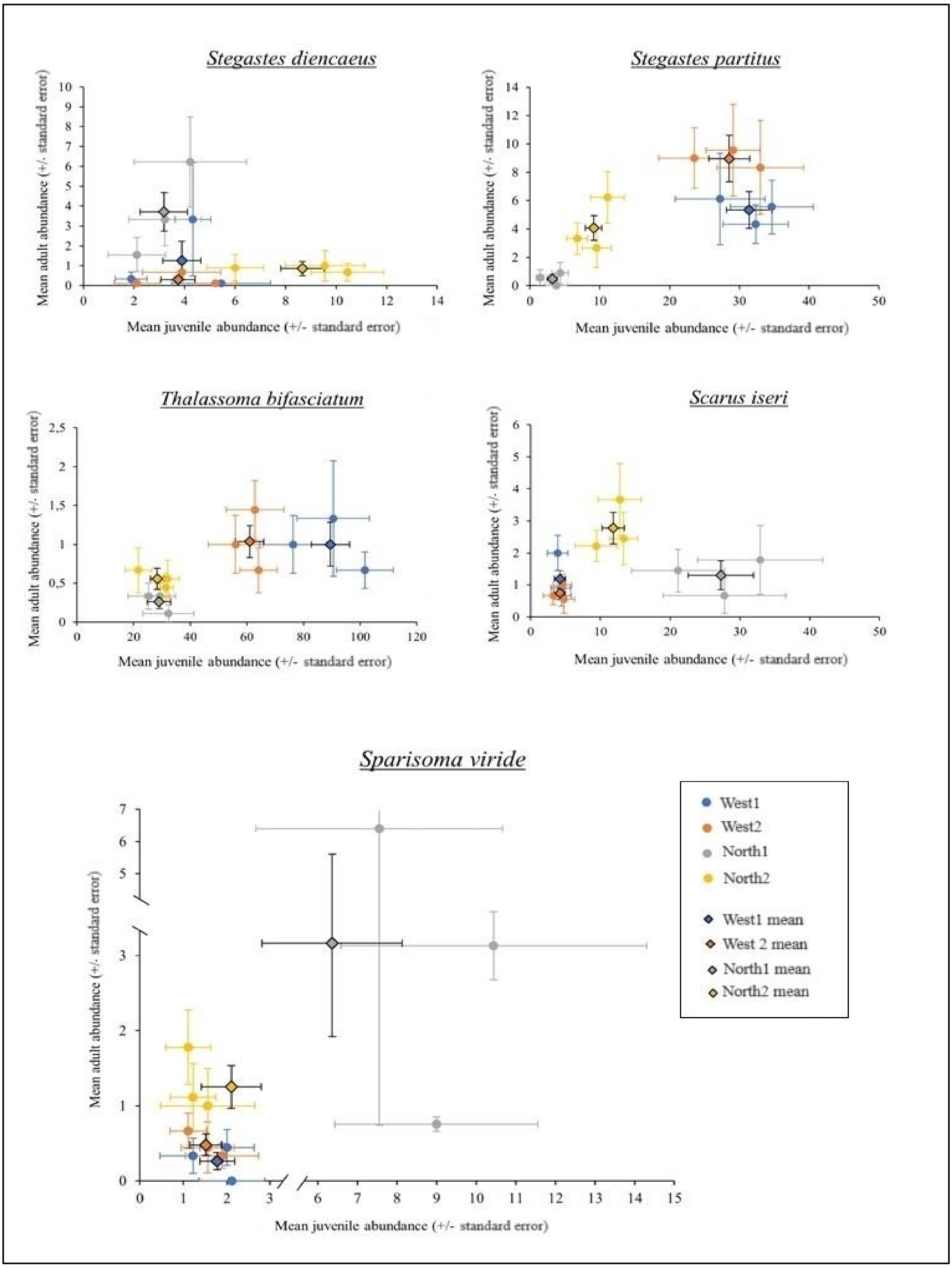

Figure 1 Representation of mean adult abundance function of mean juvenile abundance for each transect (rounds) with error type and mean adult abundance function of juvenile abundance per

site (diamonds) with error type, for the five species. Each color represents a site: West1 in blue, West2 in orange, North1 in grey and North2 in yellow.

4. Discussion and conclusion

Overall, mixed results were founded with some support for (*T. bifasciatum* and *S. iseri*) and against (*S. diencaeus*, *S. partitus* and *S. viride*) our original expectation that juvenile abundance would be a better predictor of adult abundance for sedentary species than for mobile ones at both the transect and site scales. Thus, the sedentary *versus* mobile classification does not adequately help explain our results.

At the transect scale, the lack of relationships between adult and juvenile abundances might reflect a mismatch between the size of the transects and the size of home range, particularly for the sedentary species. Indeed, the point-intercept transect method is adequate for covering a site but is not necessarily suited to the detailed description of a small part of the reef as used by species with a small home range. In the case of *S. diencaeus* and *S. partitus*, the transect may pass through an area outside adult territory where juveniles are located, or *vice versa*, which may bias the abundance of adult and juvenile individuals observed. In the case of *T. bifasciatum*, due to the low number of adults compared with juveniles, there is less chance of counting them if the transect does not pass over the area they are living. Finally, these species are all very attached to the places where they settle (Warner and Hoffman, 1980; Cheney and Côté, 2003; McDougall and Kramer, 2007; White and Warner, 2007), so knowing the abundance of juveniles could still help predict the abundance of future adults on a site.

At the site scale, it is likely that the site scale analyses lacked power due to the small number of sites. Indeed, high correlation coefficient and correlation p-value obtained above 0.1 for *S. partitus* and *T. bifasciatum* could possibly became significant with higher number of sites in the study.

Another factor which could explain results obtained is the behavior of each species. To begin*,* *S. diencaeus* is a species described as recruiting directly to the reef, and with juvenile attracted by the presence of their conspecifics proof of habitat quality (Cheney and Côté, 2003; Turgeon *et al.*, 2010). However, it is a territorial species, not living in groups, with aggressive behavior towards individuals of other species but also of the same species (Cheney and Côté, 2003; Solandt *et al.*, 2003). Adults and juveniles seem therefore to share the habitat. In a study conducted in Barbados, adult territories were describing as contiguous on spurs (finger-like projections of the reef towards the sea) and juveniles were observed in large numbers in the furrows adjacent to these spurs, between adult territories (McDougall and Kramer, 2007). The characteristics of this species may explain the trends observed between adult and juvenile abundance. At transect scale: juveniles are living in adjacent habitat to those of adults, the transect method used if passing through one habitat but not the other maybe bias the number of individuals at each stage on a part of the reef. At site scale, juveniles and adult didn't show linear relationship, but juveniles are more numerous on sites where adult abundance is low: given the territoriality of adults, we can assume that juveniles will tend to settle on reefs where adult numbers are lower, to avoid the agonistic behavior of adults. This could explain the negative correlation coefficient we found in the present study, even if it was low and if the correlation p-value was not significant. Then, *S. partitus* is a species where adult and juvenile stages are using the most complex structures on the reef (Nemeth, 1998; Johnson and Hixon, 2010). The choice of complex reefs allows them to escape predators and to have sufficient prey to avoid competition with young conspecifics (Nemeth, 1998; Hixon *et al.*, 2012). Indeed, although this species is territorial, no behavior against juveniles of the same species has ever been observed. However, juveniles and adults tend to spread out on the reef: juveniles were observed separately from adults, but in proximity and with the same configuration (complex structure to limit predation). Indeed, it has been observed that juveniles do not change their "living environment" in terms of distance as they grow to adulthood (Nemeth, 1998; Johnson and Hixon, 2010; Figueira *et al.*, 2008). The fact that adult and juvenile abundances were not related at the transect level could be due to this repartition on site and the transect method used (as explained before). At the scale of the site, as there is no agonistic behavior on the part of adults towards juveniles, and as both stages use complex structures on the coral, the presence (in low or high abundance) of adults probably attracts juveniles. Indeed, this high abundance indicates the presence of a large, favorable habitat for new arrivals, which could encourage them to move in. This could explain the high correlation coefficient found for this species. *T. bifasciatum* is also species that settles directly on the reef and exhibit small home range. Juvenile individuals tend to return to the same reefs as adult conspecifics where they cohabit, and even if it is a territorial species, adult only developed agonistic behavior towards other species (Warner and Hoffman, 1980; White and Warner, 2007). This behavior could explain the relation founded between juvenile and adult at the transect scale and the high correlation coefficient at site scale. Then, *S. iseri* is a species which have large home ranges that can cover an entire reef (Jaxion-Harm *et al.*, 2012; Hylkema *et al.*, 2015; Green *et al.*, 2015). This species has been described using seagrass beds, mangroves, or coral as nursery areas (Nagelkerken and Van Der Velde, 2003; Nagelkerken *et al.*, 2007; Jaxion-Harm *et al.*, 2012), adults and juvenile are thus living at two distinct scales. Indeed, adults move toward the entire reef, whereas juvenile hide in little places. Moreover, this species has a complex social structure at the adult stage. Indeed, individuals can live in 1) groups territorial adults individuals defended a delimited area from conspecifics, 2) groups of individuals in initial or terminal phase with low aggressiveness which are staying at the same place, or 3) large groups of schooling fish generally from a single life phase, which perform extensive daily migrations (Feitosa *et al.*, 2021). These various possibilities of social organization in *S. iseri* may lead to two hypotheses. The first is that, after their development in nursery areas, individuals would join groups of non-aggressive adults. The second is the opposite: after their development, the individuals would be confronted with groups of aggressive adults, and thus don't integrate adult population. This second hypothesis could possibly explain why no relation between juvenile and adult abundance was found at the transect and site scale in the present study.

Finally*, S. viride* is a species living in groups of varying size, from 3 to over 20 individuals, which means that these species require reefs with large quantities of food (Van Rooij *et al.*, 1996; Overholtzer and Motta, 2000). The parrotfish family they belong to is known to search for the availability and quality of food and habitat (Gust, 2002; Johansson *et al.*, 2012; Heenan *et al.*, 2016). We can therefore assume that juveniles return to a reef where conspecifics live, since this indicates to them a place where habitat and food will be suitable. They take shelter in adjacent nursery areas or directly on the reef (Overholtzer and Motta, 2000; Nagelkerken and Van Der Velde, 2003; Nagelkerken, 2007) to complete their development and then join the adult groups. In the present study, juvenile possibly choose coral reef where adult is already present has nursery area. This could explain why juveniles and adults are related at both transect and site scales.

Some of the species described and studied in this study are of significant ecological interest to coral reefs. Damselfish and parrotfish are reef herbivores, helping to protect corals from algae, with which they are in constant competition for light (Heenan *et al.*, 2016). *T. bifasciatum* is a so-called cleaner fish for reef individuals and is therefore of significant ecological interest for the health of other reef fish (Johnson and Ruben, 1988). In addition, parrotfish are of commercial interest as they are consumed by local Caribbean populations (Vallès *et al.*, 2015). Therefore, this study helps to define the scale at which these species of interest should be considered to apply protective measures for the conservation of coral reefs and continue to promote local fishing.

In this study, juvenile abundance is a good predictor of adult abundance at small (transect) scale for *T. bifasciatum*, and at small and large (site) scale only for *S. viride*. Certain biases in the study methodology may distort the results obtained for the two sedentary species *S. partitus* and *T. bifasciatum* at site scale. However, the third sedentary species, *S. diencaeus*, does not seem to show any relationship between juvenile and adult abundance, due to the behavior adopted by individuals of this species. Similarly, the results for the two mobile species are very different, due to the behavior of individuals in the adult stage. In conclusion, although juvenile recruitment affects adult populations of the same species, predicting or estimating adult abundance from juvenile abundance involves complex mechanisms specific to each species.

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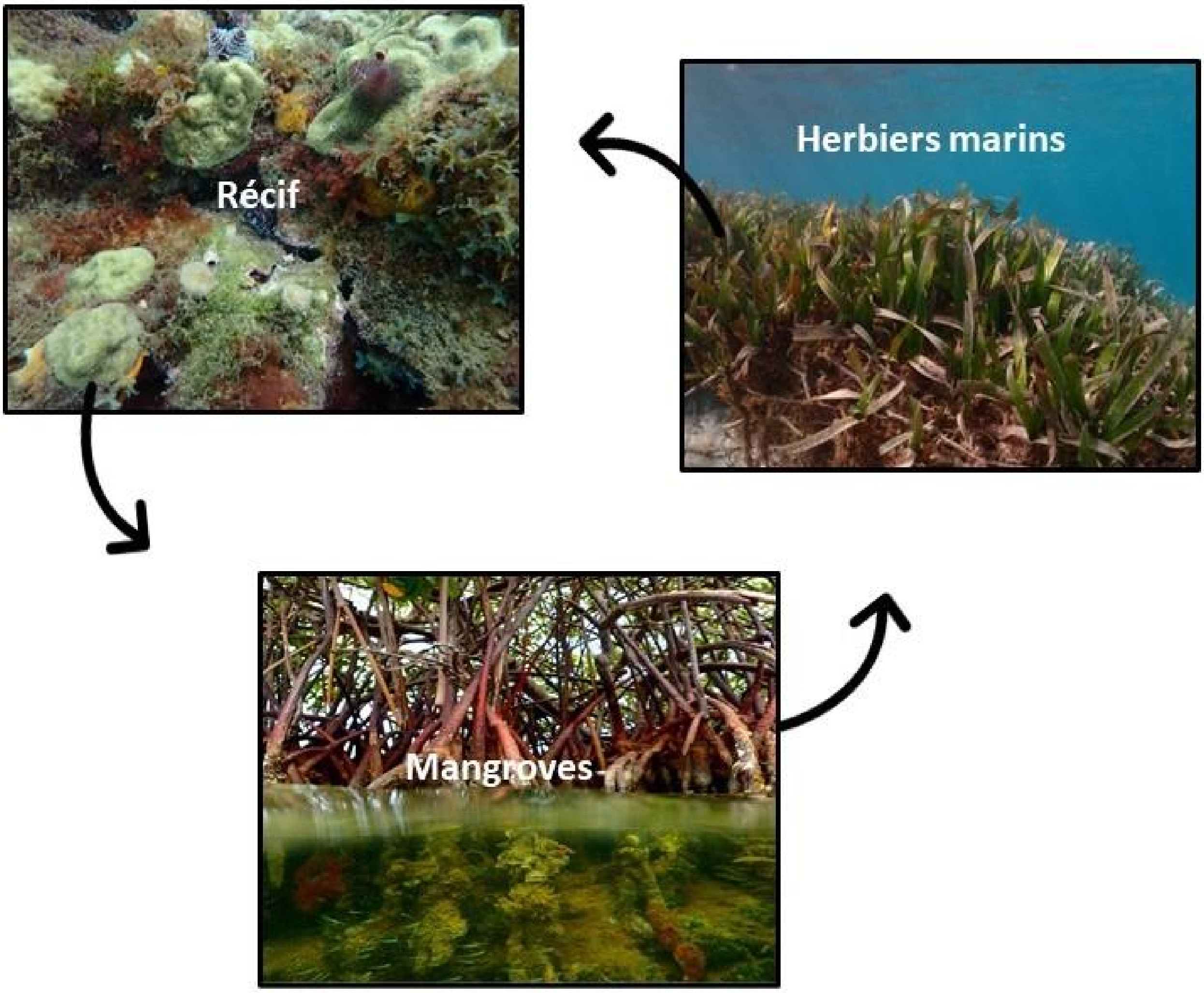
Chapitre 2 : L'isotopie du cristallin, une nouvelle approche méthodologique pour retracer l'histoire de vie des poissons de récifs autour de l'île de la Guadeloupe.



Article 3 – Vignaud L., Lepoint G., Frédérich B., Cordonnier S., Lecchini D., Dromard C.R., Trace the life history of fish from the reefs of Guadeloupe using eye lens stable isotopes (en préparation)

Abstract

Reef fish are economically important to island populations, but are now threatened by man-made pollution, global warming, and overfishing. To protect them, we need to know their life history. However, the life cycle of reef fish is complex, with the possibility of transition between different habitats during ontogeny. Tracking an individual throughout its life to determine its life history is not an easy task. The use of otoliths gives information on growth during life, and muscle isotopy on food sources and therefore potential habitats used, but over a fairly short time span (the time of life when the individual was collected). A new method consists of carrying out isotopic analyses on the eye lens of adult individuals in order to retrace their entire life history. In fish, the formation of the crystalline lens begins as soon as the eggs hatch, and forms new layers as the individual grows, trapping elements from the environment (notably carbon, nitrogen, and sulfur) in each layer, without renewing or degrading over time.

In this study, adult eye lens from three species of reef fish (Microspathodon chrysurus, Lutjanus apodus and Sparisoma viride) were used to trace their life histories at several sites around the island of Guadeloupe. Carbon, nitrogen, and sulfur isotope analyses were carried out on the different layers of the crystalline rocks. Comparisons were then made between the isotopic values obtained to answer three questions: 1) Do the isotopic trends over the lifetime of individuals differ within the same species? 2) Do individual isotopic trajectories differ between sites for each species? 3) Do isotopic trends over the lifetime of individuals differ between species for the same site?

For the three species studied, the results suggested that for the same species, isotopic trends did not differ between individuals of the same species. However, isotopic values did differ between sites for each species. These differences were probably due to the use of different food sources as individuals passed through one or more habitats (depending on the site). Finally, isotopic values differed between species because of their three trophic regimes, but also as a function of their life history behavior (i.e., passage through various habitats).

The use of adult crystalline lens can therefore be a good way of tracing the entire life history of reef fish and acquiring new information to set up measures to protect the habitats used by commercialized species.

Key words : Reef fish – lens layers – isotopic composition – ontogenetic movement – diet

1. Introduction

The local populations of the Caribbean islands rely heavily on their marine resources for economic and social development. Local fishing is an important source of livelihood for the region's inhabitants, contributing to food security, employment, and tourism (Haughton, 2001; Salas *et al.*, 2011). However, one of the fishing activity challenges is to balance the exploitation and conservation of marine resources. Today, many coastal fishermen are faced with the dilemma of declining catches and increasing degradation of marine habitats (Salas *et al.*, 2011). The management and conservation of local resources is carried out by both fishermen's knowledge and scientific monitoring which provide long-term observations to understand changes in the coral ecosystem (Grant and Berkes, 2004). In Guadeloupe, the bulk of the local fishery is made up of fish (reef and pelagic populations), crustaceans such as lobsters and crabs, and mollusks with the emblematic queen conch, with high seasonal specialization related to reproduction periods or migrations (Caillart, 2002). For example, in Guadeloupe, reef fish belonging to the Lutjanidae, Haemulidae, Scaridae or Acanthuridae families, have been described as the main families of commercial interest (Vaslet *et al.*, 2009).

Reef fish have a complex life cycle with numerous ontogenetic movements (Mc Cormick and Makey, 1997; Lecchini and Galzin, 2005). At an early stage in their development (but not earliest), competent larvae move from the oceanic pelagic to the reef benthic environment, where they carry out the rest of their development (Leis *et al.*, 1996; Hixon, 1998). Once they have crossed the reef crest, they must choose a nursery habitat where to settle and develop into juveniles. On tropical islands, the main nursery areas available to competent fish larvae are represented by shallow coral reefs, seagrass beds and mangroves (Parish, 1989). During their growing, reef fish may shift from a habitat to another, according to their needs in terms of space and food resources. For example, some species move from mangrove to seagrass beds, before joining coral reefs when they reach a larger size (Shapiro, 1987; Mumby *et al.*, 2004). These migrations are of vital importance for individual survival and populations renewal because it maximizes individual growth and reduces mortality, offering young individuals' food and shelter from predators (Adams *et al.*, 2006). While competent larvae from certain fish families, such damselfish (*e.g.*, *Microspathodon chrysurus*) can directly settle on the reef and spend their entire lives there (Green *et al.*, 2015), others families, such as Scaridae (*e.g.*, *Sparisoma viride*) or Lutjanidae (*e.g.*, *Lutjanus apodus* or *Ocyurus chrysurus*) are known to pass through some nursery areas before joining the reef as adults (Nagelkerken and Van Der Velde, 2003; Verweij *et al.*, 2008; Vaslet *et al.*, 2015). These movements differ from species to species (or families), but also according to sites, that is the presence or absence of surrounding nursery areas. These variations in the use of nursery areas echo animal individuality, *i.e.,* inter-individual differences in behavior that are constant over time (Biro et Stamps, 2008). This animal individuality and its consequences on movements between coastal habitats is particularly well represented in reef fish. For example, within Scaridae, juveniles generally use nursery areas before joining reefs, but some individuals have been described using only reef corals, other only mangroves and still others only seagrass beds (Overholtzer and Motta, 2000; Nagelkerken and Van Der Velde, 2003; Nagelkerken, 2007; Jaxion-Harm *et al.*, 2012).

Another example of significant flexibility in habitat use is a study conducted in Tanzania, on four species of reef fish using nursery areas as juveniles (Kimirei *et al.*, 2011). This study showed that the use of nursery habitats differed between sites for at least three of the four species. Although each of the four species selected a predominant juvenile habitat, other habitats were also used to some extent, either in the same area or at other locations. This may have been due to habitat quality or the extent of predation (Kimirei *et al.*, 2011). Similarly, a study carried out in a bay on the Island of Curaçao on 17 species of reef fish using nursery areas at the juvenile stage showed similar results. The spatial distribution of juveniles in mangroves and seagrass beds was correlated with distance from the mouth of the bay, water transparency, amount of shelter and structural complexity of the biotope (Nagelkerken *et al.*, 2000). In addition to influencing their distribution, the geographical position of nursery areas also exerted an influence on the ontogenetic development of individuals: juveniles of three species increased in size on seagrass beds as a function of the distance between the mouth and the bay, while one bay species decreased in size with distance from the mouth. Finally, another study carried out on an island in Japan highlighted that patterns of seagrass habitat use by juvenile and adult fish changed spatially (Nakamura and Tsuchiya, 2008). So, depending on the site In which they find themselves, juvenile individuals will select their transitional habitats according to the availability and the quality of habitats. Moreover, the abundance and diversity of reef fish at different ontogenetic stages are generally higher at sites with high connectivity between reefs and nursery areas than at sites with low connectivity between habitats (Appeldoorn *et al.*, 2003).

The life history of reef fish can be studied and traced using various methodologies. Studies of isotopic compositions, especially those recorded on internal anatomical structures, can be used to recreate long-term trajectories of diets or movements between habitats (Trueman *et al.*, 2012; Tzadik *et al.*, 2017). The proportion of stable isotopes of elements such as carbon, nitrogen, and sulfur (C, N and S) varies in natural environment, especially according to the ratios between heavy and light isotopes. Stable isotope approach assumes that the "isotopic compositions" of a consumer (noted delta "δ"), which correspond to the ratios between isotopes (^{13}C:^{12}C for example) related to a standard, are intimately linked to those of the food sources consumed but also can reflect the habitat where the animal lives (DeNiro and Epstein, 1978; Hobson, 1999). Stable isotopes have therefore long been used to study the structure and functioning of food webs, the trophic ecology of populations and behavioral ecology such as migrations (Layman *et al.*, 2011). The two most commonly used elements in ecology are carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N). Carbon isotopic compositions ($\delta^{13}C$) generally reflect the sources of organic matter consumed and exhibit low fractionation factors between consumers and food resources (around 0-1‰ per trophic level), while nitrogen isotopic compositions typically increase by 1 to 5‰ with successive trophic levels (average 2.3‰ in marine biota), allowing $\delta^{15}N$ values to be used as an indicator of trophic position and of nitrogen sources (MacCutchan *et al.*, 2003). Finally, sulfur isotopic compositions, measured by with $\delta^{34}S$, is increasingly used as a third tracer to disentangle sources in aquatic systems, as it can help differentiate between pelagic and benthic inputs. Indeed, benthic primary producers exhibit lower $\delta^{34}S$ values than pelagic primary producers, and so their consumers have lower values too (Connolly *et al.*, 2004; Newsome *et al.*, 2007; McCauley *et al.*, 2014). In coral reef habitats, sulfur isotopes can discriminate outer reef and oceanic habitats from inner reef habitat (Gajdzik *et al.*, 2016; Mittelheiser *et al.*, 2023). As isotopic compositions can vary spatially, these can be used as natural markers of habitat shifts by individuals, for example during ontogenetic migrations of juveniles from nursery areas to reefs (Cocheret de la Morinière *et al.*, 2003) or during the settlement of fish larvae, from pelagic to demersal habitats (Herzka *et al.*, 2001).

Not all tissues, usually targeted for isotopic studies, can be used to trace the life history of reef fish. Indeed muscle, liver, or blood samples, for example, undergo metabolic turnover on a weekly or monthly scale, which limits the retrospective period that can be studied (Tieszen *et al.*, 1983; Trueman *et al.*, 2012). Otoliths, fins, and scales, on the other hand, are characterized by an accretion of constituent elements as individuals grow, which means that they can be used to collect data on the life history of individuals, from their earliest to adult stages (Jones, 1986;

Trueman and Moore, 2007; Woodcock and Walther, 2014; Tzadik *et al.*, 2017). In recent years, the use of the crystalline lens (or ocular lens) in isotopy has been proposed (Bell-Tilcock *et al.*, 2021). The crystalline lens is a metabolically inert structure, which like otolith *annuli* is formed of layers that are deposited sequentially (Wallace *et al.*, 2014; Peebles and Hollander, 2020). Lens development begins in the early embryonic stage (Grainger, 1992) and, as fish grow, lens cells are deposited in concentric layers, like the layers of an onion (Wallace *et al.*, 2014; Bell-Tilcock *et al.*, 2021). The lens core, composed of nuclear fiber cells in the center, is the oldest part of the lens and the most recent growth of the fish is recorded in the outermost layer (Peebles and Hollander, 2020). Therefore, the lens of adult fish offers the possibility of reconstructing $\delta^{13}C$ and $\delta^{15}N$ trajectories throughout the fish's life and allows the inference of ecological interpretations from them (Wallace *et al.*, 2014). Since 2014, numerous studies have experienced the use of fish lens, with an isotopic approach. Topics have included the accumulation of chemical pollutants in organisms such as mercury (Miraly *et al.*, 2022; Stounberg *et al.*, 2022), the study of inter-individuals variations in diets or over their lifetimes (Wallace *et al.*, 2014; Quaeck, 2017; Simpson *et al.*, 2019; Liu *et al.*, 2020; Wallace *et al.*, 2023) but also the spatial movements of individuals during their lifetime (Wallace *et al.*, 2014; Wallace, 2019; Faletti and Stallings, 2021; Vecchio *et al.*, 2021; Buell-Fleming, 2022; Michaud, 2022). Studies have generally focused on carnivorous reef species, targeted by fishing activities (Wallace *et al.*, 2014; Curtis *et al.*, 2020; Faletti and Stallings, 2021; Vecchio *et al.*, 2021; Michaud, 2022; Wallace *et al.*, 2023). Despite their major ecological importance, no studies have been carried out on small reef-associated species such as damselfish, or herbivores such as Acanthuridae and Scaridae.

In the present study, we seek to trace the life history of three reef species (*Microspathodon chrysurus*, *Lutjanus apodus* and *Sparisoma viride*) in studying trajectories in their feeding habits, habitat shifts and behavioral patterns (sedentary vs mobile species) during ontogeny. *Microspathodon chrysurus* is a benthic-feeder omnivorous fish: juveniles eating copepods or small crustaceans, and adult eating on copepods, shrimps, or sponges, but can also eat microalgae in high proportion (around 50%). This species which lives on coral reefs at both juvenile and adult stages is found most of the time in cavities and holes from reef formations. This sedentary species is highly territorial and did not shift in habitat during ontogeny (Emery, 1973; Robertson, 1984; Welsh *et al.*, 2013). *Lutjanus apodus* is a carnivorous species, with juvenile feeding on invertebrates and adults on invertebrates as well as other fish. Contrary to *M. chrysurus*, the ontogeny of these species is characterized by a habitat shift from nursery area such as seagrass meadows and/or mangroves to reef environment (Verweij *et al.*, 2008; Garcia *et al.*, 2014; Vaslet *et al.*, 2015). This species is considered as mobile on the reef (Hitt *et al.*, 2011). Finally, *Sparisoma viride* is an herbivorous species at both juvenile and adult stage (Burkepile *et al.*, 2022), with changes in algal material between the two stages (Overholtzer and Motta, 1999). This species also undergoes a habitat shift during ontogeny using seagrass meadows or mangroves as nursery areas as juvenile and coral reefs as adult (Overholtzer and Motta, 2000; Nagelkerken and Van Der Velde, 2003; Nagelkerken, 2007; Jaxion-Harm *et al.*, 2012).

For these three species, we measured isotopic compositions of C, N and S, and study isotopic trajectories along the different layers of the adult crystalline lens in order to answer several questions: 1) Do the isotopic trends over the lifetime of individuals differ within the same species? Can we define a high or low individuality based on the life traits of each species? 2) Do individual isotopic trajectories differ between sites for each species? This could highlight the influence of sites on ontogenetic shifts in diet and habitat for each species; 3) Do isotopic trends over the lifetime of individuals differ between species for the same site? This could suggest that differences in species' life history behavior led to different habitat uses.

2. Material and method

2.1. Sampling site

The present study was carried out in Guadeloupe Island, Lesser Antilles (16°15'N; 61°30N). Several coastal ecosystems are present around the island: fringing reefs (*i.e.*, reefs growing near the coastline), barrier reefs (*i.e.*, continuous barrier parallel the coastline separated by wider lagoons) and patch reefs (*i.e.*, highly diversified non-reef building coral communities), but also seagrass meadows and mangroves (Figure 1).

2.2. Fish sampling

Three teleost species belonging to three families were studied: the yellow tail damselfish *Microspathodon chrysurus* (Pomacentridae), the schoolmaster snapper *Lutjanus apodus* (Lutjanidae), and the stoplight parrotfish *Sparisoma viride* (Scaridae). Fishes were sampled from September 2022 to November 2022 at nine sites around the island (Figure 1). Due to logistical issues, it was not possible to catch all species at all sites (Figure 1B). Adults were collected by spearfishing, hand nets or fish traps, while juveniles were sampled with hand nets.

The juvenile and adult's stages were identified using scientific articles (Potthoff *et al.*, 1987 for *Microspathodon chrysurus*), identification guides (Humann and Deloach, 2018) and Fish Base (Froese and Pauly, 2022). The main criteria used to differentiate adults from juveniles were the color of the individuals and their length (Table 1).
Fishes were euthanized with an immersion in a solution of eugenol diluted with seawater, and then placed on an ice box with ice. Adults and juveniles were measured (total length in cm) and weighted (in g). A sample of the white dorsal muscle was taken from adult fish and oven-dried 48h at 60°C. Eyes were removed and conserved in a freezer until analysis. Eyes were then dissected to extract the lens, which was placed under a microscope to be measured to the nearest mm to establish a relation between lens size and standard length of individuals.

For each adult individual (n = 5 per site for *M. chrysurus*, n = 5 per site for *L. apodus* except for Les Saintes et Marie Galante sites where n = 3, and n = 5 for S. viride except for Pointe de la Grande Vigie site where n = 2) the lens was taken out of the eye through a lateral incision using a scalpel. The lens of either the left or right eye can be used, since there is no difference in the number of layers or isotopic composition of lenses belonging to the same individual (Faletti and Stallings, 2021). The lens was placed in a glass dish filled with distilled water to rinse it, and the epithelium (thick layer protecting the lens) was removed using flat forceps and discarded, because its isotopic composition differs from those of lens layers (Faletti and Stallings, 2021). Lens layers were removed using micro-forceps and lens delamination was completed once the lens nucleus was reached (*i.e.,* the innermost part of the lens, forming a hard transparent ball from which no layer can be removed). Lens were photographed between each layer removal under a binocular equipped with a camera and the lens diameter was measured (in mm) for each layer using this picture (IS Capture software). Each layer was placed individually in a pre-weighed tin cup, oven-dried during 48 hours at 60°C and weighted (to the µg precision). The number of layers obtained per individual in this study varied according to species (Table 1), and ranged from 6 to 14, which corresponds to values previously reported in the literature (Wallace *et al.*, 2014; Faletti and Stallings, 2021).

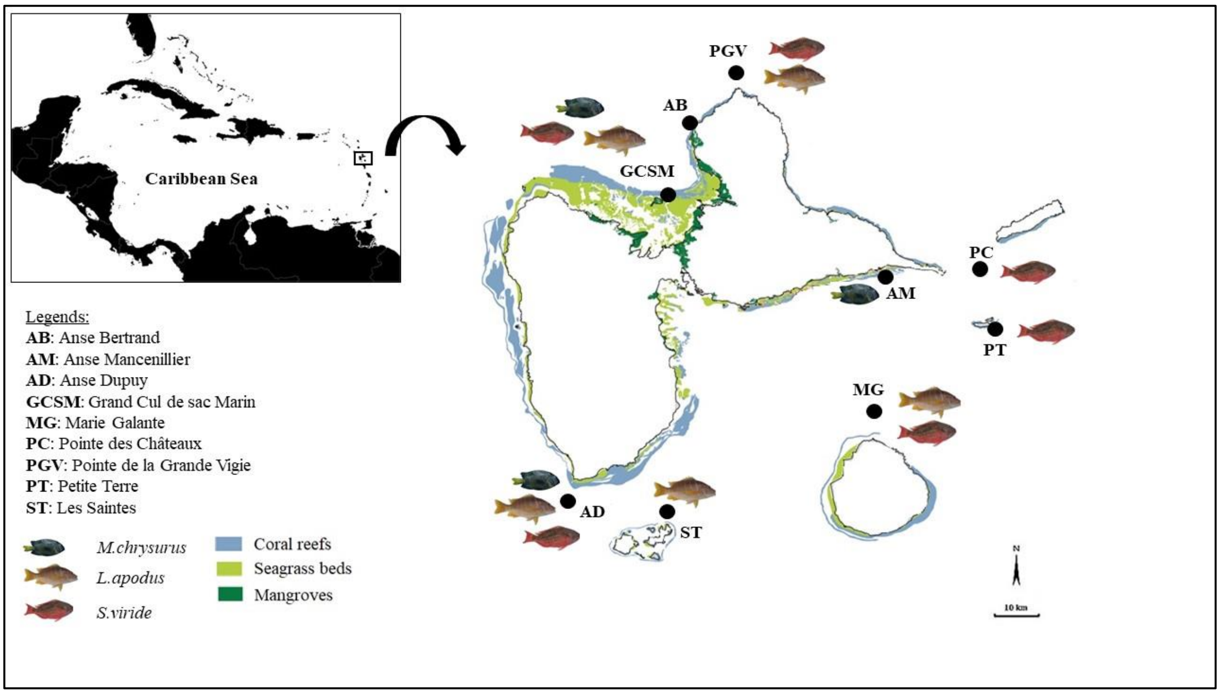


Figure 1 Location of coastal habitats around Guadeloupe according to Bouchon *et al*. (2008), and location of the nine sampling sites and relative species sampled at each site.

Table 1 Standard length range (SL in cm) of juveniles and adults of each fish species, total number of individuals studied (n) and mean number (min-max) of lens layers found and studied in each case.

	Juveniles		Adults		
Species	n	SL range (cm)	n	SL range (cm)	Mean number of lens layers (min-max)
Microspathodon chrysurus	8	4.5 – 10	13	10 – 25	8.0 (6 – 11)
Lutjanus apodus	13	3.0 – 15	34	15 – 38	11.3 (7 – 14)
Sparisoma viride	6	3.0 – 15	31	15 – 43	9.6 (8 – 11)

2.3. Benthic component

For sites common to all three studied species (Anse Dupuy, Grand Cul Sac Marin), primary producers were collected to provide isotopic baselines respective to each habitat (Table 2). Samples were collected by hand, placed in separate containers, and kept on ice during transport. Each sample was then placed in a tube and freeze-dried until analysis. To complete this database of isotopic baselines, isotopic compositions of various benthic components and potential food sources were obtained from previous studies on similar sites (Dromard *et al.*, 2015) (Table 2).

Each sample of primary producers was ground and weighed before being placed in a tin cup. For the macroalga *Galaxaura oblongata*, which naturally contains carbonates, a sub-sample was acidified with hydrochloric acid (HCl) to eliminate calcified inorganic matter, which has a less negative carbon isotopic composition than organic matter (De Niro and Epstein, 1978). This sub-sample was rinsed with distilled water and then placed in an oven for 48 h at 60°C to dry before being placed in a cup. Other samples were not acidified and directly dried following the same methodology.

2.4. Stable isotopes analyses

Measurements of isotopic compositions of benthic components and lens layers were done using a mass spectrometer coupled with an elemental analyzer.

For fish lens layers, isotopic compositions as well as carbon, nitrogen, and sulfur concentrations ([C]%, [N]% and [S]%) were performed using an isotope ratio mass spectrometer (preciSION) and an elemental analyzer (Vario Microcube, Elementar) respectively. Isotopic compositions were expressed by standard delta notation (δ values in ‰) according to the following formula:

$\delta = [(R_{sample} / R_{standard} - 1)] \times 1000$,

where R is the ratio of a heavy isotope to a light isotope (^{13}C:^{12}C, ^{15}N:^{14}N or ^{34}S:^{32}S). $R_{standard}$ correspond to international standards (Vienna Pee Dee Belemnite for $\delta^{13}C$, N2 in atmospheric air for $\delta^{15}N$, and Canyon Diablo troilites for $\delta^{34}S$).

2.5. Calculation of $\Delta^{13}C$, $\Delta^{15}N$ and $\Delta^{34}S$

Fractionations between isotopic compositions obtained with the outermost layer and a selected inner layer have been noted $\Delta^{13}C$, $\Delta^{15}N$ and $\Delta^{34}S$ for carbon, nitrogen and sulfur, respectively. To obtain comparable values, the inner layer chosen had to be almost identical in diameter in all individuals and have reach an isotopic equilibrium. This layer could therefore not correspond to the innermost layer of the lens which still retains partly the stable isotopes composition of oceanic larval stage (*i.e.*, unreached isotopic equilibrium). For sulfur, isotopic values for the innermost layers could not be obtained (too little biological material). Thus, the inner and outer layers selected where not the same than for $\Delta^{13}C$ and $\Delta^{15}N$ (Table 3).

Table 2 Details (average, minimum and maximum diameter, and fish length) of inner and outer layer of lens used for the isotopic fractionation.

Species	Isotopic fractionation	Inner layer		Outermost layer	
		Mean diameter (min-max)	Fish length (mm)	Mean diameter (min-max)	Fish length (mm)
M. chrysurus	$\Delta^{13}C$ and $\Delta^{15}N$	1.64 (1.42 - 2.1)	30	3.87 (2.44 - 4.96)	120
	$\Delta^{34}S$	2.04 (1.82 - 2.6)	5	4.07 (3.74 - 4.42)	13
L. apodus	$\Delta^{13}C$ and $\Delta^{15}N$	2.30 (2.02 - 3.52)	40	7.76 (5.2 - 10.86)	250
	$\Delta^{34}S$	2.12 (1.9 - 2.56)	4	5.06 (4.46 - 5.54)	16
S. viride	$\Delta^{13}C$ and $\Delta^{15}N$	1.40 (1.22 - 1.66)	3.8	4.19 (2.54 - 5.62)	29
	$\Delta^{34}S$	2.6 (2.24 - 3.14)	17	4.40 (3.56 - 5.62)	29

2.6. Statistical analyses

All statistical analyses were performed with the R Core Team (2023), a language and environ ment for statistical computing, Vienna, Austria.

Firstly, the relationship between standard length of fishes (adults and juveniles) and the diameter of lens, for each species was investigated with two regression models (linear and polynomial) using the "lm" function of the package "stats". The two models were then, compared with each other using a one-way ANOVA, testing the null hypothesis that the fits of the two models are equal and that the polynomial regression model is not significantly better than the linear regression model. In the results, if the p-value is > 0.05, this means that the null hypothesis is accepted and that linear regression is representative of the data; on the contrary, if the p-value is < 0.05, this means that the null hypothesis is rejected, and that polynomial regression represents the data better than linear regression.

Secondly, a comparison of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values between white muscle from adults and lens (outermost layer) was carried out to determine whether the two tissues could be complementary in isotopic analyses. A Wilcoxon-Mann-Whitney test was used, as the number of data was less than 30 for each species.

Thirdly, individual trajectories for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were graphically compared for each species at each site. Additionally, obtained values were statistically compared 1) between individuals of the same species in order to test differences at the level of the individual, 2) for each species between sites, and 3) between species for a similar site using non-parametric Kruskal-Wallis tests, followed by a Dunn multiple comparison tests, when the first results showed significantly different. Similarly, $\Delta^{13}C$, $\Delta^{15}N$ and $\Delta^{34}S$ (fractionations between outermost and inner layer values) were also compared 1) between individuals of the same species for each species, 2) between sites for each species, and 3) between species for sites GCSM and AD, where the three species were found together. These comparisons were also conducted using Kruskal-Wallis tests, supplemented by Dunn multiple comparison tests.

3. Results

3.1. Relation between standard length of individuals and lens diameter

For *Microspathodon chrysurus* and *Lutjanus apodus*, linear regressions were the most significant relationship between standard length of individuals and lens diameter (ANOVA, p-value > 0.05). On the other hand, for *Sparisoma viride*, this relationship did not appear to be linear and was represented by a polynomial regression (ANOVA, p-value < 0.05) (Figure 2).

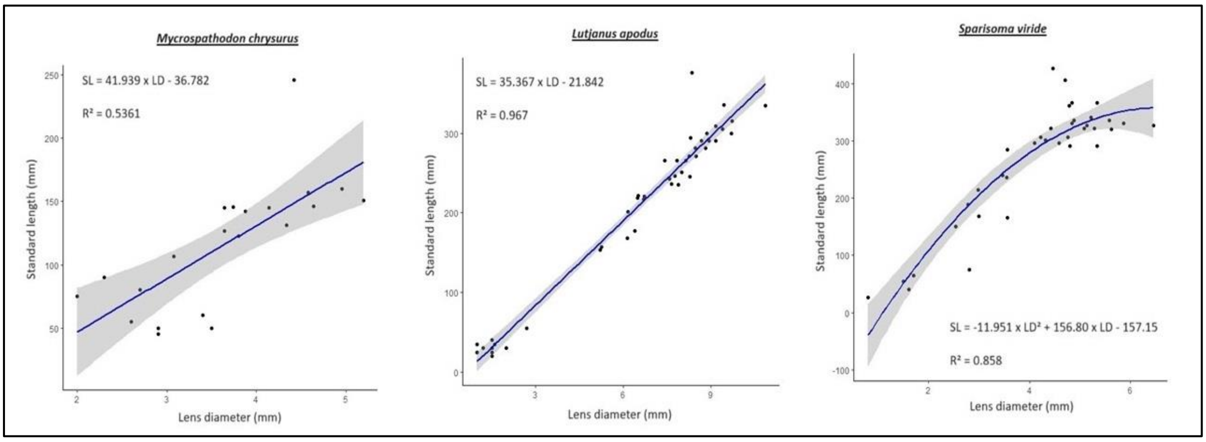


Figure 2 Relationships between standard length (SL) and lens diameter (LD) for *Microspathodon chrysurus* (n = 21), *Lutjanus apodus* (n = 47) and *Sparisoma viride* (n = 37), tested with linear and polynomial regressions

3.2. Comparison between white muscle and lens isotopic compositions

Whatever the species, the $\delta^{13}C$ values obtained with the last lens layer samples did not differ from those obtained from white muscle samples (Mann-Whitney-Wilcoxon, p-value > 0.05). For $\delta^{15}N$ values, the only significant difference between both tissues was observed for *S. viride* (mean difference of 1.35 ‰ ± 0.61). $\delta^{34}S$ values differed significantly between muscle and lens samples for the three species (Mann-Whitney-Wilcoxon, p-value < 0.05). $\delta^{34}S$ values were greater in muscles rather than in lens (mean values increased by +1.58 ‰ ± 0.10 for *M. chrysurus*, +7.06 ‰ ± 5.07 for *L. apodus* and +2.33 ‰ ± 0.02 for *S. viride*).

3.3. Comparisons between isotopic compositions of adult's outer lens layer between sites and between species

There were no differences in $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values measured in between adults individuals (the outer lens layers) from the same species (Kruskal-Wallis, p-value > 0.05).

For *M. chrysurus*, $\delta^{15}N$ values measured in the outer lens layer significantly differed between sites (Table 4). Thus, individuals of GCSM site exhibited lower $\delta^{15}N$ (mean ± SD : 6.7 ± 0.2‰) values than individuals of the two other sites (7.5 ± 0.4‰ and 7.5 ± 0.6‰). There were no differences in $\delta^{13}C$ and $\delta^{34}S$ values between sites for this species. For *L. apodus,* only $\delta^{13}C$ values differed between sites with sites GCSM and MG showing higher values (-16.4 ± 4.5‰ and -14.4 ± 0.4‰ respectively) than AD site (-11.9 ± 0.7‰). For *S. viride,* none of the isotopic values varied significantly according to sites (Tables 4).

On the two sites occupied by the three studied species, *i.e.,* GCSM and AD, mean values of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ differed between species (Table 5). At GCSM site, $\delta^{15}N$ and $\delta^{34}S$ of *L. apodus* adults differed from those of the two other species, exhibiting higher values of $\delta^{15}N$ and lower values of $\delta^{34}S$. At AD site, *S. viride* exhibited lower nitrogen values (5.9 ± 0.9‰) than *M. chrysurus* and *L. apodus* (respectively 7.5 ± 0.4‰ and 9.1 ± 1.5‰). On the same site, *S. viride* was characterized by intermediate carbon isotopic composition, between those of the two other species, but statistically different. Then, *L. apodus* exhibited lower $\delta^{34}S$ values (11.3 ± 4.1‰) than *M. chrysurus* (20 ± 0.6‰).

Table 3 Results of Kruskal-Wallis tests comparing A) isotopic compositions of the outer lens layer between sites and B) $\Delta^{13}C$, $\Delta^{15}N$ and $\Delta^{34}S$ (fractionation between outermost and inner layer values) of individuals between sites. Results in bold show significant differences between sites.

	$\delta^{13}C$			$\delta^{15}N$			$\delta^{34}S$		
A)	χ^2	df	p-value	χ^2	df	p-value	χ^2	df	p-value
M. chrysurus	4.860	2	0.088	9.488	2	**0.009**	0.125	2	0.939
L. apodus	9.588	4	**0.048**	0.963	4	0.915	6.135	4	0.189
S. viride	9.896	5	0.078	4.985	5	0.418	6.263	4	0.180
	$\Delta^{13}C$			$\Delta^{15}N$			$\Delta^{34}S$		
B)	χ^2	df	p-value	χ^2	df	p-value	χ^2	df	p-value
M. chrysurus	0.42	2	0.811	4.02	2	0.134	2.4	2	0.301
L. apodus	3.439	4	0.487	11.962	4	**0.018**	9.417	4	0.051
S. viride	11.443	5	**0.043**	6.572	5	0.254	2.109	4	0.716

3.4. Trajectories and variations of isotopic composition during life history of fish

There were no differences in $\Delta^{13}C$, $\Delta^{15}N$, and $\Delta^{34}S$ values between individuals of the same species (Kruskal-Wallis, p-value > 0.05).

No significant differences in the $\Delta^{13}C$ values were found between sites for *M. chrysurus* and *L. apodus* (Table 4). Indeed, when analyzed visually, $\delta^{13}C$ values tended to increase or remained stable over the lifetime of the fish, represented by the increase in lens diameter (Figures 3 and 4). On the other hand, $\Delta^{13}C$ differed between sites for *S. viride* (Table 4), with values measured at AD site differing from those measured at GCSM et PGV, but also values from GCSM different from those at PC site. $\delta^{13}C$ values tended to remain stable over the lifetime of the fish at AD, whîle these values followed a U-shaped curve at GCSM and PGV (Figures 3 and 4). Moreover, $\delta^{13}C$ values seemed to increase along the U-shaped curve for GCSM site, whereas its decreased at PC site.

Concerning $\Delta^{15}N$ values, there were no differences between sites for *M. chrysurus* and *S. viride* (Table 4). Indeed, for these two species, $\delta^{15}N$ values tended to increase or remain stable over the lifetime of the fish at all sites (Figures 5 and 6). However, for *L. apodus*, $\Delta^{15}N$ differed between AD, GCSM and the other sites (Table 4). Then, $\Delta^{34}S$ did not differ between sites for the three species (Table 4 and Figures 7 and 8).

When looking at the sites that were common to the three fish species, there were no significant difference in the $\Delta^{13}C$, $\Delta^{15}N$ and $\Delta^{34}S$ values between species for AD (Table 5). However, for GCSM, *L. apodus* $\Delta^{15}N$ values were higher than those of *S. viride*. Indeed, *L. apodus* $\delta^{15}N$ values seemed to increase over the lifetime of the fish at GCSM, whereas it seemed to decrease for *S. viride* on the same site (Figures 5 and 6).

Table 4 Results of Kruskal-Wallis tests used to compare isotopic values of the outermost layer ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) and $\Delta^{13}C$, $\Delta^{15}N$ and $\Delta^{34}S$ between fish species, on the two sites in which they were found together (AD: Anse Dupuy and GCSM: Grand Cul-de-Sac Marin). Bolded results represented significant differences.

Sites	$\delta^{13}C$			$\delta^{15}N$			$\delta^{34}S$		
	χ^2	df	p-value	χ^2	df	p-value	χ^2	df	p-value
GCSM	5.020	2	0.081	8.791	2	**0.012**	6.144	2	**0.046**
AD	9	2	**0.011**	10.493	2	**0.005**	7.854	2	**0.020**
	$\Delta^{13}C$			$\Delta^{15}N$			$\Delta^{34}S$		
	χ^2	df	p-value	χ^2	df	p-value	χ^2	df	p-value
GCSM	0.422	2	0.810	7.736	2	**0.021**	2.050	2	0.359
AD	5.660	2	0.059	3.840	2	0.147	4.821	2	0.090

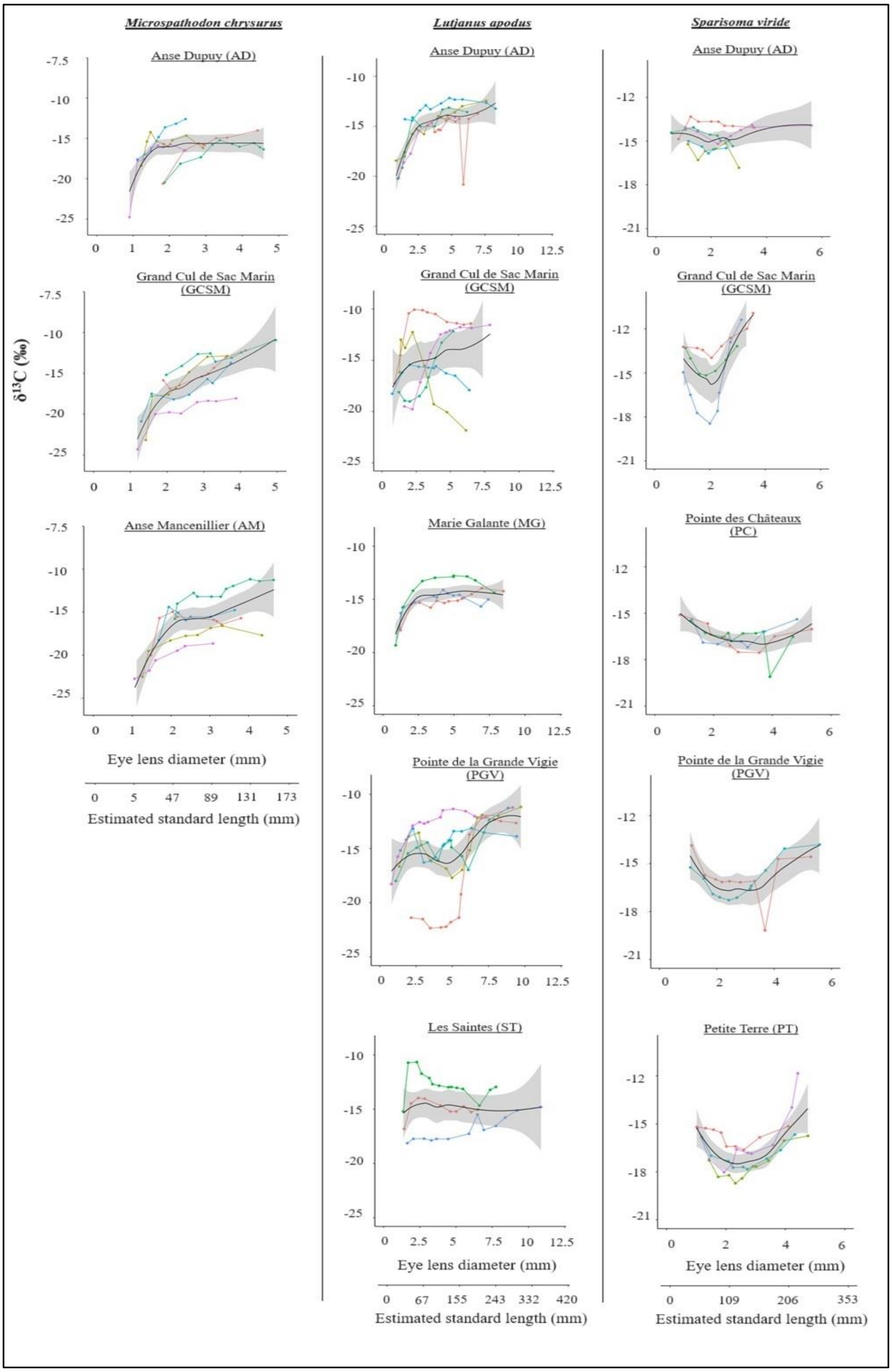


Figure 3 Individual (colors) and loess (black) curves of $\delta^{13}C$ eye lens function of eye lens diameter, for *M. chrysurus*, *L. apodus* and *S. viride* at each site.

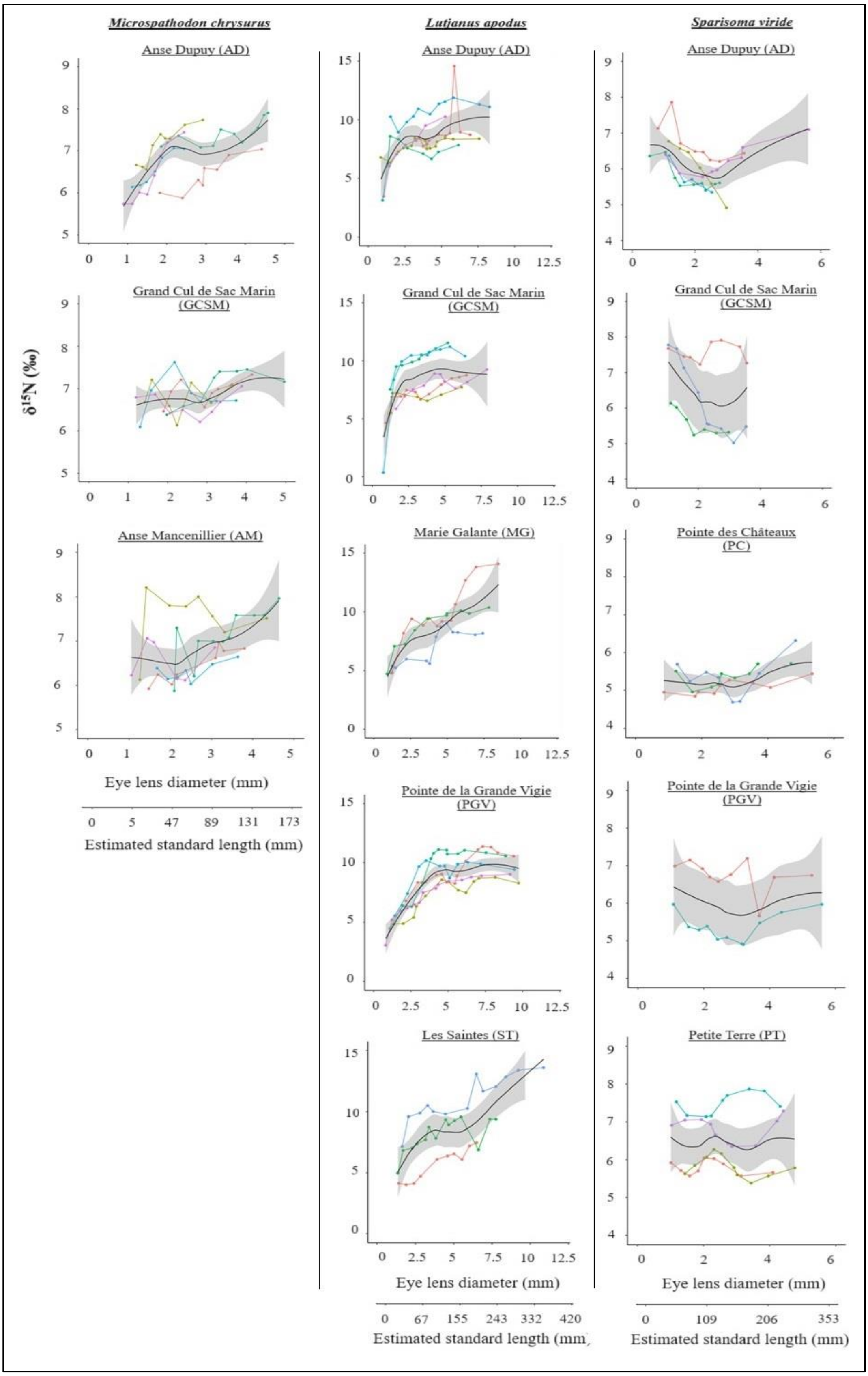


Figure 4 Individual (colors) and loess (black) curves of δ^{15}N eye lens function of eye lens diameter, for *M. chrysurus*, *L. apodus* and *S. viride* at each site.

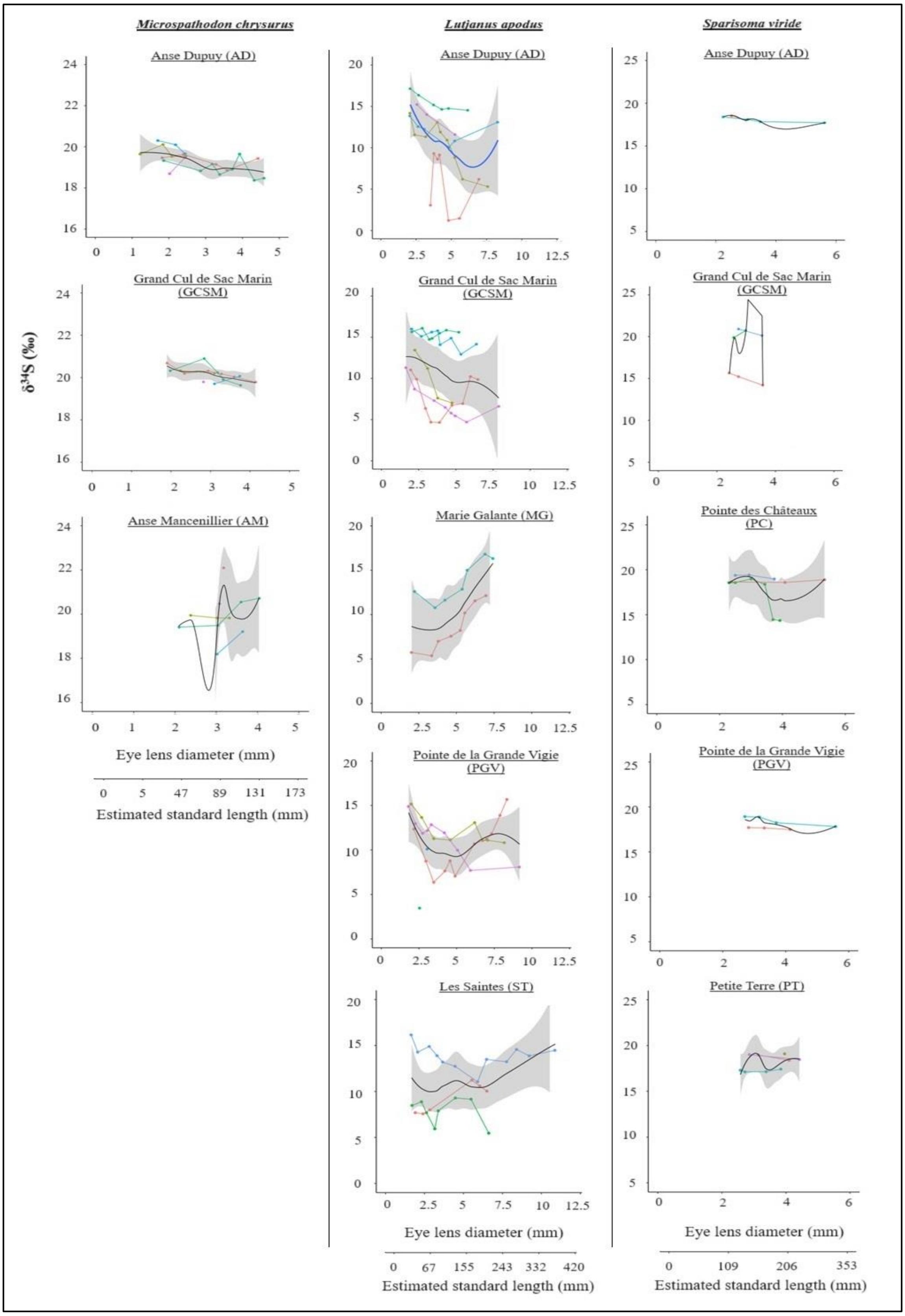


Figure 5 Individual (colors) and loess (black) curves of δ^{34}S eye lens function of eye lens diameter, for *M. chrysurus*, *L. apodus* and *S. viride* at each site.

4. Discussion

4.1. Relation between standard length individuals and lens diameter

In this study, the relationship between lens diameter and individual size was modelled using two types of regression. For *M. chrysurus* and *L. apodus*, a linear relationship fitted the data better than a non-linear one, while for *S. viride*, the relationship did not appear to be linear. As the crystalline lens increases over the life of the fish, leading to an increase in tissue volume throughout life, there is an almost isometric growth in lens diameter relative to body size (Bassnett & Beebe, 1992; Kröger, 2013). However, the relationship between lens diameter and body size is species-specific. Indeed, in the study conducted by Quaeck-Davies *et al.* (2018), it has been shown that the relationship between lens diameter and body size, while linear for all species, was species-specific.

These results confirm that lens diameter and body size are related for three reef fish species belonging to different families. We can therefore assume that the same applies to other reef fish species. However, the linear relationship already found in other studies is not respected for one of the three species, so even if the lens diameter increases with the size of the individuals, the relationship between them must first be tested for a correct interpretation of the results.

Nevertheless, the data collected in the present study may be subject to certain biases. Firstly, the number of individuals used is relatively low, particularly for juveniles. For *M. chrysurus*, *L. apodus* and *S. viride*, we studied 21, 47 and 37 individuals respectively, including 8, 13 and 6 juveniles. This number of individuals, often less than 30, may have led to biases in the relationships found for each species. On the other hand, the adult individuals used were collected at different sites, and the juveniles could not be collected at all the adult collection sites. This could induce diversity in the life histories of the individuals and therefore contribute to different relationships.

We recommend increasing the number of measurements to access to a more accurate relationship between size of individuals and lens diameter, in order to use the latter parameter as a *proxy* of the stage of development.

4.2. Comparison between white muscle and lens isotopic ratios

For the three reef fish species, carbon isotopic values did not differ between adult white muscle and lens. In contrast, nitrogen isotope values differed for *S. viride* only, and sulfur isotope values differed for all species, with a lower sulfur value in the lens than in the muscle. In previous studies, the comparisons of the isotopic composition of lens and muscle samples showed that $\delta^{13}C$ values either did not differ or could be enriched in the lens compared to muscle (Falleti & Stalling, 2021; Rosinski *et al.*, 2023). However, nitrogen isotopic compositions generally did not differ between the two tissues, unlike to what we found for *S. viride* (Quaeck-Davies *et al.*, 2018; Falleti & Stalling, 2021; Rosinski *et al.*, 2023). Finally, it appears that isotopic sulfur compositions may be lower in the lens than in muscle in adult fish (Rosinski *et al.*, 2023), as it was the case in the present study.

These results indicate that the isotopic compositions (for carbon and nitrogen) of the outer lens layer of reef fish can be used to study the isotopic niche of adult, in the same way as studies carried out on muscle, and that lens values can be compared with those of muscle widely present in the literature. If the results for the outer layer of the lens are similar to those for muscle, this potentially means that each layer of the lens will give similar values to muscle over the lifetime of the fish. This underlines the value of using the adult lens to obtain information on the whole of an individual's life, and not just at a given point in time, as is the case with muscle. For other components, such as sulfur, it is necessary to test the differences between the lens and white muscle to determine whether there is an enrichment or a depletion. The results of this study show that sulfur appears to be enriched in white muscle for three species from different families and confirms the findings of previous studies on other species. We could therefore assume that sulfur is generally depleted in the lens of fish. What's more, using the eyes rather than the flesh of the fish could make it possible to collect data on individuals already fished for commercial purposes, for example, and thus limit the collection of adults in the environment.

4.3. Variations in isotopic composition over the life cycle of fish

4.3.1. Inter-individual variations

Without going into detail for each site, mainly due to the lack of data, the isotopic compositions of the outermost layer, reflecting adult life, but also the fractionation values (difference between the outermost and innermost layers) corresponding to the life history of the fish, were compared between individuals. For the three species, there were no differences between individuals.

These results suggest that, irrespective of the site from which individuals originate, individuals of each species are characterized by similar ranges of isotopic compositions, reflecting mainly their trophic niche and main habitat. Indeed, even if small variations can be observed between the diets of juveniles and adult, their general trophic level remains similar. *Microspathodon chrysurus* eats on coral or sponges, and on benthic sources (copepods, ostracods, amphipods) at juvenile stage. Adults feed also on sponges, benthic sources, and filamentous algae (around 50%) (Ciardelli, 1967; Emery, 1973). *Lutjanus apodus* juveniles tend to consume prey present in seagrass beds or mangroves, such as shrimps, crabs, or other crustaceans, while adults also consume fishes. The main difference is that juveniles use smaller and softer prey compared to adults (Szedlmayer and Lee, 2004; Case *et al.*, 2008). Then, *S. viride* is herbivorous at both juvenile and adult stages, even if ontogenetic variations of their diet have been described before (from calcareous algae for juveniles to brown or green macroalgae for adults; Overholtzer and Motta, 1999; Burkepile *et al.*, 2022). Thus, despite some variations of the diet between juveniles and adults, the trophic level of the three species stays similar during their lifetime.

Isotopic compositions in sulfur obtained in the results generally decrease during the lifetime of each individual (from the inner layer to the outmost layer). Benthic primary producer exhibits lower $\delta^{34}S$ values than pelagic primary producer and so their consumers could exhibit lower values too when recruiting on benthic habitats (Connolly *et al.*, 2004; Newsome *et al.*, 2007; McCauley *et al.*, 2014). Thus, these results suggest the same process of habitat change for all individuals, notably the transition from oceanic pelagic to reef benthic habitat during the colonization process (Dufour and Galzin, 1993 ; Caley, 1993 ; Lecaillon and Lourié, 2007).

4.3.2. Inter-sites variations

For each species, isotopic compositions and fractionations have been compared between sites, revealing significant spatial variations.

For *L. apodus* and *S. viride*, isotopic values taken over the lifetime of individuals differ. The $\Delta^{15}N$ values differ for *Lutjanus apodus*, suggesting different use in food sources according to sites, and the $\Delta^{13}C$ values differ for *S. viride*, suggesting a site-specific use of different habitats. At the juvenile stage, *L. apodus* juveniles tend to consume small invertebrates such as zooplankton, annelids, crabs, or shrimps (Cocheret de la Morinière *et al.*, 2003; Nagelkerken & Van der Velde, 2004; Vaslet *et al.*, 2015). It is a species known to undergo habitat changes during its life history, that often lead to dietary changes, and therefore shifts in the isotopic compositions of individuals. To avoid intensive predation, juveniles generally develop in nursery areas, such as mangroves or seagrass beds before returning to reefs (Kimirei *et al.*, 2013; Garcia *et al.*, 2014; Vaslet *et al.*, 2015). Juveniles, which live and feed in the mangroves during the day, move to the seagrass beds to complete their nutrition at night (Verweij *et al.*, 2007). Movements between coastal habitats (seagrass beds and mangroves) during ontogeny could be responsible of the differences in the nitrogen isotopic fractionation of individuals between sites. It could explain why nitrogen isotopic fractionation ($\Delta^{15}N$ values) at GCSM site (where mangroves and seagrass beds are present) differed from the other sites. Then, some reefs are not located close to mangroves, which may result in young settling directly on the reef and possibly using seagrass bed at night. They can feed on coral reef only, or on an association of sources from both coral reef and seagrass beds. In the two cases, they didn't use food sources of mangroves. These possibilities could explain why nitrogen isotopic fractionation at AD site (where seagrass beds are present but not mangroves) differs from GCSM site and from the other sites.

On the same way, *S. viride* could also undergo ontogenetic habitat shifts (Overholtzer and Motta, 1999; Burkepile *et al.*, 2022). Indeed, juveniles can directly integrate reefs where conspecifics live, or can also take shelter in nursery areas such as seagrass bed before integrating groups of adults on reefs (Overholtzer and Motta, 2000; Nagelkerken and Van Der Velde, 2003; Nagelkerken, 2007). The difference in carbon composition over lifetime between sites can probably be explained by the difference in the habitat composition at each site. Indeed, juvenile which are not using nursery habitat will use food source with different isotopic composition, than those passing by nursery habitat. In the present study, AD site differs from GCSM and PGV sites. AD and GCSM sites are characterized by the presence of seagrass beds (mangroves also present at GCSM), while there are maybe less nursery areas at PGV. Similarly, the results for the GCSM site differ from those for the PC site, where there are maybe few nursery areas. We can thus suppose that the several habitats present on a site, as well as the behavior of individuals, can influence the use of food resources by consumers, and so, influence the isotopic composition of individuals along their lifetime.

Then, for *M. chrysurus* and *L. apodus,* there were differences in the isotopic composition of adults between sites. The values of $\delta^{15}N$ values differ for *M. chrysurus* suggesting a change in food source used between sites, and the $\delta^{13}C$ values differ for *L. apodus*, suggesting change in habitat use for feeding between sites. *M. chrysurus* is a species known to live exclusively on the reef at both juvenile and adult stages, in colonies of *Millepora* and *Acropora palmata* (Emery, 1973; Waldner & Robertson, 1980), caves and crevices (Emery, 1973; Leal *et al.*, 2013) in slightly deeper areas for adults. By consequences, the difference in $\delta^{15}N$ values observed between adults individuals from GCSM and those from AD and AM could be explained by a natural spatial variation of the baseline's isotopic composition. Unfortunately, this hypothesis could not be tested as we do not know the isotopic composition of the food sources at each site. These differences can also be due to the heterogenous diet of *M. chrysurus* and the availability of each food resource at each site. Indeed, *M. chrysurus* is characterized by a diversified diet, including corals (mainly *Millepora* spp.), benthic sources (copepods, ostracods, amphipods) and sponges for juveniles (Ciardelli, 1967; Emery, 1973; Leal *et al.*, 2013), and consume diverse crustaceans and filamentous algae for adults, which could reach 50% of their diet (Ciardelli, 1967; Emery, 1973; Robertson, 1984). Then, for *L. apodus* adults it has already been shown in adult large carnivores that, when the distance travelled to find food increases, the prey assemblages used may differ (Cocheret de la Morinière *et al.*, 2003). This may be responsible for the differences in adult carbon isotope compositions between sites. In the present study the carbon isotopic composition differs between AD and GCSM, AD and MG, and MG and PGV sites. The food source can thus be different in accessibility and composition explaining the differences observed. Fish from the AD site are enriched by 4.6‰ in carbon compared with those from the GCSM site and by 2.6‰ in carbon compared with those from the MG site. Assuming a mean enrichment of 1.5 ± 0.5‰ for carbon between sources and consumers (Sweeting *et al.*, 2007), it is possible to link the isotopic compositions of individuals with potential feeding sites. The values found for individuals at the AD and PGV sites could be linked to the use of seagrass beds habitats, whose average isotopic composition in the Caribbean ranges from -9.9 to -13.2 ‰ (Fry *et al.*, 1982; Nagelkerken and Van der Velde, 2004). For the GCSM site, on the other hand, the individuals' feeding grounds could be mangroves. Indeed, it has already been shown that carbon isotope composition values were lower in fish feeding in mangroves than in fish feeding in seagrass beds (Nagelkerken and Van der Velde, 2004). These different feeding locations between sites could therefore be at the origin of the differences in carbon isotopic compositions between adults.

Concerning results of $\delta^{34}S$, the spatial and ontogenetic difference observed between sites was noticed for *M. chrysurus*. Benthic primary producers generally have lower $\delta^{34}S$ values than pelagic primary producers, and this trend is reflected in consumers' isotopic compositions (Connolly *et al.*, 2004; McCauley *et al.*, 2014). Thus, the decrease in $\delta^{34}S$ values over time, for individuals collected at GCSM and AD sites, attests to a shift from pelagic to benthic environments during life, which is the case during the colonization process. At AM, some individuals exhibited an increase in their $\delta^{34}S$ values during their development. Here, we can hypothesize that the food sources consumed by these individuals could be related to pelagic food sources, which is the case of *M. chrysurus,* which can consume zooplankton as one of its food sources (Emery, 1973).

4.4. Inter-species variations

Microspathodon chrysurus, *Lutjanus apodus* and *Sparisoma viride* have be collected jointly on two sites (AD and GCSM).

At AD, *Lutjanus apodus* and *Microspathodon chrysurus* adults exhibited similar isotopic compositions in carbon and nitrogen, which can be explained by a close diet (omnivore and carnivore). These two species differed from *Sparisoma viride* which presented lower δ^{13}C and δ^{15}N than *M. chrysurus* and *L. apodus*. As carbon and nitrogen provide information on the diet of individuals, the difference in isotopic values can be explained by the fact that *S. viride* is an herbivorous species (Burkepile *et al.*, 2022), associated with a low trophic level. *L. apodus* and *M. chrysurus* don't have the same diet but these species use a wide range of food sources including crustaceans (Ciardelli, 1967; Szedlmayer and Lee, 2004). It could therefore explain the similar isotopic composition of the two omnivorous and carnivorous species at AD.

At GCSM, adults of the three species presented differences in their isotopic compositions as well as differences in their Δ values. The differences between isotopic signatures of *S. viride* adults and those of *L. apodus* adults have been previously explained by an important difference in their diet (herbivorous *vs* carnivorous diets). However, in GCSM site, the values obtained for *L. apodus* adults are also different from those obtained for *M. chrysurus* adults, 89hile this time *S. viride* and *M. chrysurus* adults values did not differ. Adult *M. chrysurus* is known to have diversified food sources, a large proportion of which (around 50%) may be represented by microalgae such as diatoms (Ciardelli, 1967; Emery, 1973; Robertson, 1984). At GCSM, it could therefore be a major food source used by *M. chrysurus* adults which would explain its isotopic composition, which is closer to that of *S. viride* at this site. The difference between the Δ^{15}N values of *L. apodus* and *S. viride* can be explained on the one hand by the difference in trophic diet during their life (herbivores vs. carnivores) and on the other hand, by the different ontogenetic movements during the life of the individuals (passage through nursery areas such as mangroves at GCSM for *L. apodus*) which leads to the use of different food sources.

Then, at AD and GCSM, δ^{34}S values obtained for *L. apodus* differed from those obtained for the other two species, exhibiting lower values for *L. apodus*. The carnivorous diet of this species, which consumes a large proportion of Crustacean but also of other fish (Cocheret de la Morinière et al., 2003), may explain the low δ^{34}S values obtained compared with the other two species. Being at a higher level of the trophic chain, it accumulates negative values from its prey and therefore has more negative values than the lower levels of the trophic chain, which include *M. chrysurus* and *S. viride*.

4. Conclusion

In this study, isotopic trends over the lifetime of individuals do not appear to differ within each of the three species studied. However, it would be interesting to increase the number of individuals per site to carry out tests not only within a species, but within a species and for each of the sites studied. It has been shown that, depending on the sites studied, isotopic trajectories during the life of individuals can differ. Differences in isotopic values highlighted ontogenetic changes in diet, which may be due to the food sources present at each site, their ability to collect some categories of food sources and/or to the passage of individuals through different coastal habitats (for *L. apodus* and potentially *S. viride*). Finally, isotopic trends over the lifetime of individuals differ between the three species, when studying at a same site. This can be explained by the diets of the three species, and the differential use of food sources during their lifetimes conditioned by their transition through different habitats such as nursery areas. The isotopic values obtained from the lens of adult fish did not differ from those obtained from their muscle, except for sulfur, for which muscles appear to be enriched. Using the lens of adult fish is therefore a good way of tracing the life history of individuals.

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Supplementary materials

Table 5 Table of mean (± SD) δ13C, δ15N and δ34S, and for Δ13C, Δ15N and Δ34S values for each species at each site.

Species	Site	Mean δ13C ± SD (‰)	Mean δ15N ± SD (‰)	Mean δ34S ± SD (‰)	Mean Δ13C ± SD (‰)	Mean Δ15N ± SD (‰)	Mean Δ34S ± SD (‰)
M.chrysurus	AD	-11.6 ± 0.9	7.5 ± 0.4	20 ± 0.6	1.2 ± 1.7	1.1 ± 0.3	-0.9 ± 0.4
	AM	-13.7 ± 1.4	7.46 ± 0.6	19.8 ± 0.9	1.7 ± 0.4	0.5 ± 1.1	1.3
	GCSM	-11.8 ± 1.4	6.7 ± 02	19.9 ± 0.2	2.4 ± 1.6	0.4 ± 0.5	-0.8 ± 0.1
L.apodus	AD	-11.9 ± 0.7	9 ± 1.5	11.3 ± 4	1.5 ± 1.1	1.1 ± 1.2	-3.6 ± 1.3
	GCSM	-16.4 ± 4.7	9.2 ± 1.5	8.3 ± 4.1	0.34 ± 7.3	1.3 ± 0.8	-3.4 ± 2.3
	MG	-14.4 ± 0.4	10.5 ± 3	19.1	0.4 ± 0.7	3.7 ± 1.9	1.4 ± 1.6
	PGV	-12.6 ± 1.2	10 ± 1	7.6	3.1 ± 3.5	3.2 ± 0.9	-4.1 ± 0.7
	ST	-13.5 ± 1.1	10.6 ± 3.1	15.4 ± 3.1	0.1 ± 2.7	3.2 ± 0.8	0.7 ± 2.6
S.viride	AD	-15.1 ± 1.2	5.9 ± 0.9	18.6 ± 0.2	-0.4 ± 06	-0.4 ± 1.1	-0.9 ± 0.3
	GCSM	-11.3 ± 1.6	6 ± 1.1	16.3 ± 3.6	3.2 ± 2.9	-1 ± 1	-1.4
	PC	-16 ± 0.6	5.8 ± 0.4	19	-0.52 ± 0.7	0.42 ± 0.3	-2.3 ± 2.7
	PGV	-14.2 ± 0.5	6.4 ± 0.5	18.3	1.6 ± 0.7	0.1 ± 0.7	-0.2
	PT	-14.6 ± 1.9	6.5 ± 0.9	18.8 ± 0.1	1 ± 0.7	0.1 ± 0.1	-0.3 ± 0.4

Table 6 Results of Dunn multiple comparison test following Kruskal-Wallis test to compare adult isotope values for each species between sites. Results in bold are significant.

Species	Dunn multiple comparison test		
	Isotopic ratio	Sites	p-value
M. chrysurus	$\delta^{15}N$	AD-AM	0.831
		AD-GCSM	**0.006**
		AM-GCSM	**0.012**
L. apodus	$\delta^{13}C$	AD-GCSM	**0.014**
		AD-MG	**0.011**
		AD-PGV	0.345
		AD-SAINTES	0.086
		GCSM-MG	0.700
		GCSM-PGV	0.109

		GCSM-SAINTES	0.643
		MG-PGV	**0.076**
		MG-SAINTES	0.448
		PGV-SAINTES	0.354

Table 7 Results of Dunn multiple comparison following Kruskal-Wallis test to compared isotopic values obtained at each site between species. Bolded results represented significant results.

Site	Dunn multiple comparison		
	Isotopic ratio	Species	p-value
GCSM	$\delta^{15}N$	*M. chrysurus – L. apodus*	**0.015**
		M. chrysurus – S. viride	0.639
		L. apodus – S. viride	**0.010**
	$\delta^{34}S$	*M. chrysurus – L. apodus*	**0.015**
		M. chrysurus – S. viride	0.257
		L. apodus – S. viride	0.163
AD	$\delta^{13}C$	*M. chrysurus – L. apodus*	1.000
		M. chrysurus – S. viride	**0.008**
		L. apodus – S. viride	**0.013**
	$\delta^{15}N$	*M. chrysurus – L. apodus*	0.228
		M. chrysurus – S. viride	**0.037**
		L. apodus – S. viride	**0.001**
	$\delta^{34}S$	*M. chrysurus – L. apodus*	**0.005**
		M. chrysurus – S. viride	0.252
		L. apodus – S. viride	0.252

Table 8 Results of Dunn multiple comparison test following Kruskal-Wallis test to compared $\Delta^{13}C$, $\Delta^{15}N$ and $\Delta^{34}S$ of individuals between sites. Bolded results represented significant results.

Species	Dunn multiple comparison test		
	Isotopic ratio	Sites	p-value
L. apodus	$\Delta^{15}N$	AD-GCSM	0.959
		AD-MG	**0.033**
		AD-PGV	**0.022**
		AD-SAINTES	**0.027**
		GCSM-MG	**0.037**
		GCSM-PGV	**0.025**

		GCSM-SAINTES	**0.030**
		MG-PGV	0.883
		MG-SAINTES	0.947
		PGV-SAINTES	0.825
S. viride	$\Delta^{13}C$	AD-GCSM	**0.006**
		AD-MG	0.357
		AD-PC	0.960
		AD-PGV	**0.037**
		AD-PT	0.063
		GCSM-MG	0.396
		GCSM-PC	**0.026**
		GCSM-PGV	0.788
		GCSM-PT	0.440
		MG-PC	0.391
		MG-PGV	0.548
		MG-PT	0.762
		PC-PGV	0.074
		PC-PT	0.125
		PGV-PT	0.673

Table 9 Results of Dunn multiple comparison test following Kruskal-Wallis test to compared $\Delta^{13}C$, $\Delta^{15}N$ and $\Delta^{34}S$ of the common sites between species. Bolded results represented significant results.

Site	Dunn multiple comparison test		
	Isotopic ratio	Species	p-value
GCSM	$\Delta^{15}N$	*M. chrysurus – L. apodus*	0.144
		M. chrysurus – S. viride	0.134
		L. apodus – S. viride	**0.006**

Chapitre 3 : Importance de la métamorphose dans la réussite du recrutement.

3.1) Modification de la forme du corps au cours de l'ontogénie

Article 4 – Vignaud L., Frédérich B., Boudault M., Chatagnon A., Rault P.L., Cordonnier S., Lecchini D., Dromard C.R., The phenotypic disparity at population level varies over ontogeny : an example using coral reef fishes, Ecology (en révision)

Abstract

The phenotypic diversity, *i.e.,* disparity, present within populations is of crucial importance for their adaptation but it is also needed for the operation of natural selection. To date, very few studies questioned the variation of disparity levels within species populations over the ontogeny. The complex life cycle of many coral reef teleost fishes is made of ontogenetic ecological shifts, and thus provides an ideal system to study the distribution of disparity over ontogeny. Here, the disparity of body shapes was quantified and studied over the ontogeny of eight coral reef fish to test the validity of two hypothesized patterns: (1) the oceanic environment seems more homogenous than the reef environment and may ultimately sustain lesser phenotypic disparity within larval populations, and (2) selective mortality and predation acting during habitat transitions may reduce the level of phenotypic diversity during reef fish growth. Body shape varied during the ontogeny of all studied species, with a lengthening of the overall body shape and a shortening of the cephalic region. Conversely to the other species, *S. coruscum* has a more massive and wider body in adults and juveniles than in post-larval stage. The largest amount of body shape variation occurred between the post-larval and the adult stages, probably associated with the major ecological transition between the oceanic and the reef environment. Interestingly, shape variation between juvenile and adult stage is also driven by ontogenetic shift in species ecology. Supports on the two main hypotheses were mixed. Indeed, the level of body shape disparity did not vary during the ontogeny of some species when the peak of disparity levels being present at different stages depending on the species. The distribution of body disparity level over ontogeny does not follow a general rule, but depends on a mixture of external (*e.g.*, habitat diversity) and internal (*e.g.,* physiological state of metamorphosis) factors. Future similar studies are certainly needed to test whether phylogeny

or ecology would be the main driver of the ontogenetic dynamics of phenotypic disparity in reef fishes.

Key words : Body shape – morphology – habitat shifts – geometric morphometrics - diversity

1. Introduction

Individual apparent characteristics such as morphology, physiology or behavior is defined as its phenotype. Phenotypic variation corresponds to variation in these characteristics among individuals of a population and is generally highly adaptive. This phenotypic variation is universal and is mainly due to environments which vary (Whitman and Agrawal, 2009). Character variability among individuals in a population can be directly observed at birth. Indeed, an individual's phenotype at birth is determined in part by the transmission of genes and by the environmental conditions during its development (Byers, 2008; Plard *et al.*, 2016). However, the variability of phenotypes can also occur later during ontogeny. Abiotic and biotic factors can interact with an individual's development and thus disrupt the correspondence between its phenotype and the environment. In response to different environmental conditions, phenotypes may vary during growth, a process known as phenotypic plasticity (Nicoglou, 2015). Phenotypic variation within one generation is almost always non-genetic, and is often adaptive, enabling individuals to cope with environmental modifications (Meyers and Bull 2002; DeWitt and Scheiner, 2004).

Ontogenesis itself can therefore be seen as a continuous variation of phenotypes to adapt to the environments in which the individual evolves (Schlichting and Smith, 2002). Phenotypic variation can ensure that organisms are best adapted to their environment and thus limit mortality. For example, mortality in early life stages varies according to phenotypes: different cohorts may have developed under dissimilar environmental conditions and/or come from genetically different source populations, leading to variation in the distribution of phenotypes and therefore their greater or lesser vulnerability in an environment (Johnson *et al.*, 2014). However, it would be interesting to study how this diversity is distributed between the different stages, and whether this level of phenotypic diversity (*i.e.,* disparity) is more or less important at certain stages of life, or whether it is distributed in the same way throughout ontogeny.

In coral reefs, teleost fishes have a complex life cycle that generally takes place in two distinct environments: the pelagic environment where most of larvae live and the reef environment for the juveniles and the adults (Leis *et al.*, 1996; Hixon, 1998). The transition of the larvae from the pelagic to the reef environment is known as settlement (Dufour and Galzin, 1993). During this key period, post-larvae metamorphose into juveniles, under the influence of thyroid hormones (Bishop *et al.*, 2006; Holzer *et al.*, 2017; Roux *et al.*, 2019). This process gives rise to morphological (*e.g.*, general body, scales, otolith shape), physiological (*e.g.*, vision) and behavioral changes to adapt to their new environment (McCormick *et al.*, 2002; Frédérich *et al.*, 2010; Frédérich *et al.*, 2012; Vignon, 2012; Cortesi *et al.*, 2016; Fogg *et al.*, 2022; Martinez-Leiva *et al.*, 2023). Juveniles have all the characteristics of the adults except for size (smaller) and sexual maturity (Danilowicz, 1997; Mc Cormick *et al.*, 2002). During settlement, they must choose their habitat among the many potential substrates (remain on the reef or settle for a time in nursery areas), intra- and interspecific competitors, and predators (Parish 1989; Planes *et al.*, 1993; Balon, 1999; Nagelkerken *et al.*, 2000a).

The habitat transitions that occur during ontogeny are subject to different selection forces. In the early life stages, the transition from pelagic oceanic to benthic reef environment is subject to natural selection and predation: individuals that have not developed optimally enough to make the transition between the two environments will generally not survive and would be easy preyed (Searcy and Sponaugle 2001; Sponaugle and Grorud-Colvert, 2006). Once on the reef, the choice between different habitats is linked to minimizing the risk of mortality and maximizing growth rate. The presence of sufficient resources (habitat and food), or predation, are therefore also selective forces that influence phenotypic adaptation and habitat choice (Lima and Dill, 1990; Benard, 2004).

Due to their complex life cycle with habitat transitions at different stages and the various selective forces to which they are subjected, reef fishes offer a unique opportunity to study variation in the level of phenotypic diversity (disparity) during ontogeny: whether the different selection forces associated with habitat transitions create disparity or, on the contrary, reduce it during the growth of individuals. Thus, the present study aims to quantify and compare phenotypic variation in populations of reef fishes over their ontogeny. In the post-larval stage, individuals are adapted to an oceanic pelagic environment, unlike the juvenile and adult stages which, after metamorphosis, have a morphology adapted to the benthic reef environment. In some species, juveniles use nursery habitats and do not join the adult habitat directly. Accordingly, the morphology of post-larvae, juveniles and adults would differ due to specific habitat adaptations (McCormick and Makey, 1997; Frédérich *et al.*, 2012). We expect the diversity of phenotypes (*i.e.*, disparity level) within populations would vary during ontogeny and we will aim to decipher two broad hypotheses. On one hand, the oceanic environment seems more homogenous than the reef environment and may ultimately sustain lesser phenotypic disparity within larval populations. On the other hand, selective mortality and predation acting during habitat transitions may reduce the level of phenotypic diversity during reef fish growth.

2. Materials and methods

2.1. Fish sampling

The present study was conducted in Guadeloupe island, Lesser Antilles (16°15'N; 61°30N). Several coastal ecosystems are present in the island: fringing reefs (*i.e.*, reefs growing near the coastline), barrier reefs (*i.e.*, continuous barrier parallel the coastline separated by wide lagoons) and patch reefs (*i.e.*, highly diversified non-reef building coral communities), but also seagrass meadows and mangroves (Bouchon *et al.*, 2008).

Eight teleost species belonging to five different families were studied: the doctor fish *Acanthurus chirurgus* (Acanthuridae), the five-band surgeonfish *Acanthurus tractus* (Acanthuridae), the schoolmaster snapper *Lutjanus apodus* (Lutjanidae), the yellowtail snapper *Ocyurus chrysurus* (Lutjanidae), the reef squirrelfish *Sargocentron coruscum* (Holocentridae), the striped parrotfish *Scarus iseri* (Labridae), the stoplight parrotfish *Sparisoma viride* (Labridae) and the beaugregory *Stegastes leucostictus* (Labridae). *Acanthurus chirurgus* and *A. tractus* are gregarious herbivorous fishes, grazing in seagrass beds as well as on the reef whatever its ontogenetic stage (juvenile or adult) (Cocheret de la Morinière *et al.*, 2003; Nagelkerken and Van Der Velde, 2003; Duran, 2018). *Scarus iseri* and *Sparisoma viride* are herbivorous fishes, grazing in seagrass beds at the juvenile stage, and in reef areas at the adult stage. Both species present thus a habitat shift during their ontogeny and use seagrass meadows as nursery areas. They lived alone or in very small groups (Nagelkerken and Van Der Velde, 2003; Dromard *et al.*, 2017). *Lutjanus apodus* and *Ocyurus chrysurus* are carnivorous fishes, feeding on invertebrates and fishes. The ontogeny of these two species is also characterized by a habitat shift: juveniles live in seagrass meadows and/or mangroves, and adults in reefs. They are solitary but *Ocyurus chrysurus* can also form groups (Verweij *et al.*, 2008; Vaslet *et al.*, 2015). *Sargocentron coruscum* is a nocturnal carnivorous species associated to the reef during its entire lifespan. *Stegastes leucostictus* is an omnivorous species, feeding on small invertebrates and filamentous algae, and lives at the edge of seagrass beds and reefs. Their juveniles and adults share the same habitat and they mainly feed in seagrass beds (Vaslet *et al.*, 2015).

Three ontogenetic stages were studied: post-larvae (*i.e.*, fish settling on reef habitats), juvenile and adult stages. Post-larvae and juvenile fishes were collected from January 2022 to March 2023 at sites: Anse du Mancenillier, Ilet du Gosier, Ilet à Cochon, Port Louis, Banc-Frotte-Ton-Cul, Banc-des Anneaux, Anse Bertrand and Vieux Fort (Figure 1). Post-larvae were collected by using crest nets and trap CARE (Collected by Artificial Reef Ecofriendly) (Lecaillon and Lourié, 2007). Juveniles were collected by seine and dip nets. After their capture, post-larval and juvenile fishes were euthanized with an immersion in a solution of eugenol diluted with seawater, and then placed on ice. All adult specimens were collected by fishermen in April 2022 and during the ACOBIOM campaign from IFREMER carried out in September 2022. The choice of the eight species depended on the fishery efficiency and the number of individuals for each species at the three ontogenetic stages.

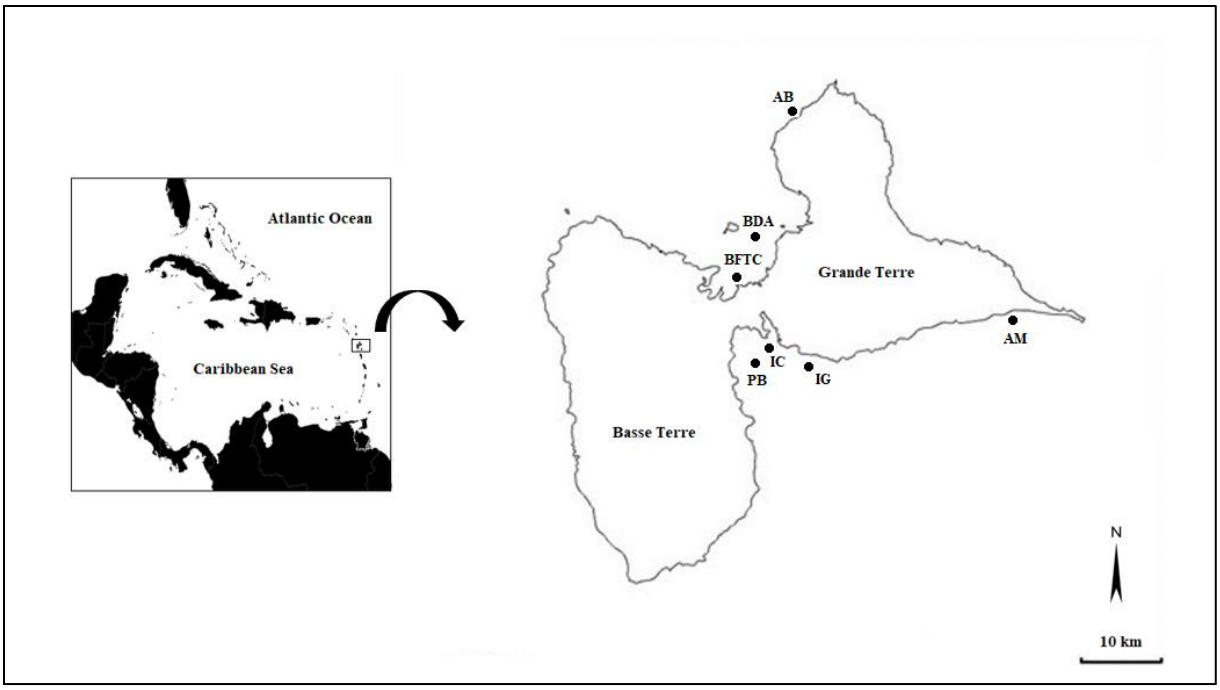


Figure 1 Location of the sampling sites: Anse du Mancenillier (AM), Îlet du Gosier (IG), Îlet à Cochon (IC), Port Louis (PL), Banc-Frotte-Ton-Cul (BFTC), Banc-des Anneaux (BDA), Anse Bertrand (AB) and Vieux Fort (VF).

2.2. Morphometry and shape analyses

The standard length (SL) of every specimen was measured to the nearest 1 mm using a Vernier caliper (Table 1). Then, each specimen was photographed in lateral view using an Olympus Tough TG- 6 camera mounted on a stem. Photographs were done in a global lateral view, with fins fully extended, and the camera was equipped with a level indicator to always obtain the same angle of view (*i.e.*, a perfect lateral view).

Table 1 Name abbreviations, number, and standard length (min-max) of specimens collected for the eight species.

Species	Abbreviations	n			Standard length (mm)		
		Post-larvae	Juvenile	Adult	Post-larvae	Juvenile	Adult
Acanthurus chirurgus	*A. chirurgus*	6	13	20	32-35	35-75	200-225
Acanthurus tractus	*A. tractus*		23	20		30-65	160-190
Lutjanus apodus	*L. apodus*		13	20		21-55	225-340
Ocyurus chrysurus	*O. chrysurus*	22	23	24	16-25	41-138	260-280
Sargocentron coruscum	*S. coruscum*	20	16	12	35-37	40-70	70-80
Scarus iseri	*S. iseri*	21	20	21	24-25	33-37	180-205
Sparisoma viride	*S. viride*		6	12		30-80	295-365
Stegastes leucostictus	*S. leucostictus*	17	16	13	10-20	22-60	60-85

We used Procrustes-based geometric morphometric methods (Bookstein, 1991; Rohlf and Marcus, 1993; Adams *et al.*, 2004) to quantify fish body shape variation and to explore the dynamic of phenotypic disparity over ontogeny. The computer program TPSDig.2, written by F.J. Rohlf (freely available at http://life.bio.sunysb.edu/morph/), was used to digitize 12 homologous landmarks (LMs) to capture body shape (Figure 2, Table 2). Conversely to the other species, *Sargocentron coruscum* has two separated dorsal fins and thus two additional LMs (LM#13 and LM #14, Figure 2) were added to capture morphological variation along the dorsal fins. All specimens were optimally aligned using a generalized Procrustes superimposition method (GPA analysis - Rohlf and Slice, 1990), the grand mean (i.e., the consensus of all specimens) was calculated, and shape variables were then generated as partial warp scores (PWs) including both uniform and non- uniform components (Bookstein, 1991; Rohlf, 1993). These shape variables were then used in the following multivariate analyses. GPA analysis and the production of shape variables were performed for each species, separately.

Figure 2 Lateral view of *Stegastes leucostictus* and *Sargocentron coruscum* at the adult stage, illustrating the landmarks (white dots) used to quantify body shape variation with geometric morphometrics.

Table 2 Landmarks position on fish body.

Landmarks	Position
1	Anterior end of the upper jaw.
2	Center of the eye.
3	Anterior insertion of the dorsal fin.
4	Posterior insertion of the dorsal fin.
5	Dorsal insertion of the caudal fin.
6	Ventral insertion of the caudal fin.
7	Anterior insertion of the anal fin.
8	Posterior insertion of the anal fin.
9	Insertion of the pelvic fin.
10	Inferior insertion of the pectoral fin.
11	Superior insertion of the pectoral fin.
12	Upper-posterior end of the operculum.

A set of different statistical analyses were performed to examine the pattern of shape divergence among ontogenetic stages (post-larvae, juvenile and adult) for the eight fish species. Every species was studied separately. First, a Principal Component Analysis (PCA) was carried out on shape variables to highlight the main axes of shape variation differentiating the ontogenetic stages. PCA plots allowed the representation of a shape space where fish body shapes are distributed and the illustration of the main axes of shape variation within species. To display shape changes associated with PC axes, we used deformation grids produced by TpsRelw (Rohlf and Slice, 1990) representing extreme positive and negative deviations along the PC axes.

Allometric variation is present during the growth of reef fishes (*e.g.,* Frédérich and Vandewalle 2011, Frédérich *et al.,* 2012) and thus, the extent of size variation within ontogenetic stages might certainly explain a fraction of shape disparity. Levene tests revealed that the variance of body size was dissimilar among ontogenetic stages for the great majority of studied species (Table 3). Accordingly, we decided to perform and duplicate all the following statistical analyses by using raw shape data and size-corrected shape data. Size corrected shape data were obtained from multivariate regression models between body shape and the logarithm of size, expressed as centroid size (Bookstein, 1991) for each species, with calculation of residuals of the regression (Klingenberg, 2016).

Statistical analyses were performed to examine the differences in morphology between ontogenetic stages. A visual exploration of the shape space defined by PC axes allowed an intuitive identification of differences among ontogenetic stages. In addition to this qualitative assessment, a Procrustes ANOVA (permutation test, 9999 iterations) followed by pairwise comparisons of Procrustes distances were performed to test if body shape differs among ontogenetic stages for each species. Procrustes distance is a univariate metric defining shape dissimilarity in the Kendall shape space (Bookstein, 1996) and we used it to quantify the amount of shape variation between two respective ontogenetic stages. Procrustes ANOVA, pairwise comparisons and information about Procrustes distances between mean shape of ontogenetic stages were obtained by using the function procD.lm() from the R-package *geomorph* and the function pairwise().

Finally, the diversity of morphologies for each species at each ontogenetic stages was examined by quantifying shape disparity. The level of shape disparity was calculated based on Procrustes variance and we performed pairwise comparisons (permutation test, 9999 iterations) between ontogenetic stages using the function morphol.disparity() in the R-package *geomorph* to test for variation among ontogenetic stages.

Table 3 Levene comparison test among the variances of ontogenetic stage for each species studied.

	Levene test		
Species	df	F	p-value
Acanthurus chirurgus	2	1.997	0.151
Acanthurus tractus	1	3.196	0.081
Lutjanus apodus	1	9.419	**0.004**
Ocyurus chrysurus	2	12.107	**$3.32*10^{-05}$**
Sargocentron coruscum	2	6.298	**0.004**
Scarus iseri	2	24.043	**$2.31*10^{-08}$**
Sparisoma viride	1	0.246	0.6267
Stegastes leucostictus	2	6.028	**0.005**

3. Results

A total of 358 specimens were studied (Table 1). The post-larvae stage could not be collected for *Acanthurus tractus* (Acanthuridae), *Lutjanus apodus* (Lutjanidae) and *Sparisoma viride* (Labridae) (Table 1).

The body shape of every fish species varied during growth. In the great majority of the studied species, the ontogenetic stages occupied different subspaces of the shape space (Figure 3). However, some overlaps between stages could be observed in *Acanthurus chirurgus*, *Ocyurus chrysurus*, *Sargocentron coruscum* and *Scarus iseri* (Figure 3).

For all the studied species, the main morphological variation captured by the first two PC axes concerned the anterior part of the head (LMs 1 and 2) and the relative position of dorsal, caudal, anal, pelvic, and pectoral fins (LMs 3 to 11). Shape variation associated with PC1 was relatively similar in every species: variation of the head length and the overall body length. In all studied species, their growth was characterized by a shortening of the nasal and ethmoid regions of the head (LMs 1 & 2) and by a proportional lengthening of the overall body shape (LMs 3 to 11) (Figure 4). Adults possessed more streamlined bodies with shorter jaws and cheeks in comparison with juveniles and post-larvae (Figure 4). However, the proportional lengthening of the body in *O. chrysurus* is accompanied by a heightening of the anterior body region (LM 3, Figure 4). *Ocyurus chrysurus* and *L. apodus* tend to have greater body lengthening than other species. The general pattern of ontogenetic shape changes in *Sargocentron coruscum* differed from the other species. Rather than a proportional lengthening of the whole-body during growth, the body shape of juveniles and adults appeared more massive than in post larvae (Figure 4). Shape variation associated with the PC2 axis concern all ontogenetic stages. Although this axis has little influence in terms of percentage changes in body shape (Figure 3), it shows variation in body shape width and length in all species.

Size variation within ontogenetic stages might explain a large part of body shape differences among stages. Indeed, for *L. apodus*, *S. iseri* and *S. viride*, body shape does not differ between ontogenetic stages when size variation was no longer considered (Table 4). For the other species, post-larvae and juveniles, or juveniles and adults generally differed significantly in their body shape (Table 4). The use of Procrustes distances allowed a simple, univariate quantification of overall body shape variation between pairs of ontogenetic stages. In *A. chirurgus* and *S. iseri*, the lowest differences in body shape were between the post-larval and the juvenile stages (Figure 5A). On the other hand, the lowest Procrustes distance value was between the juvenile and the adult stages in *S. coruscum* and *Stegastes leucostictus*. If size variation at each stage is ignored, the largest differences are observed between post-larvae and juvenile body shape in *O. chrysurus*, and between post-larvae and juveniles in *S. leucostictus* (Figure 5B).

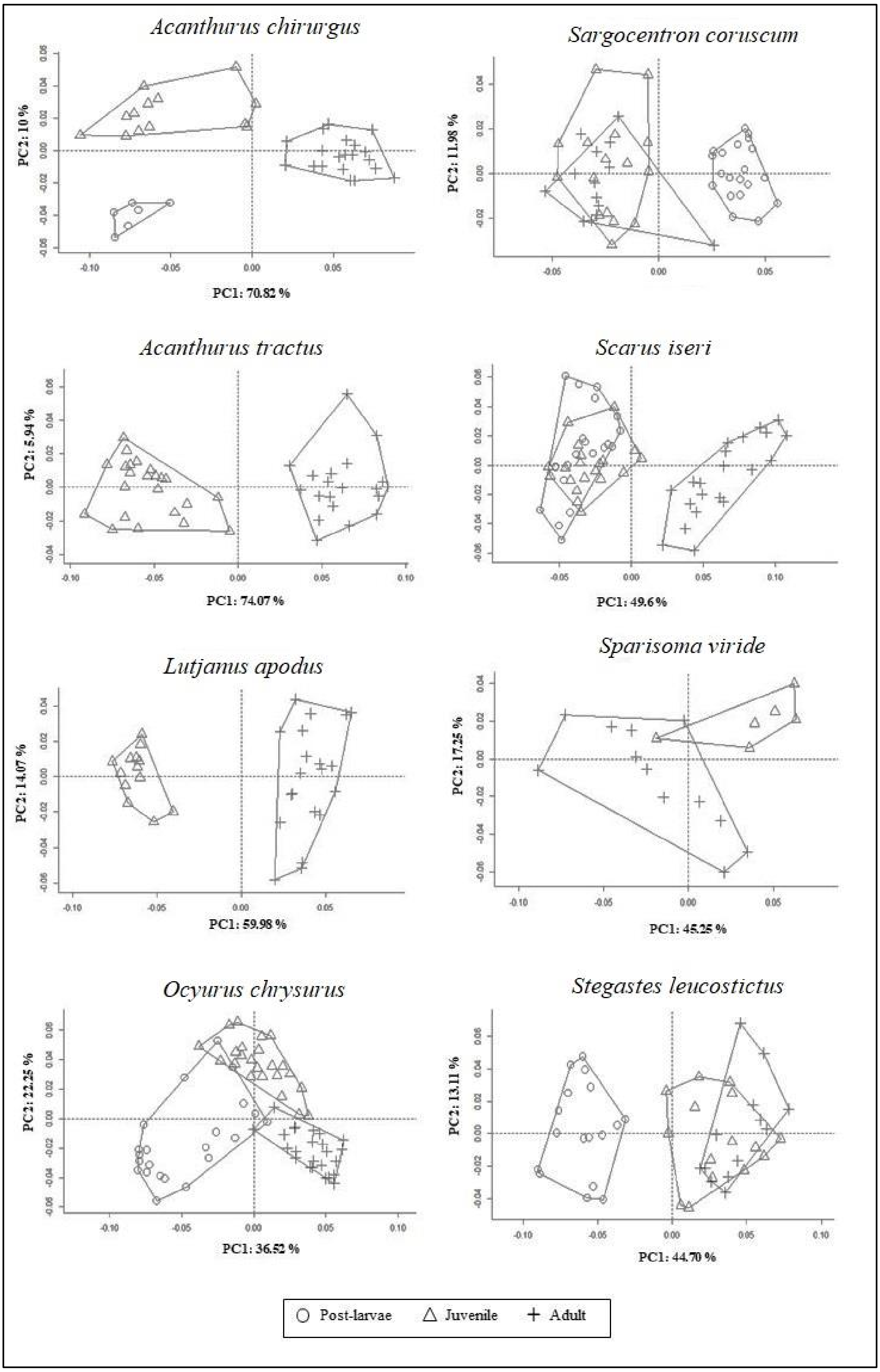


Figure 3 Principal component analysis (PCA) of the variation in body shape of the ontogenetic stages, for each species. Ontogenetic stages are indicated by different symbols and illustrated by convex envelopes.

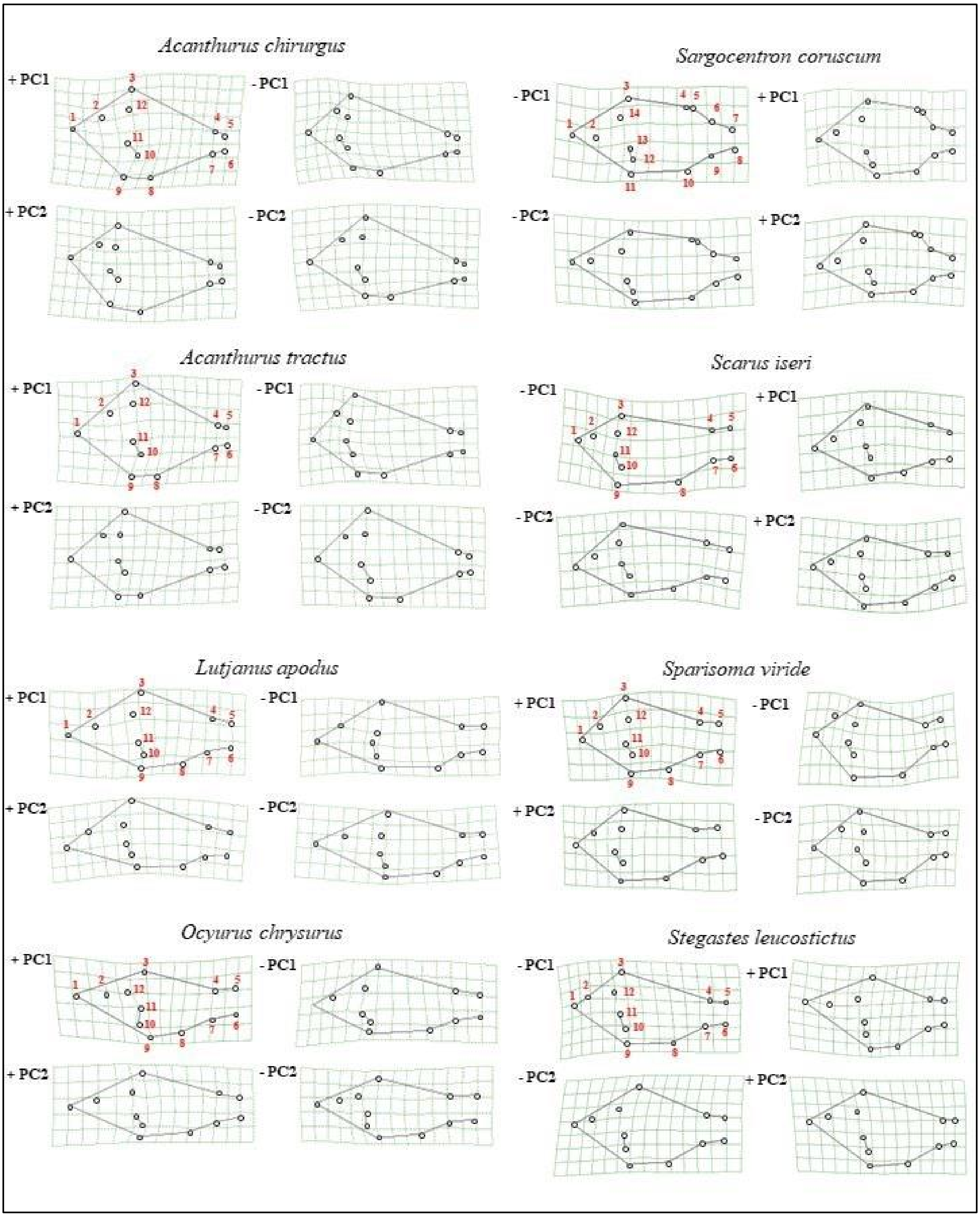


Figure 4 Deformation grids of PC1 and PC2 axis for each species. For each axis, the post-larvae stage is represented on the left and adult on the right.

Table 4 Pairwise comparisons of the differences in body shape among the ontogenetic stages for the eight species, using raw shape data and size-corrected shape data. P-values obtained by using raw shape data are shown above the diagonal and P-values obtained by using size-corrected shape data are shown below the diagonal.

		Post-larvae	Juvenile	Adult
A. chirurgus	Post-larvae		ns	< 0.001
	Juvenile	< 0.001		< 0.001
	Adult	< 0.01	ns	
A. tractus	Juvenile			< 0.001
	Adult		ns	
L. apodus	Juvenile			< 0.001
	Adult		ns	
O. chrysurus	Post-larvae		< 0.001	< 0.001
	Juvenile	< 0.001		< 0.001
	Adult	ns	< 0.001	
S. coruscum	Post-larvae		< 0.001	< 0.001
	Juvenile	< 0.001		ns
	Adult	ns	< 0.001	
S. iseri	Post-larvae		ns	< 0.001
	Juvenile	ns		< 0.001
	Adult	ns	ns	
S. viride	Juvenile			< 0.01
	Adult		ns	
S. leucostictus	Post-larvae		< 0.001	< 0.001
	Juvenile	< 0.001		ns
	Adult	ns	< 0.001	

The level of body shape disparity varied significantly during ontogeny for most of the studied species. Ontogenetic variation of disparity was not detected in *A. tractus, S. coruscum* and *S. viride*. When using raw shape data, the post-larval stage of *A. chirurgus* and *O. chrysurus* were the most disparate (Figure 6A). In *L. apodus* and *S. iseri*, the largest levels of shape disparity were at the juvenile and the adult stages, respectively (Figure 6A). When using size-corrected shape data, no more ontogenetic differences were detected in *A. chirurgus* and *L. apodus* (Fig. 6B).

Figure 5 Procrustes distance (95% confidence interval) for pairs of ontogenetic stages of the eight species. Calculations of Procrustes distance were performed when using raw shape data (A) and size-corrected shape data (B).

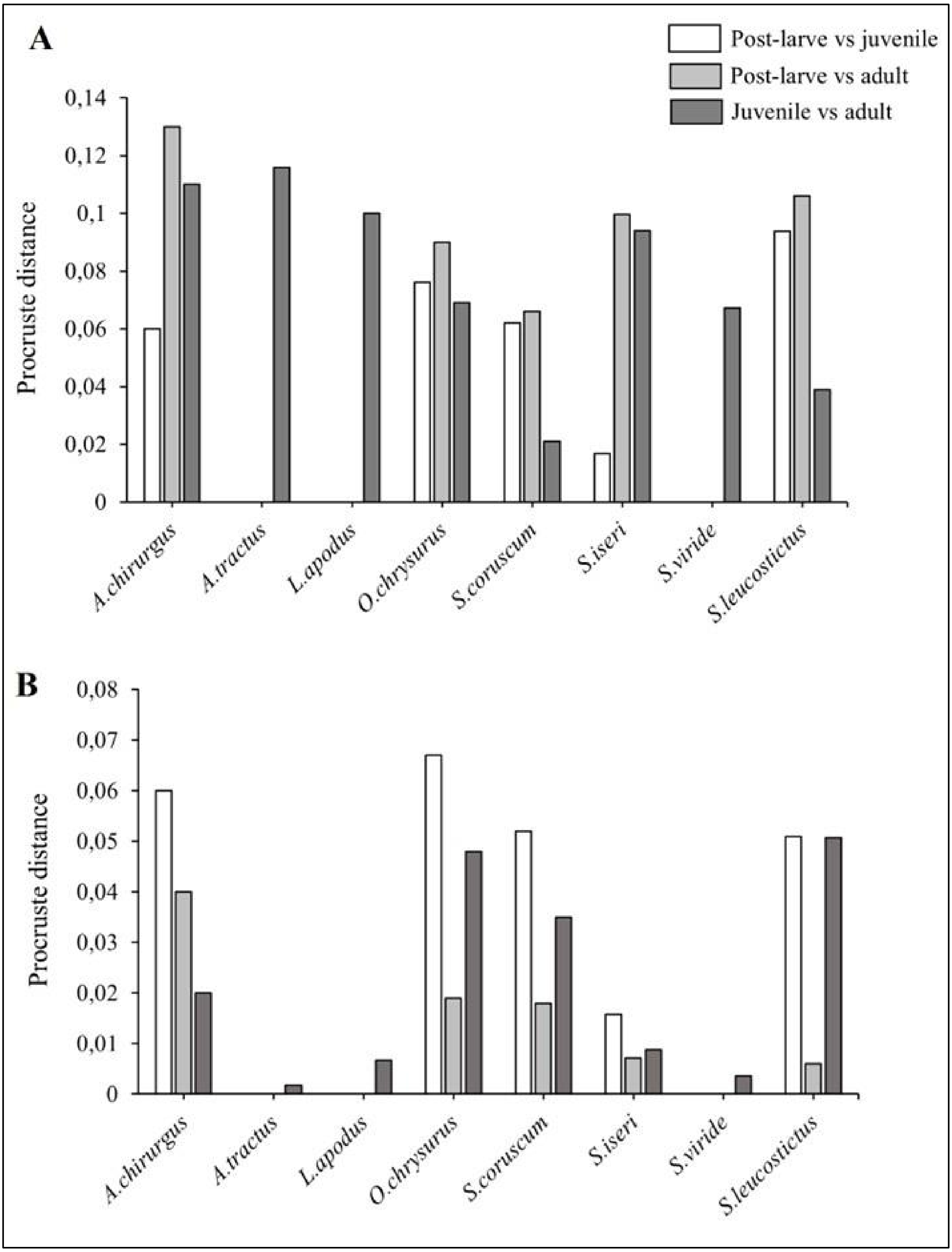
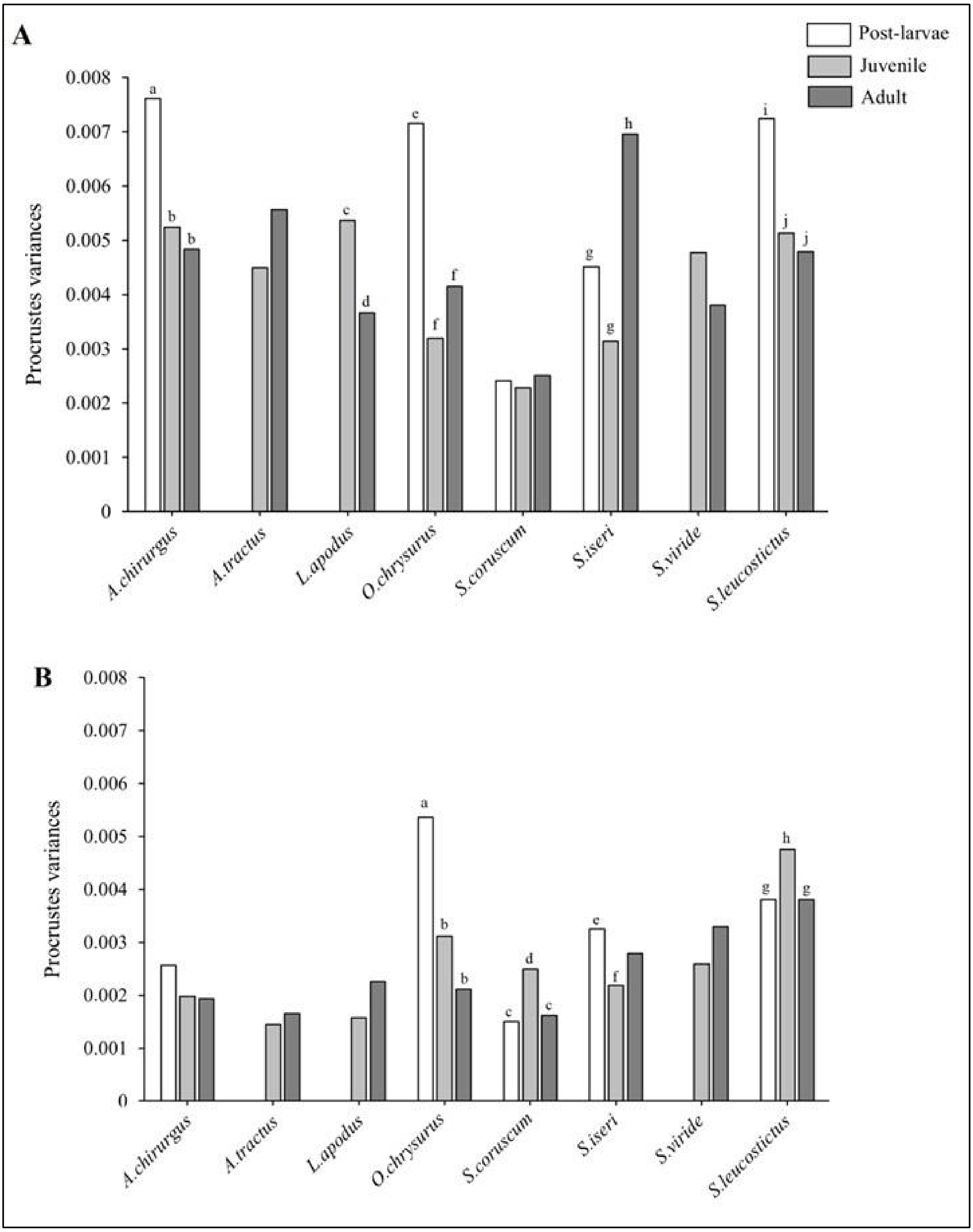


Figure 6 Levels of body shape disparity between the ontogenetic stages of the eight species. Calculations of Procrustes variance were performed when using raw shape data (A) and size-corrected shape data (B). Letters represent the differences in shape disparity between stages for each species.



4. Discussion

Size variation within each ontogenetic stage explains some differences in body shape as well as in level of disparity between stages. In every studied species, post-larvae showing morphologies optimizing survival in the pelagic environment significantly differ in body shape from their adults adapted to the reefs. Moreover, the dynamic of the variation of body shape disparity across ontogeny differs among species. *Acanthurus chirurgus*, *O. chrysurus* and *S. leucostictus* exhibit greater disparity in the post-larval stage, whereas *L. apodus* and *S. iseri* show greater disparity in the juvenile and adult stage respectively. The level of disparity does not vary among stages for *A. tractus*, *S. coruscum* and *S.viride*.

Species differ in their dynamic of body shape changes during ontogeny, and this is mainly due to the presence or the absence of ontogenetic shifts in their ecology. Body shape differences appears at least between the two extreme stages: post-larvae and adults. Adults have a more streamlined body with shorter jaws and cheeks when post-larvae showed a wide, less long body and more elongated jaws and cheeks. Only *S. coruscum* differs from the other species, by showing a more massive body shape in juveniles and adults than in post-larvae. At the post-larval stage, newly settled individuals are not yet totally metamorphosed and therefore still possess body characteristics associated with the pelagic environment. In the ocean, larvae must move horizontally and vertically in the water column to feed, protect themselves from predation (day/night migrations), and return to the reef for colonization (Leis *et al.*, 1996; Leis and Carson-Ewart 1999, 2000, 2001). To do this, they use both the characteristics of the pelagic environment, such as surface currents, which help them in their movements, and they have considerable swimming capabilities (Stobutzki and Bellwood, 1994, 1997; Dudley *et al.*, 2000). According to a study carried out on damselfishes (Pomacentridae), the critical swimming speed of individuals seems to decrease when they are settled in the benthic environment (Stobutzki and Bellwood, 1994). Accordingly, variation in body shape observed between the post-larval stage and the other two stages may therefore be linked to changes in swimming performances. Moreover, the diet of coral reef fish larvae is mainly made of resources present in the water column such as phytoplankton, zooplankton, invertebrate's eggs or nauplii, or particulate organic matter (Pepin and Penney, 1997; Pepin and Dower, 2007; Llopiz and Cowen, 2009; Llopiz, 2013; Riley and Holt, 1993). After metamorphosis, juveniles and adults often adopt a different diet from that of larvae, which is translated to morphological adaptations for the exploitation of new food resources (Frédérich and Vandewalle 2011, Frédérich *et al.,* 2012). Indeed, a head with shorter jaws and cheeks, or a differently positioned mouth, enables adaptation to feeding strategies and/or to different diet. In surgeonfish, for example, a small, ventrally oriented mouth is particularly suited to graze or to bite (Konow *et al.*, 2008). Similarly, in damselfish, these morphological changes are mainly linked to an increase in the suction feeding system (Frédérich and Vandewalle, 2011).

Except in *S. leucostictus* and *S. coruscum*, the body shape of juveniles differs from the one of adults. Such body shape changes between juveniles and adults are only observed in species showing ontogenetic shift in their ecology, which is not the case in *S. leucostictus* and *S. coruscum* (Wellington, 1992; Greenfield, 2013). These two species use the same type of habitat and have the same diet at both stages. Indeed, the territorial *S. leucostictus* occupies a wide range of benthic microhabitats, including live and dead corals, coral debris, sponges, mangrove roots and empty mollusk shells, where both juvenile and adults are observed (Longley and Hilderbrand, 1941; Emery, 1973; Itzkowitz, 1977; Wellington, 1992). It is an omnivorous species that feeds mainly on benthic invertebrates, turf algae and seagrasses at both stages (Wellington, 1992; Vaslet *et al.*, 2015). The soldierfish *S. coruscum* is nocturnal and demersal, living mainly in shallow waters, rocky bottoms, and coral reefs (Humman and Deloach, 2002; Greenfield, 2013). During the day, they hide in hollows and under massive corals (Nelson *et al.*, 2016). No studies have reported the transition of this species through nursery areas and our morphological data agree with the assumption this species recruit directly on the adult habitats. This species feeds mainly on crustaceans living on or near the bottom at both stages (Greenfield, 2013).

Studied surgeon fishes (*A. chirurgus* and *A. tractus*), parrotfishes (*S. iseri* and *S. viride*) and snappers (*L. apodus* and *O. chrysurus*) have a complex ontogeny made of shifts in habitat uses, feeding habits and behavior. After their larval phase, the juveniles of *A. chirurgus* and *A. tractus* are associated with shallow, refuge-rich habitats on restricted reef areas, rarely mangroves or seagrass beds (Nagelkerken *et al.*, 2000b; Robertson, 1988; Robertson, 1992). However, at the adult stage, these fishes use large territories, generally consisting of reefs and seagrass beds. This habitat use implies a nomadic lifestyle that juveniles do not possess, as they generally remain hidden on the reef to avoid predation (Valdes-Muñoz and Mochek, 1994; Castellanos Gell, 2012). In adults, pectoral fin attachment is more anterior and vertical, with a larger base than in juveniles. This variation in fin position has implications for swimming performance, maneuverability and turning ability. Indeed, the morphology of adult fins enable powerful pectoral swimming without compromising capabilities of maneuverability especially needed in structurally complex and turbulent environments such as coral reefs (Fulton 2007) . Juveniles of both surgeonfish species are herbivorous grazers, but their food sources diversify with the extension of territories at the adult stage (Tilghman *et al.*, 2003). Accordingly, morphological variation between juvenile and adult surgeonfish is certainly associated with changes in the diversity of habitat uses. Then, juveniles of *S. viride* and *S. iseri* use seagrass beds or mangroves as nursery areas but adults live on the entire reef (Overholtzer and Motta, 2000; Nagelkerken and Van Der Velde, 2003; Nagelkerken *et al.*, 2007; Jaxion-Harm *et al.*, 2012). The passage of juveniles through nursery areas is associated with changes in morphology between juveniles and adults, such as pectoral fin position and size (Fulton and Bellwood 2002). These species are herbivorous at both juvenile and adult stages (Burkepile *et al.*, 2022) but their ontogenetic habitat shift is associated with changes in algal resources (Overholtzer and Motta, 1999). These changes in food resources are notably linked to morphological modifications of jaws. For example, it has already been described in *Scarus trispinosus* and *Sparisoma amplum* that adults are classified as excavators, while juveniles are scrapers (Lellys *et al.*, 2019). Similarly, juveniles of *L. apodus* and *O. chysurus* pass through the mangrove during their ontogeny before reaching the reef to avoid predation (Kimirei *et al.*, 2013) whereas adults are known to live in the water column in different reef zones (Garcia *et al.*, 2014. An ontogenetic trophic shift is present in both species and is associated with the capture of larger prey (Cocheret de la Morinière *et al.*, 2003; Nagelkerken and Van der Velde, 2004b; Vaslet *et al.*, 2015). Juveniles tend to consume small, soft prey, while adults use larger, harder prey (Case *et al.*, 2008). At the adult stage, *L. apodus* and *O. chrysurus* are both carnivores, with lengthened body shape therefore linked to hunting and ram feeding strategies (Liem 1993). The body shape of adults, with a triangular head and fins evenly distributed along the body, ensures stability and maneuverability in reef waters for these predators (Moyle and Cech, 2000).

The dynamic of body shape disparity over ontogeny greatly varies among species. First, *A. chirurgus*, *O. chrysurus* and *S. leucostictus* exhibit the highest body shape disparity at the post-larval stage. Second, *L. apodus* shows the highest body shape disparity at the juvenile stage, and *S. iseri* at the adult stage. Then, *A. tractus*, *S. coruscum* and *S. viride* did not show significant differences in body shape disparity among stages. We provide thus first evidence that there is not a general rule governing a common ontogenetic dynamic of phenotypic disparity for all reef fishes. Indeed, our eight species failed to validate either of the two hypotheses proposed at the outset of this study. Among the studied species, only *S. iseri* would validate our first hypothesis along which we expected that, at the glance of inter-specific diversification over reef fish ontogeny (Frédérich & Vandewalle 2011), the heterogenous reef environment would sustain higher phenotypic disparity at adult stage than the structurally, homogenous oceanic environment. Conversely, the ontogenetic dynamic of disparity in *A.*

chirurgus, *O. chrysurus* and *S. leucostictus* agree with our second hypothesis stating that the greatest level of disparity should be observed at the larval stage. Indeed, we hypothesized that selective pressure and predation acting during the major habitat transition (reef colonization) could reduce the level of disparity during the growth of reef fish. The absence of variation in the levels of disparity over the ontogeny of *A. tractus*, *S. coruscum* and *S. viride* could be related to a process where ecological factors counter-balanced each other's leading to a constant level of phenotypic disparity over ontogeny. Finally, the juvenile stage of *L. apodus* shows the highest level of body shape diversity, which doesn't fit with both hypotheses. On the one hand, the ecology of the species could explain such a nonlinear variation in the level of shape disparity over ontogeny. *Lutjanus apodus* juveniles growth in varied nursery areas and have been described as using several areas for feeding: mangroves during the day to avoid predation and seagrass beds at night to supplement their diet (Nagelkerken and Van der Velde, 2004b; Kimirei *et al.*, 2013). As recently demonstrated by Reynaud *et al.* (2023), environments and associated ecological factors drive the phenotypic variation at the population level in the surgeonfish *Acanthurus triostegus*. Thus, we might expect that the use of several feeding habitats by *L. apodus* could sustain the greater diversity of phenotypes at the juvenile stage. On the other hand, internal factors such as a varied physiological status among individuals could also explain a higher level of disparity in juveniles. For example, the process of metamorphosis which enable the transition from post-larvae to juvenile have already been shown as source of disparity (Campinho, 2019; Keer *et al.*, 2022; Nguyen *et al.*, 2022). Accordingly, Reynaud et al. (2023) demonstrated the presence of a peak of disparity level at three days of post-settlement in *A. triostegus*, *i.e.,* some days after the metamorphosis driven by thyroid hormones (Holzer *et al.* 2017). Globally, we hypothesized that the diversity of used habitats by juveniles might drive an increase of disparity level during the first days of settlement through a process involving both external and internal factors.

5. Conclusion

Body shape and associated levels of disparity vary during the ontogeny of reef fishes. We provided evidence that body shape variation between ontogenetic stages is clearly associated with habitat, diet, and behavioral shifts. The highest level of body shape disparity can be observed at the post-larval, juvenile, or adult stage when some species do not show any variation in the level of disparity. We demonstrated there is no general rule governing the distribution of body disparity over reef fish ontogeny, but it would depend on a mix of external (*e.g.*, habitat diversity) and internal factors (*e.g.*, physiological status of metamorphosis). Our sampling of eight species remains limited and we ask for similar future studies including several species of the same family and several species having similar ecology to assess if phylogeny or ecology is the main driver of the ontogenetic dynamic of phenotypic disparity in reef fishes.

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Author contributions

Léa Vignaud, Bruno Frédérich, David Lecchini and Charlotte Dromard contributed to the study conception and design. All authors performed material preparation and data collection. Léa Vignaud, Medhi Boudault and Bruno Frédérich performed data analysis. The first draft of the manuscript was written by Léa Vignaud and Bruno Frédérich commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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3.2) Modification du régime alimentaire au cours de l’ontogénie

Article 5 – Vignaud L., Sicard A., Boudault M., Cordonnier S., Lecchini D., Dromard C.R., Isotopic niches of coral reef fishes during larval-juvenile transition, Journal of Fish Biology (en revision)

Abstract

Fish colonization (the settlement of larvae on reefs) and recruitment (the incorporation of juveniles into the adult population) are important ecological phenomena that allow for the renewal of fish populations and, as a result, the preservation of biodiversity on coral reefs. Several morphological and physiological changes occur between the pelagic life of larvae and the benthic life of juveniles, which are related to metamorphosis and the adaptation of individuals to their new way of life in the benthic reef environment. These major changes include dietary shifts, which we aimed to investigate using an isotopic approach in the current study. The isotopic niches of eight reef fish families (Acanthuridae, Apogonidae, Gobiidae, Haemulidae, Labridae, Lutjanidae, Scaridae, and Muraenidae) were measured using carbon and nitrogen stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) to study resource partitioning just before their settlement on reefs. Individuals from different fish families occupied similar isotopic niches, indicating that they used similar food resources and habitat during their pelagic migration, with the exception of the muraenid, which had higher nitrogen signatures and lower carbon signatures.

In parallel, isotopic ratios for two fish families (Haemulidae and Labridae) were measured from the first days of reef colonization to the juvenile stage to reflect dietary and habitat shifts during the larval-juvenile transition. Carbon and nitrogen ratios of haemulids and labrids become significantly enriched as a function of total length of fish, indicating an acceleration of metabolic turnover in growing individuals, a diversification of food resources used, and a transition to ^{13}C-enriched ecosystems such as seagrass beds.

Key words: fish recruitment, larval settlement, stable isotope analyses, trophic ecology

1. Introduction

Coral reefs are among the most diverse and productive ecosystems on the planet, with over 4000 fish species and 800 coral species. Coral reef fishes have a complex life cycle that takes place in contrasted environments, with a pelagic larval phase and a benthic coastal phase on the reef for juveniles and adults (Lechini and Galzin, 2003).

During this cycle, dietary shifts occur in response to habitat changes (pelagic *vs* benthic), as well as morphological and physiological changes related with individual growth. During their dispersive phase, which can last from a few weeks to a few months depending on species (Leis, 1992), larvae feeding habits are mostly based on the consumption of phytoplankton (including dinoflagellates and diatoms), zooplankton (crustaceans, appendicularians, other fish larvae), invertebrates eggs or nauplii, unicellular organisms or particulate organic matter from the water column (Llopiz and Cowen, 2009; Llopiz, 2013; Pepin and Penney, 1997; Pepin and Dower, 2007; Rîley and Holt, 1993). Larvae have good swimming abilities and well-developed sensory capabilities, allowing them to respond to a wide range of cues associated with benthic habitat and thus select a suitable habitat to colonize (Barth *et al.*, 2015; Lecchini *et al.*, 2005; Leis and McCormick, 2002; Vallès *et al.*, 2009). Some larvae maintain the same diet as during their pelagic life during reef colonization, such as serranids, which ingest copepod calanoids throughout their colonization (Llopiz and Cowen, 2009). On the contrary, other species, such as lutjanids and acanthurids, demonstrate a distinct shift in diet following colonization, switching from nauplii to appendicularians or pteropods to appendicularians, respectively (Llopiz and Cowen, 2009). Finally, during this critical developmental stage, individuals may experience a time of fasting (Leis and McCormick, 2002). Individuals undergo "metamorphosis" when they settle on shallow reefs or other nursery habitats, which is a series of irreversible physiological and morphological changes particular to the species. Metamorphosis results in a juvenile ready to "recruit," or enter the adult population. This final stage of the fish biological cycle can be related with another nutritional shift in which juveniles specialized into a certain trophic group might modify their diet when they reach adulthood (Cocheret de la Morinière *et al.*, 2003; Grover *et al.*, 1998). Dietary changes are difficult to detect at any stage of development (larvae or juvenile). Stomach and gut content analyses, one of the oldest approaches for studying fish nutrition, allow for direct observation of the eaten food sources (Cocheret de la Morinière *et al.*, 2003; Fukami *et al.*, 1999). This approach has been utilized for all phases of fish growth (from larvae to adults), however it can be problematic, particularly for identifying semi-digested or damaged food particles. Stomach or gut content analyses are also difficult for early stages of development, not only because of the tiny size of the eaten prey, but also because ingested prey can be rapidly digested and hence impossible to identify (Riley and Holt, 1993). Furthermore, meal composition may be skewed because individuals may regurgitate or defecate during capture stress (Hay, 1981). Finally, stomach contents examination offers information on the composition of the most recent meal rather than long-term food assimilation.

Stable Isotope Analyses (SIA) have been recommended as a complementary method for studying the structure and operation of trophic food-webs, trophic ecology for populations, and behavioral ecology such as migrations (Layman *et al.*, 2011; Skinner *et al.*, 2022). SIA, which is mostly focused on carbon and nitrogen isotopes, assumes that a consumer's isotopic composition is inextricably connected to that of the food sources ingested. An organism's isotopic composition denoted "δ" (delta in ‰), reflects the ratio of the abundance of the heavy to light isotope of an element ($^{13}C/^{12}C$ for carbon and $^{15}N/^{14}N$ for nitrogen), expressed relative to the globally agreed standard for that element. An organism's carbon isotopic composition ($\delta^{13}C$ values) corresponds to the isotopic composition of the organic matter he consumed plus a small fractionation factor (around 1‰ per trophic level), whereas nitrogen isotopic composition increases generally from 3 to 4‰ with successive trophic levels, allowing the use of $\delta^{15}N$ values as a proxy for trophic level. The values of these fractionation factors, however, can differ depending on the species, trophic group, or type of metabolism (Vander Zanden and Rasmussen, 2001). Individual isotopic composition can vary due to inter- or intraspecific diet variations, allowing for the measurement of several metrics (Layman *et al.*, 2007) or the comparison of "isotopic niches" (Newsome *et al.*, 2007), to study generalized *vs* specialized diet, trophic niche overlap, feeding plasticity, or food competition between or within a population (Hammerschlag-Peyer *et al.*, 2011). δ Values can also be used as natural indicators of recent habitat changes by individuals due to variations in the isotopic composition of the "baseline" that is environment specific. Thus, changes in isotopic composition can be used to assess migration of individuals during their ontogenetic development, such as the movement of juveniles from nursery areas (seagrasses and mangroves) to reefs (Cocheret de la Morinière *et al.*, 2003) or larvae migration from pelagic to demersal habitats. (Herzka *et al.*, 2001). These isotopic composition variations are strongly dependent on isotopic turnover time, which is caused by two processes: tissue development and catabolic renewal. As organisms grow, tissues are replaced by new ones, which are produced from newly ingested and digested dietary components, resulting in new isotopic composition (Hesslein *et al.*, 1993; MacAvoy *et al.*, 2001). Thus, turnover rates vary among species and during an organism's life: when an organism grows or develops quickly (as larvae or juveniles), its turnover rate is faster. Previous research, mostly on temperate fish, found that juvenile turnover times range from a few days to several weeks, but adults can have a turnover rate of one year (Bosley *et al.,* 2002). There have been few research on isotopic composition changes in reef fish, and even fewer on individuals throughout the settlement phase. Gajdzik *et al.,* (2015) discovered that the isotopic equilibrium for *Acanthurus triostegus* was not reached after 24 days, whereas some studies observed a rapid shift (16 and 10 days) in the isotopic composition of winter flounder, *Pseudopleuronectes americanus*, and red drum *Scianops ocellatus* (Bolsey *et al.*, 2002). The few research available do not allow us to determine an average turnover period for juvenile or larvae reef fish, however it is feasible that this time may be relatively short in tropical habitats, because turnover occurs faster when the ambient temperature is higher (Bolsey *et al.*, 2002). We intend to use an isotopic approach to study the larval community's partitioning of food resources and habitat shift among the larval community, as has been done in temperate or subtropical regions such as Canada (Pepin and Dower, 2007), the Gulf of Mexico (Laiz-Carrión *et al.*, 2019), and China (Mei *et al.*, 2019). We focused our investigation on six reef fish families typically found in the Caribbean during their recruitment on reefs because data on isotopic niches of reef fish are limited, particularly during the larval stage. The first goal was to compare isotopic niches of fish larvae collected shortly after their arrival on reef to see if various fish families have similar trophic niches during their larval dispersive phase. The second goal is to investigate isotopic composition variations in haemulids and labrids, two prevalent families in Caribbean reefs, from larval to juvenile stages to represent nutritional and environment shifts during their ontogenetic development.

2. Materials and methods

2.1. Sampling protocol

The current investigation was conducted on Guadeloupe Island in the Lesser Antilles (16°15'N; 61°30'N). Samplings were taken at two shallow places on a barrier reef. Algal grass and macroalgae, primarily *Dictyota* sp., and calcified algae (*Halimeda* spp. and *Amphiroa* spp.), which cover roughly 50% of the substratum, dominate the benthic composition of these two sites. *Orbicella faveolata*, *Porites astreoides*, and *Pseudodiploria strigosa* make up the coral community, which accounts for less than 10% of the benthic covering. These sites were near *Thalassia testudinum* seagrass beds, which cover a substantial portion of the lagoon. Six nights of collection were carried out between January and March 2021 in order to get a significant number of larvae per family (> 6 individuals) to describe their isotopic habitat. Three fishing gears were used throughout the collection, depending on the ontogenetic stage targeted. A crest net and a light trap were used to gather larvae. The crest net is a conical net (1 mm mesh) that is placed on the coral crest with the opening towards the current to trap larvae as they colonize the reef. The current carries the larvae into the net, where they become trapped in the collector at the net's end. To avoid cluttering the trap with plant debris and invertebrate predation, the collection was emptied every hour from 10:00 p.m. to 6:00 a.m. Ecocean created the light trap as a "CARE" (Collect by Artificial Reef Eco-friendly). This trap's operation is based on the attraction of larvae by an artificial floating light. Individuals are then caught in a vertical conical net splayed out in front of the light. Because CARE is less likely to get clogged by plant material, the trap was only emptied once, at sunrise. Both fishing gears were used during the new moon to maximize collection, a time when larvae prefer to avoid predators. As a result, recruitment of larvae on reef is often higher during the new moon (Caley, 1993; Lecaillon and Lourié, 2007).

Individuals of *Haemulon* spp. and *Halichoeres bivittatus* that had recently landed were collected using two "SMURF" (Sample Monitoring Units for Reef Fishes) that were deployed on the ocean floor at each site at a depth of 2 m. This trap consists of a small artificial reef built of coral debris that is surrounded by a metallic cage to protect recruits from predators (Vallès *et al.*, 2006). SMURF were set up a few days before the new moon to encourage the settling of newly competent larvae, who were drawn in by the trap's three-dimensional complexity and recovered nine days later by wrapping them in a thin cloth. The contents of the traps were checked and sorted after being brought to the surface in order to remove the fish. Finally, juvenile *Haemulon sciurus* and *Halichoeres bivittatus* were caught using landing nets and lures during the day. All of the people gathered were instantly preserved in pots placed in an ice box.

The ontogenetic stage (larvae, newly settled individuals, and juveniles) was assigned based on the total length of individuals and notable morphological features, such as the appearance of coloration on the body, as described by Baldwin (2013) and online ecological databases (www.coralreeffish.com). As a result, haemulids were classified into four cohorts based on their size (Online Resource 2). The first three cohorts ([8:9], [10:12], and [15:16] mm), all recognized as *Haemulon* sp., belong to newly settled individuals, whilst the largest cohort ([50:90] mm) refers to juveniles (*Haemulon sciurus*), as defined by Tupper and Juanes (1999).

The labrids were all *Halichoeres bivittatus*. Individuals ranged in length from 12 mm to 99 mm. Because the settlement size for *H. bivittatus* is 10 mm (Sponaugle and Cowen, 1997), we categorized individuals between 12 and 20 mm as newly settled, and individuals bigger than 40 mm as juveniles.

2.2. Stable isotope analysis

All individuals obtained were identified to the lowest level of identification (species, genus, or family), measured (total length to the nearest millimeter), and photographed. The samples were freeze-dried to preserve them until examination. To create a homogeneous powder, the entire body of larvae and recently settled individuals was pulverized with an agate pestle and mortar on a grid of 1 mm mesh. Only the dorsal muscle was examined in juveniles. For isotopic analysis, powdered materials were put into tin capsules. For isotope measurements, 0.4 ± 0.05 mg of powder was required. A continuous flow mass spectrometer (Thermo FisherTM, delta V Advantage) combined with an elementary analyzer (Thermo FisherTM, Flash EA 1112) was used to detect carbon and nitrogen concentrations ([C]% and [N]%) at laboratory LIENSS (La Rochelle, France). Isotopic ratios were expressed in standard delta notation (δ values in ‰) according to the following formula:

$\delta = [(R_{sample} / R_{standard} - 1)] \times 1000$

where R is the ratio of a heavy isotope to a light isotope (^{15}N:^{14}N or ^{13}C:^{12}C), R_{sample} is measured for fish and $R_{standard}$ is an international standard (Vienna Pee Dee belemnite limestone carbonate for carbon and atmospheric air for nitrogen) (Fry, 2006).

Calibration was done using reference materials (USGS-61 and USGS-62) Analytical precision was < 0.15 ‰ for both C and N based on the analyses of acetanilide (Thermo Scientific) used as internal laboratory standards.

2.3. Statistical analysis

The R studio program was used to do statistical analysis. Shapiro-Wilk tests were used to determine the normality of the data. Because the data did not have a normal distribution, isotopic composition ($\delta^{15}N$ and $\delta^{13}C$ values) were compared using the Kruskal-Wallis test, followed by pairwise comparisons using the Wilcoxon rank sum test. The models "SIBER" (Stable Isotope Bayesian Ellipses with R, Jackson *et al.*, 2011) and $\delta^{15}N$ and $\delta^{13}C$ were used to describe and compare isotopic niches between fish groups. The SIBER model enabled us to represent "ellipses" in a δ-space biplot ($\delta^{15}N$ vs $\delta^{13}C$), as illustrations of isotopic niches, and to calculate several metrics, including: 1) the Total Area metric (TA in ‰^{2}), which is the area of the minimal convex polygon containing all the individuals of a population or an ontogenetic stage (Layman *et al.*, 2007). 2) the Standard Ellipse Area (SEAc), which is the area of the theoretic confidence ellipse encompassing 40% of the data regardless of sample size (Syväranta *et al.*, 2013). We employed two separate methods to evaluate changes in the isotopic composition of haemulids and labrids during ontogenetic development. Because the size of individuals was a continuous variable, Spearman correlation tests were employed to assess the link between isotopic values and total length of individuals in labrids. For haemulids, individuals were collected in cohorts of extremely close size. Thus, we used Kruskal-Wallis tests δ to evaluate values based on size, using size classes as a factor.

3. Results

3.1. Isotopic niches of reef fish larvae according to fish families

By coupling data from the two study sites, eight fish families were collected during recruitment as larvae: Apogonidae (*Apogon* sp.), Gobiidae (*Nes longus*), Haemulidae (*Haemulon* spp.), Labridae (*Halichoeres bivittatus*), Lutjanidae (*Ocyurus chrysurus*), Scaridae (*Scarus* spp. and *Sparisoma* spp.), Lutjanidae (*Ocyurus chrysurus*) and Muraenidae (*Myrophis punctatus*) (Online Resource 1). Total length of individuals varied from 9 mm to 57 mm depending on the fish family. Mean δ^{13}C and δ^{15}N values varied from -18.2 ± 0.3 ‰ (Acanthuridae) to -21.5 ± 0.2 ‰ (Muraenidae), and from 4.2 ± 0.6 ‰ (Scaridae) to 5.4 ± 1.1 ‰ (Labridae) respectively (Table 1).

Table 1 List and number of larvae samples collected (n), mean Total Length of individuals (TL ± SD, in mm), mean isotopic compositions in carbon and nitrogen (δ^{13}C ± SD and δ^{15}N ± SD, expressed in ‰), Total Areas (TA in ‰^{2}) and Standard Ellipse Areas corrected (SEAc).

		n	**TL ± SD (mm)**	**δ^{13}C ± SD (‰)**	**δ^{15}N± SD (‰)**	**TA (‰^{2})**	**SEAc (‰^{2})**
Acanthuridae	*Acanthurus chirurgus*	8	35.6 ± 1.8	-18.2 ± 0.3	4.4 ± 0.3	0.54	0.35
Apogonidae	*Apogon* sp.	15	11.6 ± 1.4	-18.6 ± 0.5	4.6 ± 1.0	1.79	0.90
Gobiidae	*Nes longus*	19	13.8 ± 1.4	-19.4 ± 0.2	4.7 ± 0.8	1.84	1.15
Haemulidae	*Haemulon* spp.	9	9.0 ± 0.0	-18.9 ± 0.6	4.9 ± 0.7	1.40	0.60

Labridae	*Halichoeres bivittatus*	12	15.6 ± 2.3	-19.8 ± 0.4	5.4 ± 1.1	2.58	1.58
Lutjanidae	*Ocyurus chrysurus*	15	20.1 ± 1.9	-19.5 ± 0.6	4.5 ± 0.8	2.29	0.97
Muraenidae	*Myrophis punctatus*	7	53.4 ± 2.8	-21.5 ± 0.2	5.2 ± 0.3	0.26	0.23
Scaridae	*Scarus* spp. and *Sparisoma* spp.	8	11.0 ± 1.3	-19.7 ± 0.3	4.2 ± 0.6	0.75	0.53

Isotopic compositions of larvae significantly varied among fish families for carbon (Kruskal-Wallis, $\chi^2 = 62.78$, df = 7, p-value < 0.001) but not for nitrogen (Kruskal-wallis, $\chi^2 = 12.23$, df = 7, p-value = 0.09). Pairwise comparisons indicated that δ^{13}C values differences were mostly due to muraenids which exhibited low values in ^{13}C relative (-21.5‰) to the rest of the community (between -18.2 and -19.8‰). Bayesian ellipses were represented with the model SIBER for each larvae family (Figure 1). Total Areas varied from 0.26 ‰^{2} for muraenids to 2.58 ‰^{2} for labrids. When corrected by the sample size of each population, Standard Ellipse Areas (SEAc) varied from 0.23 ‰^{2} for muraenids to 1.58 ‰^{2} for labrids (Table 1). Total Areas generally overlapped between ellipses of the different fish families (Figure 1).

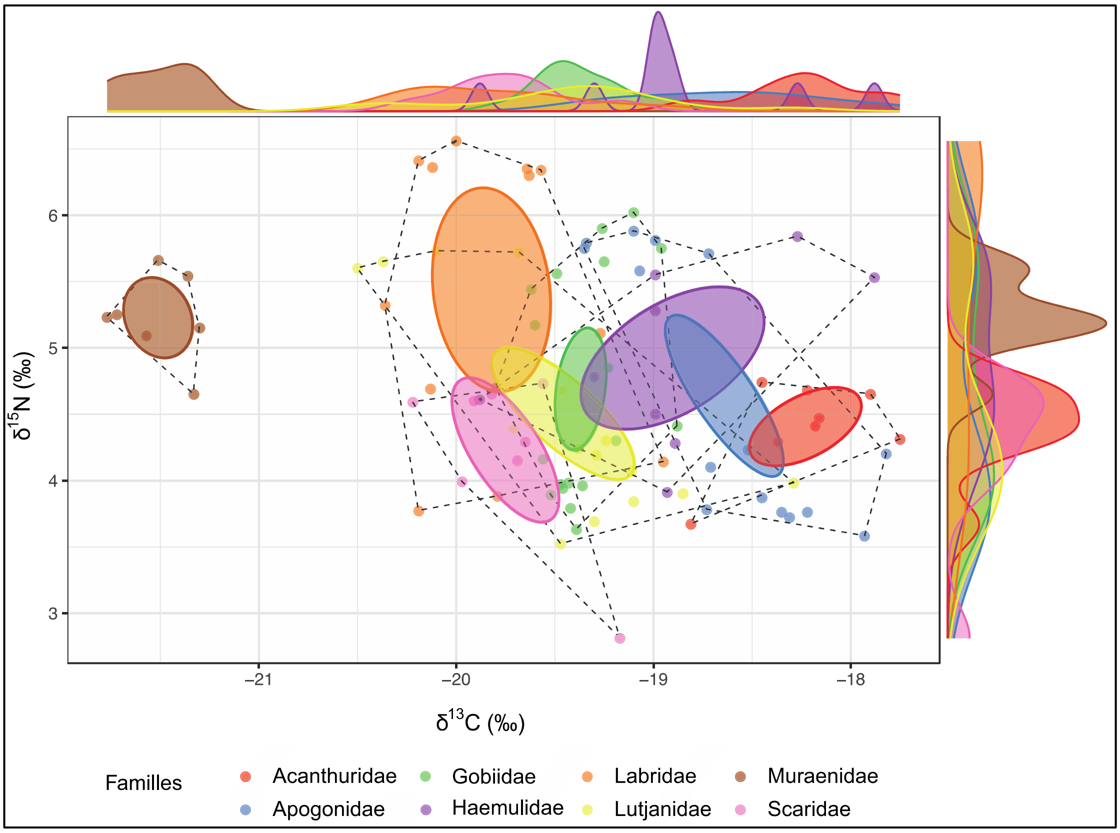

Figure 1 Isotopic niches of different fish families at larval stage, represented by their isotopic composition ($\delta^{13}C$ *vs* $\delta^{15}N$ values in ‰) and density plots of isotopic signatures. Black dotted lines indicate Total Areas (TA), and solid lines show Standard Ellipse Areas corrected (SEAc).

3.2. Isotopic niches during larval-juvenile transition

For haemulids, newly settled individuals were identified to the genus level (*Haemulon* spp.), while juveniles correspond to *Haemulon sciurus.* $\delta^{13}C$ and $\delta^{15}N$ values were significantly different among size classes (Kruskal-Wallis, $\chi^2 = 31.32$, p-value < 0.0001 for carbon and $\chi^2 = 31.03$, p-value < 0.0001 for nitrogen), and post-hoc pairwise comparisons tests indicated that significant differences were found between all stages when compared two by two, except between the two smallest size classes ([8:9] and [10:12] that exhibited similar isotopic composition). Carbon and nitrogen isotopic compositions of haemulids increased within the size of the individuals, *i.e.*, according to their stage of development (Figure 2).

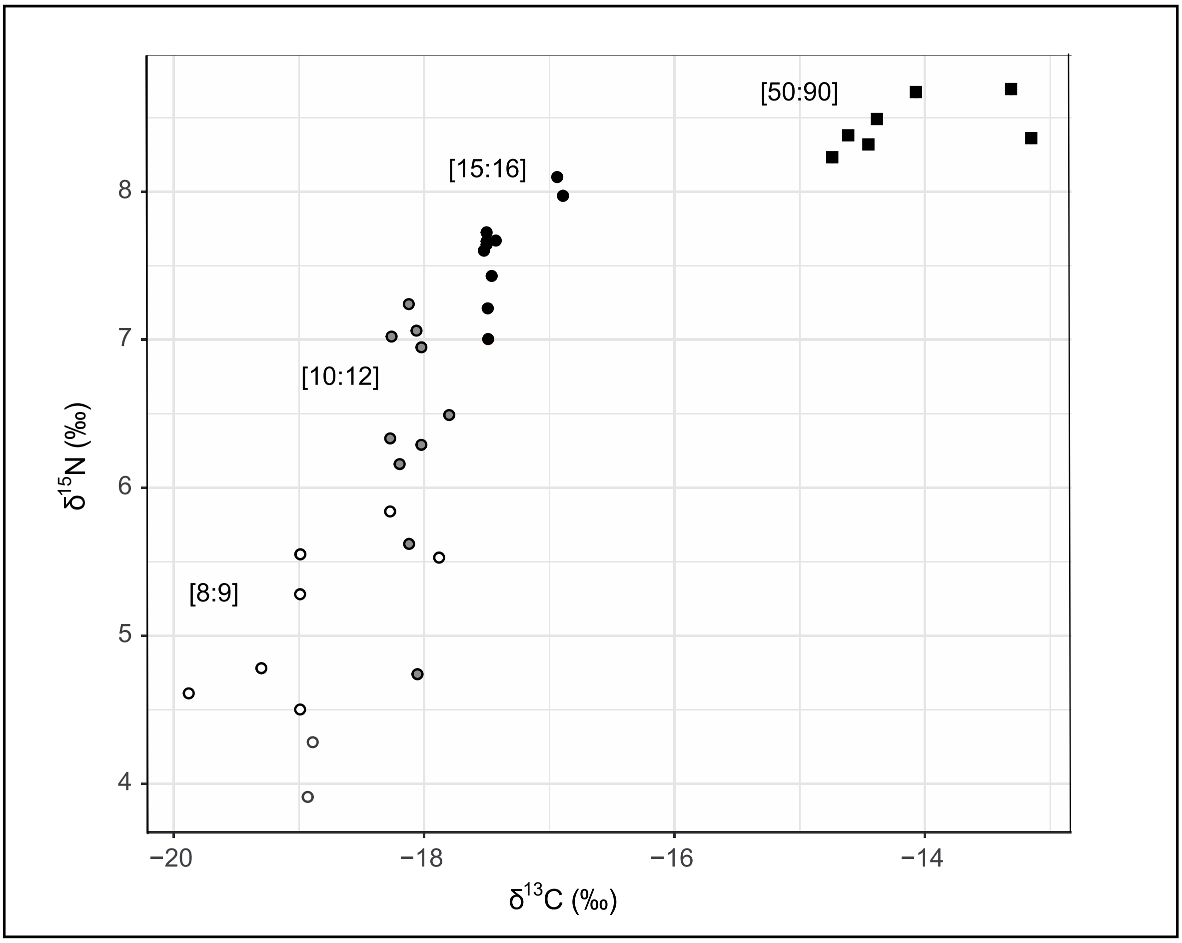

Figure 2 $\delta^{13}C$ *vs* $\delta^{15}N$ values (in ‰) of *Haemulon* spp. function to the size classes of individuals: [8:9] mm (white circles), [10:12] mm (grey circles) and [15:16] mm (black circles) for newly settled individuals and [50:90] mm (black squares) for juveniles.

For labrids, $\delta^{13}C$ and $\delta^{15}N$ values were positively correlated to the total length of individuals (Spearman, p-value < 0.01, $r = 0.82$ and p-value < 0.01, $r = 0.77$, respectively). $\delta^{13}C$ and $\delta^{15}N$ values increased with the length of individuals (Figure 3).

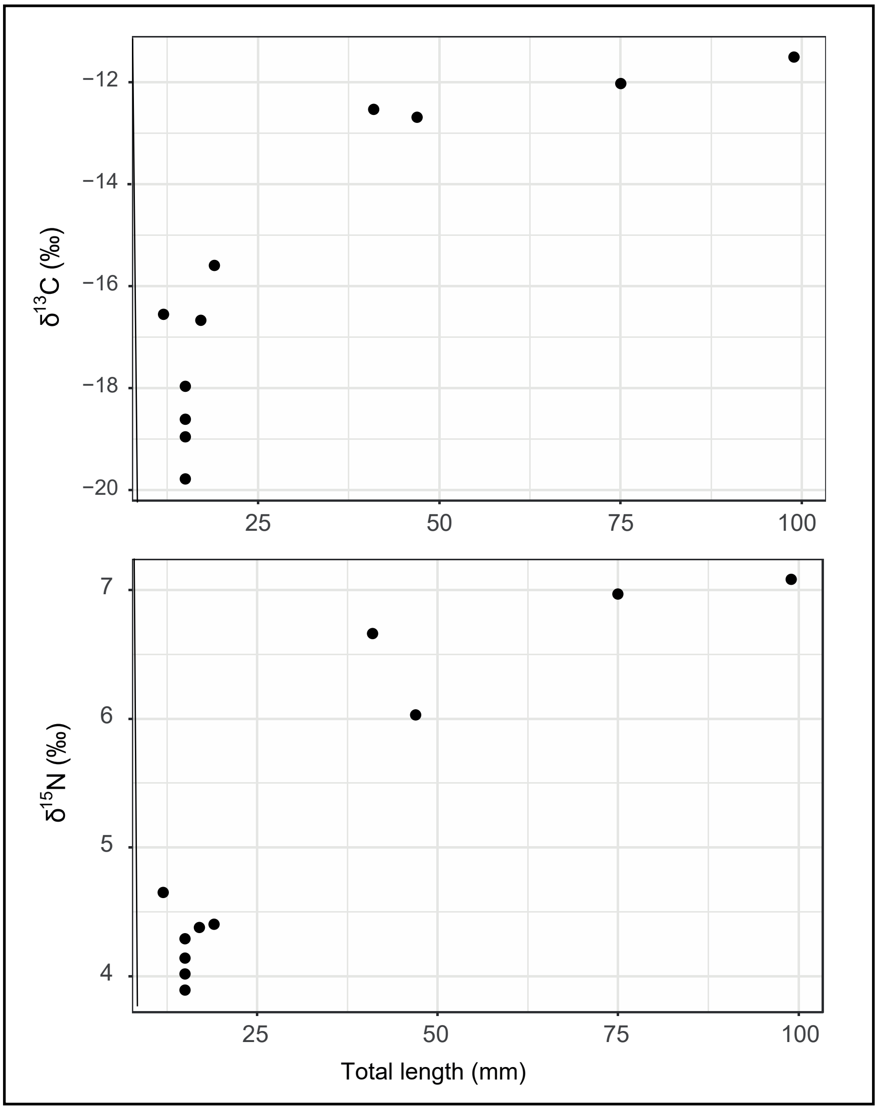

Figure 3 $\delta^{13}C$ and $\delta^{15}N$ values (in ‰) *vs* total length (TL in mm) of *Halichoeres bivittatus*.

4. Discussion

4.1. Isotopic niche variation in reef fish families during the larval stage

The isotopic niche of eight fish families was explored during the era of individual settlement in the current study. Carbon isotopic composition differed between families, and pairwise comparisons revealed that the discrepancy was attributable to Muraenidae having lower $\delta^{13}C$ values than other fish families. On the contrary, the nitrogen isotopic composition did not differ by fish family. Given that stable isotopes provide information on an individual's dietary intake over a period of days to weeks (Vander Zanden *et al.*, 1998; Bosley *et al.*, 2002; Gajdzik *et al.*, 2015), $\delta^{13}C$ and $\delta^{15}N$ values measured in newly settled individuals reflect the isotopic composition of the food sources they ingested and assimilated prior to reef colonization. The diet of larvae may change in terms of prey composition in a pelagic environment, but the isotopic baseline varies little, which may explain the lack of apparent interspecific heterogeneity in the isotopic niche of larvae during the pelagic phase. In other words, larvae, regardless of family, may eat on similar food resources, or at least on food sources with similar isotopic signatures.

According to gut content analyses, the majority of fish larvae ingest phytoplankton and zooplankton during their pelagic larval phase, such as copepods, harpacticoids, calanoids, or appendicularians (Llopiz and Cowen, 2009; Pepin and Penney, 1997). Previous research in the Caribbean region has found that phytoplankton and zooplankton have similar isotopic compositions (De Figueiredo *et al.*, 2020; Fry and Quiones 1994; Land *et al.*, 2000; Thayer *et al.*, 1983). $\delta^{13}C$ values for phytoplankton range between -17 and -22 ‰, -18 and -21.8 ‰ for zooplankton, and $\delta^{15}N$ values range between 2 and 6 ‰ for both (De Figueiredo *et al.*, 2020; Fry and Quiones 1994; Land *et al.*, 2000). Furthermore, several of these studies found that distinct phylla of zooplankton (copepods, small decapods, harpacticoids, and so on) had similar isotopic signatures, making it difficult to distinguish in the analysis of larvae nutrition (De Figueiredo *et al.*, 2020; Pepin and Dower, 2007). In parallel, diet convergence can be described by larvae's lifestyle, which moves and feeds on multispecific "patches" that can accommodate a significant number of individuals (Barth *et al.*, 2015; Victor, 1984). According to certain research, these aggregations can span tens of kilometers (Victor, 1984). As a result of their shared displacement, larvae use similar resources and have similar isotopic signatures. Previous investigations utilizing gut content analysis (Llopiz and Cowen 2009; Riley and Holt 1993; Sampey *et al.*, 2007) support this concept, as do the substantial overlaps of larvae isotopic niches (*i.e.*, Total Areas of Ellipses) discovered in the current study. Muraenid isotopic compositions, with high carbon and nitrogen isotope values, were the most noticeable isotopic difference within the population. These results were consistent with recent measurements of muraenid isotopic values in the Gulf of Mexico (Quattrini *et al.*, 2019). The uniqueness of their isotopic niche indicates that muraenids use different food resources than other fish families and/or have a distinct lifestyle during this pelagic period. Muraenids, like most reef fish families, have a morphologically different pelagic larval stage called "leptocephalus" (Miller, 2009). Muraenids feed at varying depths and preferentially devour particulate organic matter, including bacteria, protists, fecal matter, and other detritus such as marine snow particles (Miller *et al.*, 2011; Quattrini *et al.*, 2019). These foods are also more digestible than crustaceans and can be easily digested and integrated into the tissues of larvae. Previous research on the stomach or gut contents of muraenids revealed that, unlike the majority of fish larvae, zooplankton is not consumed by muraenids during the pelagic phase (Mochioka and Iwamizu, 1996). As a result, leptocephali occupy a separate trophic niche, as evidenced by a distinct isotopic niche, allowing muraenids to avoid competition for food resources with other fish families in the open ocean (Quattrini *et al.* 2019). The computed Standard Ellipse Areas (SEAc) for each fish family were tiny. These values can imply a low food plasticity, which is a selection of a low diversity of prey, or an intake of prey with similar isotopic signatures, as explained in the preceding paragraph. Narrow isotopic niches can also represent larvae's wide-ranging environment and can be considered habitat generalists during pelagic migration (Flaherty and Ben-David, 2010; Jackson *et al.*, 2011).

4.2. Variation of isotopic niches during larval-juvenile transition

Isotopic niche changes in *Halichoeres bivittatus and Haemulon spp*. were investigated during the larval-juvenile transition. Carbon and nitrogen isotope compositions grew rapidly with individual size in both species and genera. Immediately following settlement, the fish undergo fast morphological, anatomical, and metabolic changes associated with metamorphosis, allowing newly settled larvae to develop into juveniles adapted to benthic reef life. These significant alterations occur in a matter of days. We discovered a quick change in the isotopic composition of haemulids and labrids after their settlement, followed by a stabilization of these values when the animals reached their juvenile stage. These rapid alterations were linked to isotope turnover rates, which must be high during metamorphosis due of individuals' rapid growth rates (Herzka *et al.*, 2001). Both fish families showed a considerable rise in $\delta^{13}C$ and $\delta^{15}N$ values with size, indicating a greater integration of ^{13}C and ^{15}N in animal tissue during metamorphosis. Carbon isotopic compositions reveal the origin of organic matter consumed by humans and can be used to distinguish between "offshore" and "inshore" carbon. Thus, benthic primary producers have higher $\delta^{13}C$ values than pelagic primary producers (Newsome *et al.*, 2007). As a result, shifts in $\delta^{13}C$ values in individual tissues represent the episode of settling, followed by recruitment and the transition between pelagic and benthic habitats. For haemulids and labrids, the difference in $\delta^{13}C$ values between recently settled individuals and juveniles was noticeable.

Similarly, $\delta^{15}N$ values increased with individual size, indicating a shift in diet toward more proteinaceous dietary resources. Larvae of haemulids and labrids feed on zooplankton, mainly copepods (Llopiz and Cowen, 2009; Sampley *et al.*, 2007), while juveniles are mostly consuming tanaidacea and decapods for *Haemulon sciurus* (Cocheret de la Morinière *et al.*, 2003) and echinoids, polychaetes, gastropods and decapods for *Halichoeres bivittatus* (Randall, 1967). The increase in $\delta^{15}N$ values during ontogeny could possibly indicate a metabolic shift toward improved nutrition incorporation into tissues. Finally, growing larger is related with increased $\delta^{15}N$ values, indicating a gain in trophic status during ontogeny (Hammerschlag-Peyer *et al.*, 2011; Newsome *et al.*, 2007; Wells and Rooker, 2009). Ontogenetic niche shift occurs in 80% of animal species, and the different life phases are thus considered functionally separate groups (Hammerschlag-Peyer *et al.*, 2011).

4.3. Limitations of the study

Isotopic measurements are typically taken from the white muscle of organisms, which serves as the primary protein reservoir in fish. The dorsal muscle could not be extracted for study due to the tiny size of the individuals obtained. As a result, we measured the isotopic values of the entire fish body, as has been done in earlier research on fish larvae (Herzka *et al.*, 2001; Kume *et al.*, 2021). The utilization of the entire organism can result in biases in the isotopic values obtained, particularly because samples include the isotopic composition of the contents in the stomach and gut. However, based on past research, we believe that element inputs *via* digestive material may be insignificant in comparison to the overall fish tissue employed for analysis. Pepin and Peney (2000), for example, estimated that the total stomach contents of fish larvae rarely surpass 2% of total body weight. The second limitation of this study is the minimal number of participants. Because of the tiny size of the individuals, their fragility during handling, and the constraints during identification, sampling larvae and other individuals at an early stage of development is often challenging. These findings add to our understanding of the larvae's ecology and the peculiarities of their isotopic niche, although more sample would be required to improve the statistical tests' power.

5. Conclusion

To summarize, except for Muraenidae leptocephali, the majority of larvae ingest comparable types of prey or fish with similar isotopic composition and inhabit a tight isotopic niche in the open sea. By eating on distinct food resources during the pelagic phase, the latter avoids a major portion of the interspecific competition, resulting in niche partitioning for this family. Isotopic niche for *Haemulon* spp. and *Halichoeres bivittatus* exhibited ontogenetic variations with increasing $\delta^{13}C$ and $\delta^{15}N$ values according to the size of individuals, revealing a change in the origin of consumed sources of carbon (offshore *vs* inshore, pelagic *vs* benthic, Newsome *et al.*, 2007) and a shift in the trophic level of individuals.

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Statements and Declarations

Competing interests

The authors have no competing interests to declare that are relevant to the content of this article.

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Financial interests

The authors declare they have no financial interests.

Ethical approval

All procedures of collect and killing of fish were approved by the Comity of ethic of the University of Antilles and was conducted in accordance with the Guidelines of the European Union Council. The collect of fish (species, number, and method) has been approved by Direction de la Mer of Guadeloupe, who delivered a sampling authorization (N°465/2020 and N°158/2021)

Authors contribution

LV, DL and CD contributed to the study conception and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written by LV and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability statement

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Supplementary materials

Figure 4 Photo of fish larvae collected during the present study a) *Acanthurus chirurgus*, b) *Apogon aurolineatus*, c) *Haemulon* sp., d) *Halichoeres bivittatus*, e) *Ocyurus chrysurus* and f) *Sparisoma* sp.

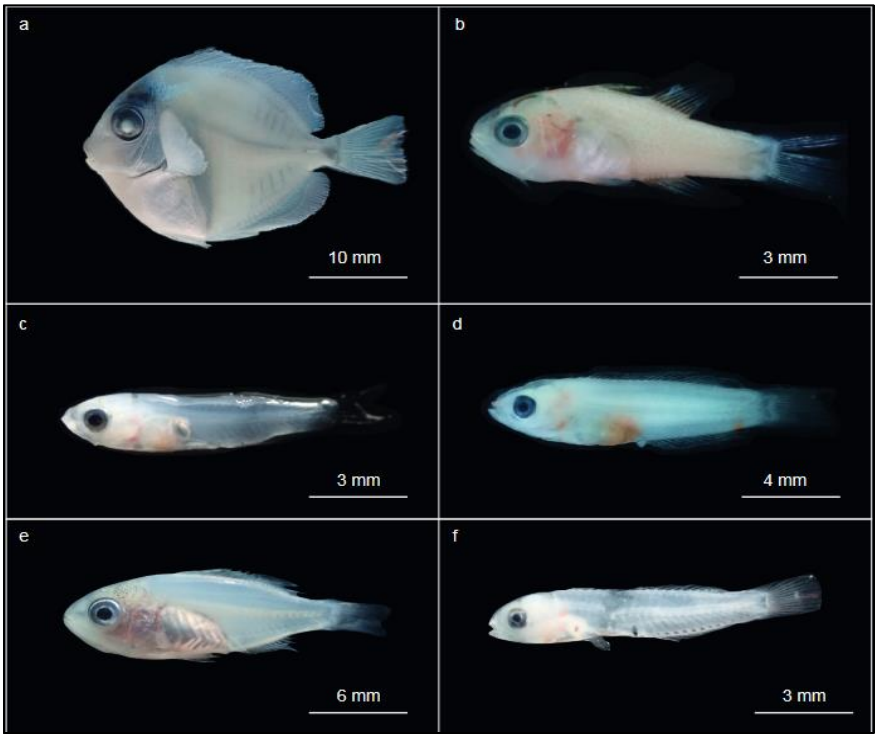
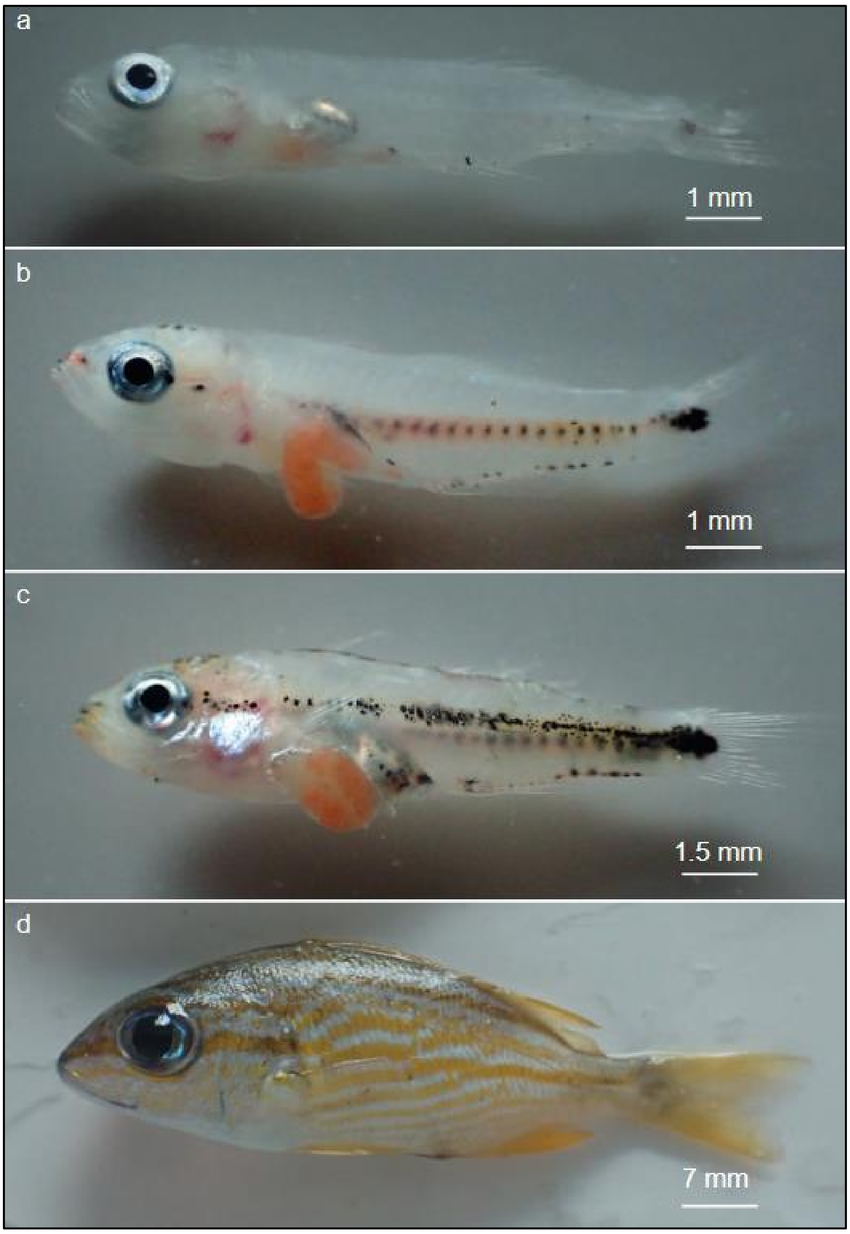


Figure 5 Photo of haemulids individuals collected. Newly settled individuals at different size classes: a) [8:9] mm, b) [10:12] mm, c) [15:16] mm and d) juvenile ([50:90] mm). Individuals on pictures a, b and c have been identified to the genus level *Haemulon* spp., d has been identified to the species level (*Haemulon Sciurus*).



Conclusion générale et perspectives

Les poissons de récifs jouent un rôle crucial pour les populations humaines insulaires des Petites Antilles. Ils jouent un rôle écologique (relations proies-prédateurs ou régulation des algues, Belwood *et al.*, 2004) mais aussi économique (tourisme et sécurité alimentaire, Moberg & Folke, 1999). L'amélioration des connaissances concernant leur biologie et leur écologie est indispensable pour penser des modèles de gestion, de protection et de conservation. Pour cela, il est important d'étudier leur répartition, leur comportement mais surtout de leur cycle de vie.

Le recrutement des poissons est une étape cruciale du cycle de vie des poissons de récifs au cours duquel les individus juvéniles intègrent les populations adultes de même espèce. Lors de ce processus, les individus peuvent soit recruter directement sur le récif, généralement dans la zone la moins profonde du récif, soit recruter sur d'autres habitats côtiers, associés aux récifs coralliens, tels que les mangroves et les herbiers marins, qui jouent le rôle de zones de nourriceries. Après avoir atteints leur taille d'évitement (pour laquelle ils sont moins vulnérables face à la prédation), les individus rejoignent le récif pour intégrer la communauté récifale. Ces déplacements entre différents environnements (pélagique au stade larvaire puis benthique au stade juvénile et adulte) mais aussi entre différents types d'habitats (mangrove, herbier, récif) sont des informations clés pour comprendre le cycle de vie complexe des poissons de récif et entreprendre des mesures de conservation. Quelle que soit la zone de recrutement initiale, le recrutement est associé à de nombreux changements morphologiques, anatomiques et écologiques qui permettent à chaque individu d'être parfaitement adapté à son nouvel environnement. Ces modifications sont également des éléments majeurs dans la compréhension du développement ontogénétique des poissons de récifs.

Au cours de cette thèse, différentes études ont été menées afin de décrire et comprendre 1) la dynamique de recrutement des poissons en Guadeloupe, 2) les mouvements entre les habitats côtiers et 3) les modifications morphologiques et écologiques, notamment de l'alimentation, au cours de l'ontogénie.

Recrutement des poissons de récifs de la Guadeloupe

La première étude réalisée dans le cadre de ma thèse nous renseigne sur la dynamique spatiale et temporelle des populations de juvéniles, regroupant ici 21 espèces étudiées sur six sites d'étude. Les principaux résultats ont montré que le recrutement de la communauté juvénile de poissons de récifs varie fortement dans l'espace et dans le temps autour de l'île de la

Guadeloupe. Dans l'espace, la localisation géographique des sites étudiés, et le type de récifs associé à chaque site, influencent la présence de juvéniles. Il semble que l'abondance de juvéniles soit plus importante sur les sites localisés au nord de l'archipel, et à l'ouest de la Basse-Terre, ainsi que sur des récifs de type non bioconstruits. Dans le temps, la communauté juvénile varie en fonction des saisons, avec une plus grande abondance des individus lors de la saison humide, soit entre mi-avril et mi-novembre.

Bien que ces résultats soient en accord avec les précédentes études menées sur le sujet dans d'autres îles de la Caraïbe (Stimson, 1990 ; Tupper & Hunte, 1994 ; Adams *et al.*, 2002), il est possible que les variations observées soient principalement reliées aux espèces les plus abondantes de la communauté, et ne soient pas représentatives de toutes les espèces de poissons de récifs. Un renforcement de l'effort de la collecte de données permettrait sûrement de prendre en compte des espèces moins abondantes, moins fréquemment rencontrées sur les récifs. De la même manière, une augmentation du nombre de sites (ce qui n'était pas envisageable dans le cadre de la thèse) permettrait de renforcer les données sur la dynamique de recrutement en élargissant le nombre d'espèces rencontrées. Par ailleurs, les observations ont été faites sur une année, mais le comportement des populations peut potentiellement varier d'une année à une autre, notamment dans le cadre du changement climatique qui perturbe le cycle des saisons. Il se peut donc intéressant de mettre en place des comparaisons interannuelles, en complétant les résultats de cette première étude par des recensements ultérieurs de la communauté juvénile et en programmant les observations sur plusieurs années.

L'abondance des juvéniles peut être un bon prédicteur de l'abondance des adultes de même espèce sur les récifs à petite échelle, (transect) et/ou large échelle (site) en fonction de l'espèce étudiée. En effet, les résultats de la deuxième étude réalisée dans le cadre de cette thèse ont mis en évidence le fait que chacune des cinq espèces étudiées présente des schémas de prédiction différents. Ces schémas ne semblent pas dépendre du caractère sédentaire ou mobile des espèces, mais plutôt des comportements développés envers les congénères. Ces relations intraspécifiques peuvent effectivement conditionner le choix du site de recrutement et l'installation des juvéniles au sein d'un territoire. Par exemple, les juvéniles ne s'installeront pas sur un site si les adultes affichent des comportements agonistiques envers les juvéniles. On retrouve ce type de comportement chez trois des cinq espèces étudiées, et pour ces trois espèces l'abondance des juvéniles n'était pas un bon prédicteur de l'abondance des adultes.

La technique d'observation utilisée, le transect, peut être un biais dans l'étude puisqu'il peut ne pas représenter correctement le territoire d'une espèce au sein d'un site. En effet, la méthode des transects point-intercept est adéquate pour décrire la composition benthique d'un site dans son ensemble, mais ne permet pas la description détaillée des micro habitats utilisés par les espèces de petite taille (par exemple *S. diencaeus* et *S. partitus* dans notre étude). Cette étude pourrait donc être complétée par l'ajout d'une autre méthode d'observation, en fonction du domaine vital de chaque espèce étudiée.

Ce premier chapitre dédié au processus de recrutement nous apporte tout d'abord des informations sur la dynamique spatiale et temporelle du recrutement des poissons de récifs en Guadeloupe. Ces résultats sont en accord avec d'autres études réalisées à travers le monde mais aussi en Caraïbe (Shulman, 1985 ; Booth & Beretta, 1994 ; Tupper & Hunte, 1994 ; Caselle & Warner, 1996 ; Sponaugle & Cowen, 1997 ; Tolimieri *et al.*, 1998 ; Valles *et al.*, 2009). De même, des études précédentes menées, dont certaines dans la zone Caraïbe sur la côte du Panama, ont déjà montré que la dynamique du recrutement des poissons de récif peut affecter directement la distribution et l'abondance des adultes sur les récifs coralliens (Sale, 1977 ; Victor, 1986 ; Jones, 1990). Les résultats de ce premier chapitre viennent donc ainsi infirmer certains patrons de dynamique de recrutement, précédemment décrits dans la Caraïbe.

Les connaissances apportées sur la dynamique spatiale et temporelle du recrutement, ainsi que son rôle sur le renouvellement des populations adultes, sont particulièrement utiles pour la gestion et la conservation des poissons de récifs. A titre d'exemple, ces résultats apportent des informations sur les récifs, qui pourraient être identifiées comme des zones hautement productives en termes de recrutement, et qui pourraient être placés sous un statut de protection particulier. De la même manière, les données temporelles pourraient permettre d'identifier des périodes de l'année au cours desquelles appliquer des mesures de protections, afin d'établir un équilibre entre l'exploitation et le maintien des stocks des poissons de récifs. Ces mesures sont particulièrement importantes dans le contexte actuel où les récifs coralliens subissent de nombreuses et fréquentes perturbations.

Mouvements ontogénétiques entre les habitats côtiers

Certaines espèces de poissons de récifs sont caractérisées par des déplacements entre différents habitats côtiers au cours de leur vie, tels que les zones de nourricerie (mangroves, herbiers) et les récifs coralliens. Lors de ces transitions entre habitats, qui sont souvent de nature ontogénique, les individus affichent généralement un changement du régime alimentaire, ce qui peut être dû aux ressources alimentaires disponibles sur les différents types d'habitats. Ces transitions sont souvent liées à l'espèce et dépendent fortement de la zone de recrutement, c'est-à-dire de la présence ou non de zones de nourricerie lors de la colonisation larvaire.

Au cours de troisième étude, les transitions entre habitats et histoires de vie des individus ont été étudiées par les trajectoires isotopiques mesurées dans les couches du cristallin des yeux des poisson adultes de trois espèces connues pour avoir des histoires de vie différentes. Tout d'abord, les valeurs isotopiques en carbone et azotes obtenues à partir de la couche la plus externe du cristallin des poissons adultes, ne diffèrent pas significativement de celles obtenues à partir de leur muscle dorsal, tissu qui est habituellement utilisé en écologie. Ces résultats montrent que les données issues du cristallin peuvent donc se substituer à celles du muscle, ou du moins traduisent des informations similaires à celles récoltées à l'aide du muscle. Pour le souffre, en revanche, le muscle semble enrichi en souffre par rapport au cristallin.

L'utilisation du cristallin permet également de retracer l'histoire de vie des poissons en mesurant les compositions isotopiques des différentes couches, de la plus externe à la plus interne. Ainsi, les résultats de cette étude ont montré que les trajectoires isotopiques au cours de la vie des individus semblent similaires pour les trois espèces étudiées, si l'on considère une large échelle spatiale. Les différences de valeurs isotopiques mettent en évidence des changements ontogéniques de régime alimentaire, qui peuvent être dûs aux sources alimentaires présentes sur chaque site, et/ou au passage des individus dans différents habitats côtiers. Entre les trois espèces, les tendances isotopiques au cours de la vie des individus diffèrent lorsqu'elles sont étudiées sur un même site. Ceci peut s'expliquer par les régimes alimentaires différents des trois espèces, et l'utilisation différentielle des sources de nourriture au cours de leur vie, conditionnée par leur transition à travers différents habitats tels que les zones de nurserie.

L'utilisation des couches du cristallin reste cependant une méthode à perfectionner. En effet, les couches les plus internes étant très fines et petites, il peut être difficile de les différencier et plusieurs couches peuvent être utilisées ensembles par erreur. Les valeurs obtenues peuvent alors réunir les informations issues de plusieurs stades ontogénétiques. Sachant que les cristallins des deux yeux des individus adultes auraient le même nombre de couches, et enregistrent les mêmes isotopes au cours du temps (Faletti & Stallings, 2021), une comparaison entre le nombre de couche et les valeurs obtenues pour les deux yeux d'un individu pourraient permettre de remarquer les possibles erreurs. Il serait aussi intéressant de comparer les valeurs isotopiques des couches les plus internes avec celles du muscle d'individus collectés à un stade précoce (larves ou juvéniles), afin de voir si une relation peut être mise en évidence comme pour les adultes. Enfin, cette étude pourrait être complétée en augmentant le nombre d'individus utilisé pour chaque espèce par site (seulement cinq à chaque fois dans cette étude) afin de confirmer les résultats obtenus. De même, une description précise des habitats et des analyses isotopiques des sources de nourritures potentielles (autres que végétales) à chaque site, pourraient permettre une meilleure interprétation des résultats.

Ce chapitre permet tout d'abord de mettre en avant une méthode innovante et relativement accessible, pour étudier l'histoire de vie des poissons. L'utilisation des yeux, qui ne sont généralement pas consommés par les humains, pourrait permettre de meilleures collaborations avec des pêcheurs professionnels et d'utiliser pour la recherche des individus pêchés à des fins commerciales. Une telle collaboration permettrait d'en apprendre plus sur la vie des poissons de récifs, tout en allant dans le sens de leur protection en évitant les pêches supplémentaires pour les recherches scientifiques.

Ce chapitre met également en avant l'utilisation et l'importance des habitats associés aux récifs coralliens pour les poissons de récifs au cours de leur développement ontogénique. Ils attestent d'une connectivité entre les différents habitats côtiers de la Guadeloupe, déjà mis en évidence sur d'autres îles par d'autres méthodes (Worm *et al.*, 2006 ; Polidoro *et al.*, 2010). L'amélioration des connaissances sur l'utilisation de ces habitats côtiers par les poissons, et notamment ceux d'intérêt commercial, peut aider à la conservation des populations de poissons, en s'appuyant sur des mesures de gestion et de protection des habitats, tels que les zones de nourricerie par exemple (comme le récent arrêté préfectoral n°329-2023, interdisant le mouillage des navires sur les herbiers marins situés dans les eaux intérieures de la Guadeloupe).

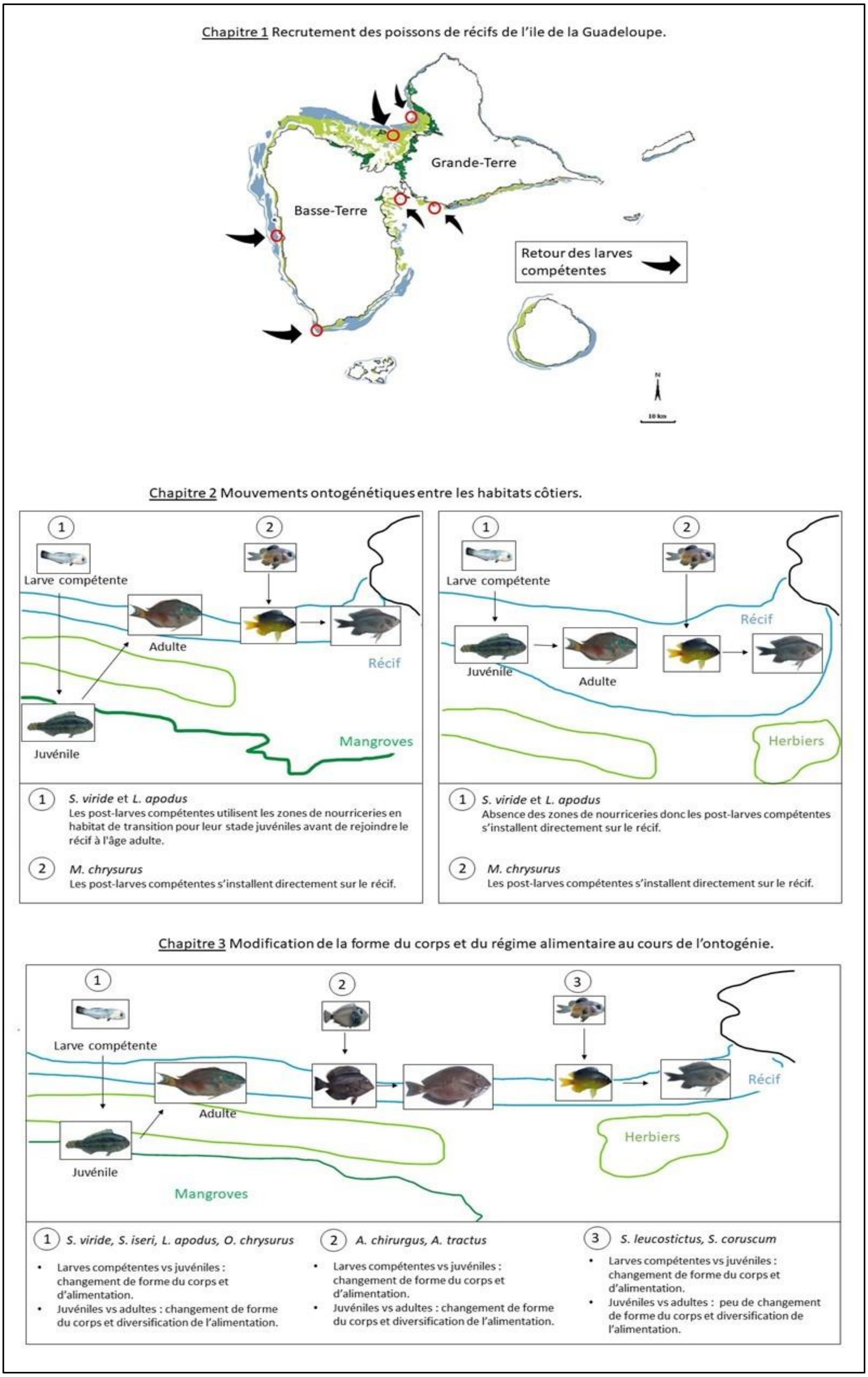
Modification de la forme du corps et du régime alimentaire au cours de l'ontogénie

Au cours de leur développement, les poissons subissent des changements radicaux, d'un point de vue morphologique, anatomique, comportemental et écologique d'une manière générale. La forme du corps et la diversité des phénotypes associés (disparité) varient au cours de l'ontogénie des poissons de récifs. La variation de la forme du corps entre les stades ontogénétiques est clairement associée à l'habitat, au régime alimentaire et aux changements de comportement de chaque espèce. Au contraire, la distribution de la disparité corporelle au cours de l'ontogenèse dépend d'un mélange de facteurs externes (par exemple, la diversité de l'habitat) et internes (par exemple, l'état physiologique de la métamorphose). L'échantillonnage de la quatrième étude réalisée dans le cadre de la thèse a ciblé huit espèces appartenant à cinq familles différentes : Acanthuridae (*Acanthurus chirurgus* et *Acanthurus tractus*), Holocentridae (*Sargocentron coruscum*), Lutjanidae (*Lutjanus apodus* et *Ocyurus chrysurus*), Pomacentridae (*Stegastes leucostictus*) et Scaridae (*Scarus iseri* et *Sparisoma viride*). La forme du corps a varié au cours de l'ontogénie de toutes les espèces étudiées, avec un allongement de la forme générale du corps et un raccourcissement de la région céphalique. La plus grande variation de forme du corps s'est produite entre les stades post-larvaire et adulte, probablement associée à la transition écologique majeure entre l'environnement océanique et l'environnement récifal. Ensuite, la variation de forme entre le stade juvénile et le stade adulte semble également être due à un changement ontogénétique dans l'écologie des espèces. En fonction des espèces, le niveau de disparité des formes corporelles n'a soit pas varié au cours de l'ontogénie, ou présentait un pic à différents stades (post-larvaire, juvénile ou adulte). Cette étude pourrait donc être complétée par l'ajout d'espèces d'écologie similaire, dans chaque famille, afin d'évaluer si la phylogénie ou l'écologie représente le principal moteur de la dynamique ontogénétique de la disparité phénotypique chez les poissons de récifs.

Le régime alimentaire est un élément clé du développement qui varie également au cours de l'ontogénie des poissons de récifs. Le changement de régime alimentaire entre larves et adultes est difficile à étudier car elles sont petites, transparentes et vivent dans la zone pélagique. De ce fait, peu d'études ont pu mettre en évidence le régime alimentaire des larves de poissons. Dans notre étude, nous avons étudié neuf espèces dont nous avons comparé les niches isotopiques à l'aide d'analyses isotopiques. La majorité des larves étudiées dans le cadre de ma thèse (à l'exception des larves leptocephali des Muraenidae par exemple) présentaient des compositions isotopiques très proches. Cela est dû au fait que *i)* elles consomment les mêmes proies, ou *ii)* elles ingèrent des proies qui présentent des compositions isotopiques similaires. Cela met en évidence leur comportement grégaire dans la zone pélagique, caractérisé par un déplacement et un nourrissage sous forme de " patchs " multi spécifiques (Barth *et al.*, 2015 ; Victor, 1984). En raison de leur déplacement conjoint, les larves utilisent des ressources similaires et affichent ainsi des signatures isotopiques similaires.

Parallèlement, nous avons mis en évidence le changement du régime alimentaire au cours du recrutement, et cela pour deux espèces (*Haemulon sp.* et *Halichoeres bivittatus*). L'enrichissement des compositions isotopiques en carbone en ^{13}C traduit directement le passage d'une vie pélagique à benthique (Newsome *et al.*, 2007) et l'utilisation de sources de carbone différentes au cours de cette transition. Ce changement de milieu de vie et de régime alimentaire au cours de l'ontogénie est aussi associé à un changement de niveau trophique des individus, représenté par l'augmentation des valeurs isotopiques en azote, soit un enrichissement des compositions isotopiques en ^{15}N. Dans cette étude, seules deux espèces ont été utilisées pour suivre les changements de régimes alimentaires au cours de l'ontogénie. Ce choix a été dicté par les échantillons disponibles à la suite des campagnes d'échantillonnage. De plus, chaque espèce n'a pu être suivie que sur un seul site d'étude. Il serait donc intéressant de compléter cette étude en utilisant d'autres espèces, sur plusieurs sites autour de l'île, afin d’améliorer la base de données sur les changements ontogénétique de régime alimentaire chez les poissons de récifs. Néanmoins, la pêche des larves est difficile du fait des campagnes de pêche nocturnes et des déplacements aléatoires de larves.

Ce dernier chapitre apporte des informations sur les changements morphologiques et écologiques au cours de l’ontogénie des poissons de récifs. Certaines de ces informations sont novatrices, notamment en ce qui concerne les poissons de récifs. Les changements observés infirment les résultats du chapitre précédent, qui attestent de la connectivité entre les différents habitats côtiers de la Guadeloupe, et de la transition des individus au cours de leur développement. Ces résultats renseignent aussi sur le mode de vie et le rôle de chaque espèce de poissons de récifs au sein de l'écosystème corallien, mais aussi du méta-écosystème qui regroupe les récifs et les écosystèmes associés. Il est explicite ici que la réduction ou la disparition des habitats associés, pourrait engendrer des conséquences écologiques graves sur la pérennité des populations de poissons de récifs. Ces études sur les changements ontogénétiques de la forme du corps et du régime alimentaire des poissons de récifs, pourront servir de sources de comparaisons pour de prochaines études sur le sujet, et peuvent permettre d’investiguer des modifications de l’environnement récifal dans le temps.



Chapitre 1 Recrutement des poissons de récifs de l'ile de la Guadeloupe.

Chapitre 2 Mouvements ontogénétiques entre les habitats côtiers.

① *S. viride* et *L. apodus*
Les post-larves compétentes utilisent les zones de nourriceries en habitat de transition pour leur stade juvéniles avant de rejoindre le récif à l'âge adulte.

② *M. chrysurus*
Les post-larves compétentes s'installent directement sur le récif.

① *S. viride* et *L. apodus*
Absence des zones de nourriceries donc les post-larves compétentes s'installent directement sur le récif.

② *M. chrysurus*
Les post-larves compétentes s'installent directement sur le récif.

Chapitre 3 Modification de la forme du corps et du régime alimentaire au cours de l'ontogénie.

① *S. viride, S. iseri, L. apodus, O. chrysurus*

- Larves compétentes vs juvéniles : changement de forme du corps et d'alimentation.
- Juvéniles vs adultes : changement de forme du corps et diversification de l'alimentation.

② *A. chirurgus, A. tractus*

- Larves compétentes vs juvéniles : changement de forme du corps et d'alimentation.
- Juvéniles vs adultes : changement de forme du corps et diversification de l'alimentation.

③ *S. leucostictus, S. coruscum*

- Larves compétentes vs juvéniles : changement de forme du corps et d'alimentation.
- Juvéniles vs adultes : peu de changement de forme du corps et diversification de l'alimentation.

Figure 1 Schéma récapitulatif des résultats de la thèse sur le recrutement des poissons de récifs, les mouvements ontogénétiques et les changements de forme du corps et d'alimentation associés.

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