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Life-history dynamics in the protogynous cleaner wrasse *Labroides dimidiatus*

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General Summary

All living organisms share the fundamental goal of surviving and reproducing, but finite resources force them to manage essential life-history trade-offs by deciding how much energy to allocate to each trait. This principle of allocation leads to the broad variation observed across species in demographic life-history traits such as age at maturity, lifespan, and reproductive output, with these differences shaped by ecological conditions and selection to maximize lifetime fitness.

In sequentially hermaphroditic species, the ability to change sex over a lifetime represents a complex life-history strategy. Instead of optimizing a fixed sexual role, these organisms face a dynamic challenge: determining when to shift their energy allocation between sexual functions. This shift is best explained by the size-advantage hypothesis, which predicts that sex change evolves when one sex has higher reproductive success when small or young, while the other attains greater fitness when old or large. Since protogynous species (female-to-male) most often live in polygynous haremic groups with a size-based hierarchy, in which a large dominant male monopolizes reproductive opportunities among a group of size-ranked females, it is a classical assumption that sex change is strictly controlled by social factors. Under this cohesive social queuing system, stable rank relationships are maintained by selective aggression, and it is expected that only the largest female will change sex when the male disappears.

However, this framework assumes that dominant individuals can effectively monitor and regulate subordinates. This raises a first key gap in current knowledge: what happens in systems where social structure is less cohesive? Could reduced opportunities for repeated interactions weaken social control, granting females greater autonomy over the timing of their sex change? A second key gap in understanding protogynous species concerns sex-specific life-history trajectories. While in gonochoristic (fixed-sex) polygynous systems, males are clearly the most vulnerable sex with higher mortality rates and lower longevity, it remains to be investigated if sex change could alter this pattern.

To explore these questions, I conducted a long-term observational study at Lizard Island on the Great Barrier Reef in Australia, focusing on the cleaner wrasse (*Labroides dimidiatus*). This species is an ideal fit for my study because it is a protogynous hermaphrodite that lives in noncohesive groups, with each female spending most of her time alone at her own cleaning station. From July 2022 to January 2026, I conducted about 1000 SCUBA dives totaling 1750 hours to monitor 1377 individually recognizable cleaner wrasse across eight reefs near Lizard Island, using VIE tags or natural pigmentation. Using non-invasive methods, I collected growth data with stereo-photogrammetry; documented social interactions via 20-minute underwater videos; and recorded demographic changes, such as survival, harem migrations, and sex changes, through surveys. I also used transects to assess the physical and social environment, including fish densities and reef health.

Chapter 1 demonstrates that in this protogynous species, sex-specific life-history trajectories are reversed: terminal-phase males have lower mortality rates than females. **Chapter 2** confirms that social control within the cleaner wrasse's size-based hierarchy is highly incomplete, allowing females to exercise greater agency over the timing of their sex change. Early sex change before the disappearance of the male by low-ranking individuals and rank reversals were not infrequent, and females' migration to a new harem or rapid growth increased the likelihood of sex change. Finally, **Chapter 3** specifically investigates this rapid female growth. While we did not find any clear physiological trade-offs or link to optimal cleaning efficiency, we highlight that a release from intraspecific social suppression by the dominant individual is the primary driver of rapid growth.

The results of this thesis contribute to several key conceptual advancements. They demonstrate that sequential hermaphroditism can significantly impact sex-specific life-history trajectories, challenging the classic assumption that, in polygynous mating systems, males are the most vulnerable sex. Furthermore, this research reveals that when social structures are not cohesive, size-based hierarchies do not universally function as rigidly controlled, stable queues. Ultimately, this thesis reframes sex change as a dynamic interaction of female strategies and the circumvention of intraspecific constraints.

Keywords: Cleaner wrasse, *Labroides dimidiatus*, Protogyny, Sex change, Size-based hierarchy, life-history, strategic growth, cleaning mutualism.

Résumé général

Tous les organismes vivants partagent l'objectif fondamental de survivre et de se reproduire, mais des ressources limitées les obligent à faire des compromis essentiels dans leur histoire de vie en décidant de la quantité d'énergie à consacrer à chaque trait. Ce principe d'allocation entraîne la grande diversité observée entre les espèces dans des traits démographiques tels que l'âge de maturité, la durée de vie et la production reproductive, ces différences étant façonnées par les conditions écologiques et la sélection visant à maximiser la fitness tout au long de la vie.

Chez les espèces séquentiellement hermaphrodites, la capacité à changer de sexe au cours de la vie constitue une stratégie complexe de leur histoire de vie. Au lieu d'optimiser un rôle sexuel fixe, ces organismes font face à un défi dynamique: déterminer quand réorienter leur allocation d'énergie entre les fonctions sexuelles. Ce changement s'explique le mieux par l'hypothèse de l'avantage de taille qui prévoit que la transition sexuelle évolue lorsque l'un des sexes a un succès reproducteur supérieur lorsqu'il est petit ou jeune, tandis que l'autre atteint une meilleure aptitude lorsqu'il est vieux ou grand. Étant donné que les espèces protogynes (femelle vers mâle) vivent le plus souvent en groupes harem polygyniques, avec une hiérarchie basée sur la taille, dans lesquels un mâle dominant monopolise les opportunités de reproduction parmi un groupe de femelles classées par taille, il est une hypothèse classique que le changement de sexe est strictement contrôlé par des facteurs sociaux. Dans ce système cohésif, les relations de rang stables sont maintenues par une agressivité sélective, et l'on s'attend à ce que seule la femelle la plus grande change de sexe lorsque le mâle disparaît.

Cependant, ce cadre suppose que les individus dominants peuvent réguler efficacement leurs subordonnés. Cela soulève une première lacune importante dans nos connaissances: que se passe-t-il dans les systèmes où la structure sociale est moins cohésive ? Des interactions réduites pourraient-elles affaiblir le contrôle social, permettant aux femelles une plus grande autonomie quant au moment de leur changement de sexe ? Une seconde lacune essentielle dans la compréhension des espèces protogynes concerne les trajectoires de vie spécifiques au sexe. Alors que dans les systèmes polygynes gonochoristiques (à sexe fixe), les mâles sont clairement le sexe vulnérable avec des taux de mortalité plus élevés et une longévité moindre, il reste à étudier si le changement de sexe pourrait modifier ce schéma.

Pour explorer ces questions, j'ai mené une étude observationnelle à long terme sur l'île de Lizard, sur la Grande Barrière de Corail en Australie, en me concentrant sur le labre nettoyeur (*Labroides dimidiatus*). Cette espèce est adaptée à mon étude car elle est un hermaphrodite protogyne vivant en groupes non cohésifs, chaque femelle passant la majorité de son temps seule à sa station de nettoyage. De juillet 2022 à janvier 2026, j'ai effectué 1000 plongées (1750 heures) pour suivre 1377 labres nettoyeurs identifiables via marquage VIE ou pigmentation naturelle, sur huit récifs près de l'île de Lizard. En utilisant des méthodes non invasives, j'ai collecté des données de croissance par stéréophotogrammétrie; documenté les interactions sociales via des vidéos sous-marines de 20 minutes; et enregistré les changements démographiques, tels que la survie, les migrations entre harems et les changements de sexe, au moyen d'observations directes. J'ai également utilisé des transects pour évaluer l'environnement physique et social, notamment la densité des poissons et l'état de santé des récifs.

Chapitre 1 démontre que, dans cette espèce protogynique, les trajectoires de vie spécifiques au sexe sont inversées: les mâles en phase terminale présentent des taux de mortalité plus faibles que les femelles. **Chapitre 2** confirme que le contrôle social au sein de la hiérarchie basée sur la taille chez le labre nettoyeur est fortement imparfait, ce qui permet aux femelles d'exercer une plus grande autonomie quant au moment de leur changement de sexe. Un changement de sexe précoce, avant la disparition du mâle par des individus de rang inférieur, ainsi que les inversions de rang n'étaient pas rares, et la migration des femelles vers un nouveau harem ou leur croissance rapide augmentait la probabilité d'un changement de sexe. Enfin, **Chapitre 3** étudie spécifiquement cette croissance rapide des femelles. Bien que nous n'ayons identifié ni compromis physiologiques clairs ni un lien avec une efficacité de nettoyage optimale, nous soulignons qu'une réduction de la suppression sociale intraspécifique par l'individu dominant constitue le principal moteur de cette croissance rapide.

Les résultats de cette thèse contribuent à plusieurs avancées conceptuelles clés. Ils démontrent que l'hermaphrodisme séquentiel peut avoir un impact significatif sur les trajectoires de vie liées au sexe, remettant en question l'hypothèse classique selon laquelle, dans les systèmes de reproduction polygynes, les mâles sont toujours le sexe le plus vulnérable. De plus, cette recherche révèle que lorsque les structures sociales ne sont pas cohésives, les hiérarchies fondées sur la taille ne fonctionnent pas systématiquement comme des "files d'attente" rigides et stables. Finalement, cette thèse recontextualise le changement de sexe comme une interaction dynamique entre les stratégies féminines et le contournement des contraintes intraspécifiques.

Mot-clés : *Labroides dimidiatus*, labre nettoyeur, protogynie, changement de sexe, hiérarchie basée sur la taille, histoire de vie, croissance stratégique, mutualisme de nettoyage.

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General introduction

The concept of life-history

While living organisms exhibit an incredible diversity of life cycles, they all share the fundamental goal of surviving and reproducing (Stearns 1998), two components that contribute to an individual's fitness (Wadgymar et al. 2024). The variation in the demographic life-history traits of living organisms, such as age at maturity, lifespan, and reproductive output, raises fundamental questions about the origins of this diversity (Stearns 1998). Because resources are finite, investment in one life-history trait necessarily reduces investment in others, generating fundamental physiological trade-offs (Stearns 1998). These trade-offs, such as those between current reproduction and survival, reproduction and growth, or offspring number and size, are central to life-history theory, and they ground the diversity of strategies observed in nature (Stearns 1998). Life-history theory, therefore, asks how organisms optimize the allocation of limited resources to growth, reproduction, and survival from birth to death to maximize fitness (Stearns 1976; Roff 1993; Stearns 1998; Stearns 2000).

Life-history evolution is often approached as an optimality problem, in which fitness is specifically defined, relationships between traits and fitness are established, and trade-offs among traits are used to predict the combination of traits that maximizes fitness (Stearns 2000). By linking ecological conditions to patterns of survival and reproduction, life-history theory provides a unifying framework for understanding how organisms are shaped by evolution to achieve reproductive success (Stearns 2000).

Sequential hermaphroditism: a shifting fitness target

Building on the fundamental life-history problem of resource allocation, sex allocation theory examines how organisms distribute limited reproductive resources between female and male functions to maximize lifetime fitness (Munday et al. 2006). In species with fixed sexes (gonochorism), this primarily involves an evolutionary optimization of the population sex ratio. However, for hermaphrodites, species that can either function as both sexes simultaneously (simultaneous hermaphroditism) or change sex over their lifetime (sequential hermaphroditism) (Sadovy and Shapiro 1987), sex allocation represents a highly dynamic life-history trade-off. For these species, the challenge lies not only in determining how much energy to invest in each sexual function, but when to do so across their lifespan (Munday et al. 2006). From a life-history perspective, sex change is therefore a complex optimization strategy: individuals must constantly balance the immediate physiological costs of growth, current reproduction, and survival against the future fitness payoffs of transitioning to a new sexual role.

The evolution of hermaphroditism is best understood by investigating the adaptive advantages it offers over gonochorism (Pla et al. 2022). For instance, in low-dispersal capacity or in low-density conditions where finding a mate is difficult, simultaneous hermaphroditism ensures greater reproductive success (Ghiselin 1969). Instead, when the reproductive value of one sex is highly dependent on body size, sequential hermaphroditism becomes the optimal strategy for increasing total lifetime fitness (Ghiselin 1969; Warner 1988b; Warner 1988a). The latter principle is formalized in the size advantage hypothesis (SAH), which proposes that sequential hermaphroditism evolves as an adaptive strategy when an individual reproduces most efficiently as one sex when small or young, but achieves greater fitness as the other sex when large and old (Ghiselin 1969). From a life-history perspective, sex change is a strategy that alters the timing and nature of reproduction itself, allowing an organism to reallocate reproductive effort across its lifetime, matching its sexual role to its current body size, social environment, and ecological conditions.

Sex change typically occurs in one direction: either female-to-male (protogyny) or male-to-female (protandry) (Kadota 2023). The favored direction depends entirely on which sex maximizes its reproductive value at a larger size (Pla et al. 2022), a dynamic that is tightly linked to the species' mating system (Warner 1978; Warner 1988b; Ross 1990). Protogyny is most common in polygynous mating systems, where a small number of large dominant males secure most reproductive output (Ghiselin 1969; Fricke and Fricke 1977; Kuwamura et al. 2014; Kruger 2021). In protogynous species, individuals maximize their lifetime reproductive success by beginning life as females and reproducing even at small sizes. As they grow larger and gain the competitive ability required to monopolize mates, they change sex to become terminal males, thereby achieving higher reproductive output (Benvenuto et al. 2017). This increase is due to upgrading from producing a single clutch of eggs to fertilizing the eggs of multiple females, resulting in a massive increase in both the average number of offspring produced and the overall variance in reproductive success (Benvenuto et al. 2017). If an individual remained female its entire life, it would miss out on the higher fitness payoff of the dominant male stage; conversely, if it functioned as a male from birth, it would fail to reproduce early in life due to intense competition from larger males. Thus, the shifting fitness target of sequential hermaphroditism ensures that an individual maximizes its reproductive output at every developmental stage.

Protogyny in fishes: Extrinsic and intrinsic constraints

Protogyny, as well as hermaphroditism in general, is widespread among teleost fishes, including ecologically and commercially important clades like parrotfish, wrasses, and groupers (Warner and Robertson 1978; Ross 1990; Zhou and Gui 2010; Ashman et al. 2014; Kuwamura et al. 2020). Across these taxa, individuals exhibit a diversity of sex change strategies, ranging from early to late sex change, and from no sex change to multiple sex changes (Munday et al. 2006). These strategies are influenced by the interaction between intrinsic factors such as life-history tradeoffs within individuals, and extrinsic factors, including the social and ecological environments in which they develop (Ghiselin 1969).

Most protogynous hermaphrodite fish form haremic systems (Warner and Robertson 1978; Moyer 1990; Kuwamura et al. 2020), a form of polygyny in which a dominant male monopolizes a group of females (Warner and Robertson 1978). Within these groups, social rank is strictly based on size, with the largest female occupying the highest rank below the dominant male (Moyer and Nakazono 1978; Warner 1978; Warner and Robertson 1978; Shapiro 1979; Sadovy and Shapiro 1987; Ross 1990; Devlin and Nagahama 2002; Nelson et al. 2016; Kuwamura et al. 2020). Social hierarchies are maintained through selective aggression (Hattori 1991), particularly among similarly sized individuals, as they experience high levels of conflict over resources (Enquist et al. 1987; Jennions and Backwell 1996; Cant and Johnstone 2000; Nathan et al. 2001; Bender et al. 2005). This enforces stable rank relationships and preserves size asymmetries as individuals socially queue and strategically adjust their size and growth rate in relation to those directly above in rank (Hofmann et al. 1999; Kokko and Johnstone 1999; Buston 2003a; Heg et al. 2004; Russell et al. 2004; Buston and Cant 2006; Dengler-Crish and Catania 2007; Wong et al. 2007; Young and Bennett 2010; Dubuc and Clutton-Brock 2019), thereby reducing the risk of conflict and, in more extreme cases, eviction from the social group (Taborsky 1985; Reeve 1992; Reeve and Nonacs 1997; Reeve et al. 1998; Buston 2003; Buston and Cant 2006; Wong et al. 2007). This generally leads to sex change being socially regulated, with typically the largest female changing sex at the disappearance of the male (Warner 1988a; Ross 1990). This pattern has been repeatedly documented in wrasses (Robertson 1972; Ross et al. 1983; Kuwamura 1984; Warner and Swearer 1991; Sato et al. 2018; Todd et al. 2019; Chakraborty et al. 2022; Quertermous et al. 2025), and groupers (Shapiro and Boulon 1982; Chen et al. 2020). Specific study species were the bluehead wrasse (Warner and Swearer 1991; Todd et al. 2019), the saddleback wrasse (Ross et al. 1983), the blackspot tusk fish (Sato et al. 2018), the Spanish Hogfish (Hoffman et al. 1985), the bamboo leaf wrasse (Chakraborty et al. 2022), the New Zealand spotty wrasse (Quertermous et al. 2025), and the orange-spotted grouper (Chen et al. 2020). Early studies suggested that this was also the case for the cleaner wrasse (Robertson 1972; Robertson 1974a).

However, this socially controlled framework relies on a key assumption: that dominant individuals can effectively monitor and regulate subordinates. Theoretical and empirical work across taxa shows that such control is dependent on repeated interactions, which enable dominants to detect and punish deviations, and is therefore most effective in cohesive social groups (Enquist et al. 1987; Cant and Johnstone 2000; Clutton-Brock et al. 2001; Buston 2003b; Buston 2003a; Buston and Cant 2006; Clutton-Brock et al. 2010). In systems where social structure is less cohesive, such as those characterized by female territoriality, where individuals occupy separate core areas and interact infrequently, this assumption may not hold. Reduced opportunities for repeated interactions and aggression may weaken social control, potentially allowing individuals greater autonomy in their growth and reproductive decisions. This highlights a first key gap that inspired the research focus of my thesis: how does the loss of social control in species with strict size-based hierarchies affect the timing and occurrence of sex change? And consequently, what other intrinsic and ecological factors might prove more important?

Environmental stress and sex-specific vulnerability

In addition to navigating social constraints, individuals must balance the sex-specific physiological costs of their life-history strategies against environmental pressures. In classic polygynous systems with fixed sexes, intense male-male competition imposes pronounced sex-specific trajectories: males typically grow larger, delay maturation, and experience higher energetic demands, which frequently results in higher male mortality, especially during periods of resource limitation or environmental stress (Trivers 1972; Bell 1980; Laurie and Brown 1990). This leads to a second key gap that inspired the research focus of my thesis: although these sex-specific costs and trade-offs are well documented in species with fixed sexes, they remain poorly understood in sequential hermaphrodites, where individuals experience both sexual roles within a single lifetime. In particular, it remains unclear how the physiological demands of rapid growth and sex change interact with extreme environmental events (such as marine heatwaves) to shape sex-specific vulnerability and survival in protogynous fishes.

The perfect study species: Labroides dimidiatus

General biology

Labroides is an Indo-Pacific genus of the family Labridae (Allen et al. 2002). The cleaner wrasse *Labroides dimidiatus* is the commonest and most widespread species, ranging from East Africa across the Indian Ocean and into the Pacific (Randall 1958; Robertson 1974a; Allen et al. 2002). This species is reef-associated and territorial, preferring coral or coral-sand areas in both shallow and deeper depths (0.5-40m) (Randall 1958). Our long-term field monitoring across the study sites at Lizard Island on the Great Barrier Reef, Australia, indicates that the cleaner wrasse is ubiquitous across all reef habitats and available depths. Juveniles of this species can be morphologically distinguished from adults by their black coloration and a thin, iridescent blue stripe running along the body on each side (Figure 1). Adults show no permanent sexual dimorphism and are generally pale with a black stripe running through the eye and along the back into the blue caudal fin (Figure 2) (Randall 1958; Robertson and Choat 1974; Allen et al. 2002). An individual cleaner's total length increases continuously, and the rate of such increase declines with age (Robertson 1974a; Kuwamura 1981a). Cleaner fish are typically considered juveniles until they reach a total length of 50mm, in transition but mature by 60mm, and adults thereafter (Robertson 1974a; Kuwamura 1981b). Within the monitored populations at Lizard Island, the smallest observed newly settled juvenile had a total length of 10 mm, while the largest adult measured 102 mm. In other parts of the world, the cleaner wrasse can reach 140mm. The life expectancy of *Labroides dimidiatus* is estimated at around five years, and juvenile survival in the first year is estimated at 50% (Eckert 1987).

Social structure

The cleaner wrasse is a protogynous hermaphrodite with a size-based hierarchy (Robertson 1972; Robertson 1974a; Robertson 1974b; Kuwamura 1984; Nakashima et al. 2000). Each female has her own territory within the one of the harem's male, but she spends most of her time alone at her own cleaning station (Robertson 1974a). The harem of the cleaner wrasse can either be linear, all females' territories overlap to some degree, or branching, a system characterized by sub-groups of females that do not overlap (Kuwamura 1984). This represents a non-cohesive social group in which, despite it not being directly tested, it could be logically argued that the threat of eviction is absent.

Parasitic alternative reproductive tactics are absent, as neither males nor females tolerate additional males within their territories (Kuwamura 1984) and spawning occurs exclusively between one male and one female (Robertson and Choat 1974). During the spawning act, the male and female participate in a pre-spawning dance and release gametes into the water column during an upward rush (Robertson 1974b; Robertson and Hoffman 1977; Brothers and Thresher 1985; Victor 1986). Eggs and Larvae are planktonic (Victor 1986), and juveniles later settle on the reef (Robertson 1974a; Kuwamura 1981b). Cleaner fish were observed to exhibit sexual behavior year-round, but to spawn only during certain months around the summer season at the study site (Robertson 1974a; Kuwamura 1981b; Kuwamura 1981a). During spawning season, large individual adult females spawn daily, especially soon after high tide when the outgoing current is at its peak (Robertson 1974a; Kuwamura 1981b; Kuwamura 1984; Sakai and Kohda 2001). Smaller females are not as regular but still spawn almost every day (Robertson 1974a) Bi-directional sex change has been observed (Kuwamura et al. 2020), but it appears to be entirely governed by social status (Kuwamura et al. 2011). Migration between harems was suggested as a strategy used by lower-ranking females to enhance their opportunities for sex change (Sakai et al. 2001). Classic studies demonstrated sex change suppression and hierarchical control within harems, resulting in standard sex change (Robertson 1972; Robertson 1974a; Kuwamura 1984).

Cleaning mutualism and energy acquisition

This species is a keystone protogynous species essential for maintaining reef fish diversity and abundance through mutualistic cleaning interactions (Bshary 2003; Bshary et al. 2007; Ros et al. 2011;

Waldie et al. 2011; Ros et al. 2020). Various reef fish actively visit the cleaner wrasse at their cleaning stations to have their ectoparasites removed (Randall 1958; Potts 1973; Grutter 2001), representing the cleaner's primary source of food intake (Randall 1958; Potts 1973; Potts 1973; Gorlick 1984; Grutter 1996; Grutter 1999). In this cooperative mutualism, reef fish benefit from improved health (Bshary et al. 2007; Ros et al. 2011; Waldie et al. 2011; Ros et al. 2020) while cleaners gain access to a vital food resource (Gorlick 1984; Grutter 1996). However, a conflict of interest arises as cleaners prefer fish mucus over ectoparasites (Grutter and Bshary 2003). Biting mucus constitutes cheating (Bshary 2001) and is detrimental to their client's health (Ebran et al. 1999; Reverter et al. 2018). Clients will react to cleaner mucus feeding with a visible body jolt (Bshary and Grutter 2002a). This results in an asymmetric game in which cleaners can cheat and harm clients, but clients cannot do the same (Bshary and Grutter 2002b), with predators being an exception as they could easily prey on a cheating cleaner (Trivers 1971). The latter threat is sufficient to deter cheating by cleaners and ensure high-quality service (Bshary 2001). Harmless clients are instead unable to defect a cheating cleaner and have evolved partner control mechanisms, strategies employed to prevent and penalize cheating by their partners, thereby ensuring the mutualistic nature of the interaction (Bshary and Grutter 2002b). Clients living in small territories that have access to only one cleaner adopt a punishing control mechanism involving the aggressive chasing of a cheating partner (Bshary and Grutter 2002b; Bshary and Grutter 2005). This is a temporarily spiteful behavior that imposes immediate energy costs to both partners but that yields long-term benefits to the client by discouraging future cheating (Bshary and Grutter 2002b). Larger clients with access to multiple cleaning stations can instead use partner choice as their control mechanism (Bshary and Grutter 2002b; Bshary and Grutter 2002a; Bshary and Grutter 2005). Furthermore, clients with access to multiple cleaning stations can evaluate a cleaner before an interaction by observing the cleaner's behavior with other clients. By doing so, they build an "image score" based on the observed service quality, allowing them to avoid cleaners that recently provided poor service (Bshary 2002; Bshary and Schäffer 2002; Bshary and Grutter 2006; Johnstone and Bshary 2007; Pinto et al. 2011: 20). Together, the conflict of interest and the client response selected for high strategic sophistication in cleaners as they are able to adapt their behavior to a variety of contextual features (Cant and Johnstone 2000; Bshary 2001; Bshary 2002; Bshary and Grutter 2002b; Bshary and Grutter 2002a; Bshary and Schäffer 2002; Bshary and Grutter 2005; Cant and Johnstone 2006; Pinto et al. 2011). Individuals showing locally adaptive behavior harbor relatively larger forebrains than individuals that do not (Triki et al. 2019).

General methodology and specific aims

General methodology

This thesis relies on a comprehensive, long-term observational field study conducted across eight sites at Lizard Island on the Great Barrier Reef, Australia, spanning from July 2022 to January 2026. To monitor natural social dynamics and life-history trajectories without disturbing population dynamics, we used only non-invasive methodologies. Over the course of approximately 1000 SCUBA dives and 1750 hours of direct underwater observation, we tracked 1377 individually recognizable adult and juvenile cleaner wrasses. Individual identification is achieved through a combination of Visual Implant Elastomer (VIE) tagging and distinct natural pigmentation patterns.

A core methodological component across all chapters was the continuous, high-precision measurement of individual body size, obtained using a calibrated underwater stereo-photogrammetric camera system. This allowed for the construction of deme-specific growth curves and the accurate classification of individual growth strategies. We complemented these demographic data with extensive behavioral observations, capturing 20-minute focal video recordings to quantify both interspecific cleaning interactions (e.g., cleaning duration, service quality, client jolts) and intraspecific social interactions (e.g., aggression, spatial distribution, hierarchy). Finally, regular updates of individual presence and male- or female-specific behaviors allowed us to track demographic changes, including survival rates, harem migrations, and occurrences of sex change.

Specific aims

One of the key gaps previously identified, which inspired the first aim of my thesis, was the lack of a clear understanding of sex-specific life-history trajectories in sequential hermaphrodites. Specifically, we aimed to investigate whether the classical assumption about the costs of reproduction and male-biased mortality in gonochoristic polygynous systems also applies to sequential hermaphrodites. This is researched in **Chapter 1, “Persistent male survival advantage in a protogynous hermaphrodite”,** which examines sex-specific life-history trajectories of the cleaner wrasse at Lizard Island under both normal and extreme environmental conditions. Leveraging the 2024 El Niño–Southern Oscillation (ENSO) marine heatwave, we examined survival and growth rates for males and females across the periods before, during, and after the event.

The second key gap identified, which motivated the second research aim of my thesis, concerns understanding how the loss of social control in species with strict size-based hierarchies influences the timing and occurrence of sex change, and whether intrinsic or ecological factors may instead play a more dominant role. **Chapter 2, “Flexible sex change in the cleaner wrasse: effects of social control, strategy, and population density”**, investigates the dynamics of sex change in the cleaner wrasse at

Lizard Island. This species inhabits social structures characterized by reduced group cohesion and female territoriality, which may also imply a lack of threat of eviction and therefore incomplete control. Specifically, this chapter aims to quantify deviations from strict social control by examining the frequency of early sex change, identifying females' strategies that enhance the likelihood of sex change, and evaluating the role of ecological variables in shaping growth, these strategies, and the timing of early sex change.

Finally, **Chapter 3, "Social control, not service quality, explains fast growth in the cleaner wrasse *Labroides dimidiatus*"**, builds on one of Chapter 2's findings that rapid somatic growth is a key strategy for attaining sex change. Because the cleaning behavior of the cleaner wrasse serves as the near-exclusive mechanism for energy acquisition, it provides a unique ecological arena to test whether higher foraging efficiency and strategic sophistication are the primary drivers of rapid growth. The aim is therefore to adopt a life-history perspective and investigate what enables rapid growth: (i) from an ecological and physiological perspective, whether it is fueled by increased energy intake, through increased time spent cleaning and higher service quality, or facilitated by intrinsic reproductive trade-offs, and (ii) from a game theoretical perspective, if it is the result of social control and queuing.

Figure 1: Picture of a juvenile cleaner wrasse of 20mm. The picture was taken by Letizia Pessina and Anna Viglino.

Figure 2: Picture of an adult cleaner wrasse of 70mm. The picture was taken by Letizia Pessina.

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Chapter 1: Persistent male survival advantage in a protogynous hermaphrodite fish

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Manuscript information

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Author contributions

All authors contributed to the project design. LP conducted the fieldwork, performed data and statistical analyses, and led manuscript writing. RB supervised the project and contributed to conceptual development and revision of the manuscript.

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Abstract

In many polygynous species, males face stronger intrasexual competition, higher energetic demands, and lower survival than females, especially under resource limitation or environmental stress. Such sex-specific vulnerabilities are expected to intensify with climate change. Yet, in sequentially hermaphroditic systems, where individuals change sex during their lifetime, how sex and sex change shape survival remains largely unexplored. We studied sex-specific survival and growth in the haremic, protogynous cleaner wrasse, Labroides dimidiatus, across eight reefs around Lizard Island, Great Barrier Reef. We tracked a total of 731 adult fish (individually recognizable through marking or idiosyncratic color patterns) over two years. This period included the 2024 El Niño–Southern Oscillation (ENSO), which caused a temporary 1-degree increase in water temperature, severe coral bleaching, and coral mortality at Lizard Island. Contrary to expectations from dioecious systems, terminal-phase males exhibited higher survival than initial-phase females under both normal and, in particular, ENSO conditions. While male mortality was not affected, female mortality more than doubled during the event, indicating greater physiological or energetic vulnerability. A partial explanation for the overall higher female mortality is their generally faster growth rate, which declined in both sexes during the ENSO event. Our findings challenge existing assumptions of male-biased mortality in polygynous species and highlight that sex and sex change fundamentally shape demographic responses to climate extremes.

Keywords

Sex-specific resilience, El Niño-Southern Oscillation (ENSO), Protogyny, Cleaner wrasse, Labroides dimidiatus, Male-biased survival.

Introduction

In polygynous species, males often experience intense intrasexual competition for access to mates (Kruger 2021), resulting in high reproductive skew whereby a small number of dominant males secure most reproductive opportunities (Kruger 2021). This competition imposes distinct life-history trajectories on the sexes (Trivers 1972; Bell 1980): Males typically grow larger to enhance competitive ability, delay maturation to achieve sufficient size, reproduce over fewer seasons, and often exhibit lower survival (Trivers 1972; Parker 1992; Lukas and Clutton-Brock 2014; Hämäläinen et al. 2018; Horne et al. 2020). Elevated male mortality could be partly attributed to their larger body size (Laurie and Brown 1990), which increases energetic demands and vulnerability to resource limitation during periods of food scarcity. These sex-specific costs of reproduction may carry heightened demographic consequences in the context of climate change. Males could prove more vulnerable to the related intensifying and prolonged extreme weather events.

While polygyny is typically studied in dioecious species with fixed sexes, it also exists in protogynous species, where individuals first function as females, and only a few larger individuals eventually change sex and become males that then monopolize a harem of females (Ghiselin 1969; Robertson 1974a; Robertson 1974b; Warner and Robertson 1978; Sadovy and Shapiro 1987; Ross 1990; Munday et al. 2006). This type of hermaphroditism is common in coral reef fish, including clades of great ecological and commercial importance, such as parrotfish, wrasses, and groupers (Warner and Robertson 1978; Zhou and Gui 2010; Kuwamura et al. 2020; Sakai 2023). However, how sex and sex change shape vulnerability to environmental extremes remains unknown. A key example of such extremes in the marine environment is the occurrence of the El Niño-Southern Oscillation (ENSO) (Cai et al. 2014; Cai et al. 2021; Cai et al. 2022; I.P.O.C.C. 2023; Thirukanthan et al. 2023; Huang et al. 2024: 20), which causes marine heatwaves and coral bleaching, reducing habitat quality and food availability. Yet, despite evidence of ENSO impacts on corals, fish growth, and mortality (Wellington and Victor 1985; McPhaden et al. 2006; Collins et al. 2010; Ainsworth and Gates 2016; McGowan and Theobald 2017; Hughes et al. 2018; Triki et al. 2018; McClanahan et al. 2019; Triki and Bshary 2019; Huang et al. 2021), its potential for causing sex-specific survival responses in protogynous hermaphrodites remains largely unexplored.

To address this gap, we studied the cleaner wrasse (*Labroides dimidiatus*). This species is a keystone protogynous species essential for maintaining reef fish diversity and abundance through mutualistic cleaning interactions (Bshary 2003; Bshary et al. 2007; Ros et al. 2011; Waldie et al. 2011; Ros et al. 2020). It has also emerged as a model species to study the effects of global change on behavior and cognition (Triki et al. 2018; Paula et al. 2019; Pereira et al. 2025). Both the behavior and survival of this species have previously been documented as negatively affected by extreme weather events (Triki et al. 2018; Triki et al. 2019; Pereira et al. 2025), but without studying potential sex-related differences.

We tracked individually marked fish across eight reef sites around Lizard Island, Great Barrier Reef, over a two-year period that encompassed the 2024 ENSO event. The 2024 ENSO led to sustained and extreme warming during the austral summer (NOAA 2019; Henley et al. 2024; Australian Institute of Marine Science 2025), resulting in the most severe coral cover decline on record at Lizard Island (Australian Institute of Marine Science 2025). This extreme climatic event provided a natural contrast for examining sex-specific adult survival in a protogynous species, both under "normal" conditions and under environmental stress. We measured growth and survival and contextualized these with in situ coral bleaching surveys and published water temperature measurements to describe general conditions and corroborate the negative effects of ENSO in our research area. Contrary to expectations based on male-biased mortality in other polygynous species, our results reveal that male cleaner wrasse exhibited lower mortality than females. These findings challenge existing assumptions about sex-based vulnerability and highlight the need to account for hermaphroditic systems in assessments of climate sensitivity and population dynamics.

Methods

El Niño

Normal and ENSO conditions were defined using published temperature data collected by the Australian Institute of Marine Science (AIMS) sensor buoys deployed at Lizard Island between July 2022 and November 2024 (Australian Institute of Marine Science (AIMS) 2020), in combination with thermal stress thresholds defined by the National Oceanic and Atmospheric Administration (NOAA 2019). These environmental data were complemented by field-based assessments of coral bleaching and mortality conducted at Lizard Island (Supplementary Materials 2).

Temperature records indicated that austral summer conditions in 2023 were characterized by an absence of significant thermal stress or bleaching (Australian Institute of Marine Science (AIMS) 2020), consistent with NOAA threshold criteria (NOAA 2019). In contrast, the 2024 ENSO event produced prolonged and anomalously high sea surface temperatures across the Great Barrier Reef (NOAA 2019; Henley et al. 2024; Australian Institute of Marine Science 2025), with Degree Heating Weeks (DHWs) exceeding 8, a level associated with a high probability of mass coral bleaching. This thermal anomaly coincided with the fifth recorded mass bleaching event on the GBR and the fourth global bleaching event (Australian Institute of Marine Science 2025) (Figure S1).

At Lizard Island, these conditions were accompanied by extensive coral bleaching and substantial hard coral mortality (Supplementary Material 2, Figure S2). Together, these contrasting environmental conditions provided the basis for comparing the survival and growth of cleaner wrasse males and females under baseline versus thermally disturbed reef conditions.

Site and study populations

The study took place at Lizard Island on the Great Barrier Reef in Australia in 2023 and 2024. To determine seasonal differences and detect the effects of ENSO, data were collected in summer (February to April) and winter (July to September) for both years. Eight sites were selected as our study populations based on their varying cleaner and client densities (Figure S4).

Fish were caught while SCUBA diving using hand nets (10 × 15 cm) and barrier nets (4.7 × 1.8 m or 1 × 1.2 m). To facilitate individual identification, we used visual implant elastomer (VIE) tags, a well-established methodology in small reef fishes (Jungwirth et al. 2019). Tagging was conducted underwater, with each fish kept in a hand net to maintain normal saltwater flow. From initial capture to release, the entire process took less than 2 minutes per fish. All individuals resumed normal behavior immediately after release. No non-target cleaner fish were accidentally captured.

Each adult focal individual received two injections, with each injection placed at one of four possible body locations: the front and back of both the left and right sides of the body (Figure S5). Injections were applied to the clear tissue, specifically the white or beige band located above the black band. Each injection used one of six possible colors (red, pink, yellow, green, blue, or white). This tagging scheme, which combines 2 tags, 4 locations, and 6 colors, allows for up to 1,296 unique codes. This number increases further if the order of color placement is considered (e.g., red followed by yellow is distinct from yellow followed by red). Juvenile focal individuals, typically around 40 mm in length, received only one injection, using colors most visible on their darker body coloration (red, pink, or yellow), resulting in 108 possible unique tags. In some cases, tagging was unnecessary, as individuals could be reliably identified by unique physical features such as darker or lighter pigmentation, irregularities in the lateral black band, or other distinct markings (Figure S6). Between 2022 and 2024, the dataset included 731 adult fish (120 untagged) and 495 juveniles (291 untagged). Age class was based on life stage at initial observation.

VIE tags are created using a two-part mixture consisting of a viscous pigment and a hardening agent. The hardener helps the tag maintain its structural integrity as the fish grows, preventing the gradual fading of the pigment (Northwest Marine Technology, Inc. 2017). However, because the hardening agent sets rapidly at high temperatures, causing the entire syringe to solidify and go to waste, we chose not to use it. Given the large number of fish that needed to be tagged in this study, this decision minimized material loss. Nevertheless, throughout the study, we observed no loss of marking. While the absence of a hardener occasionally led to tag expansion as the fish grew, all tags remained clearly visible throughout the observation period. To further confirm the durability of our VIE tags, a subset of previously tagged individuals was opportunistically recaptured 12-20 months after marking and examined (n = 33). All retained a clearly visible tag. These observations were used solely to verify tag durability and are not otherwise analyzed in this manuscript. Overall, our VIE tags demonstrated greater long-term retention than previously reported (Jungwirth et al. 2019).

Except for two nearby sites (Mermaid West and Mermaid East), all sampling locations were geographically isolated coral reef patches, separated by broad sandy areas or open water. As cleaner wrasses are territorial fish that do not cross open water, migration between sites is not possible. Therefore, VIE tag combinations could be reused across different sites. However, at the two closely located Mermaid sites, VIE combinations were not repeated to avoid potential tag overlap due to possible movement between the locations.

General long-term monitoring

This study is part of an ongoing long-term monitoring project that began in July 2022. During each field season, data were collected on a 5-day in-water schedule with a 1-day dry rest. Each diving day comprised three dives targeting different types of data collection, including individual-level measurements (size and behavioral video observations) and site-level surveys (fish and benthic surveys, and direct observations of social systems). Dives lasted 90-120 minutes, depending on the task, and were conducted within one of three time slots: 8 am, 11 pm, or 15 pm. Each site was visited at least two times per week, except when weather conditions or the presence of dangerous fauna prevented access. Site selection and timing were further constrained by tides, winds, and sea conditions, as some locations were shallower and/or more exposed than others.

During each dive, the primary researcher (LP) systematically surveyed the site to maintain an up-to-date record of focal fish presence or absence, covering the entire area to ensure an accurate picture of their distribution. During the period of interest for the present study, 14 additional researchers contributed to the collection of focal videos. LP was responsible for identifying focal individuals in situ, assigning them to team members for video recording, and subsequently verifying all footage to ensure individual identities were not compromised during filming. Nevertheless, all datasets used in this study, including size measurements, presence-absence records, population surveys, and fish and substrate surveys, were collected exclusively by LP, ensuring methodological consistency.

LP participated in every field trip and has conducted approximately 1,000 dives to date, totaling around 1,750 hours of underwater observation. This sustained effort involved repeated monitoring of the same individual fish, resulting in an exceptional level of familiarity with their appearance and behavior. This intensive, long-term monitoring enabled individual recognition, including that of untagged fish with distinctive markings.

Not all individuals were included in the sizing data collection due to logistical constraints. Due to overheating and battery life constraints, the time available for fish sizing at a site was limited. Therefore, individuals living at the end of the dive site were consistently excluded from the size analysis. Consequently, some fish that appear in the survival analyses are not included in the growth analyses.

Sex identification

Sex identification was based on behavioral observations in the field, a widely accepted method in fish behavioral ecology. The same approach was used in Pessina and Bshary (2026), which specifically investigated sex change strategies in the cleaner wrasse at Lizard Island. Although we did not repeat the physiological assessment in the present study, this methodology relies on well-established behavioral indicators that have been independently validated. In this species, previous research has in fact documented clear sex-specific behaviors, such as territorial displays and courtship roles, that reliably differentiate males from females (Robertson 1974b). Furthermore, these criteria have been validated through physiological methods, including gonadal inspections (Robertson 1974b). Such a non-invasive approach was essential to maintain the integrity of the long-term monitoring and avoid disrupting the natural dynamics of the cleaner wrasse population.

Several qualitative behavioral differences were used here for sex identification: (i) Flutter-Run, a rapid display involving tail fluttering and fin spreading, performed exclusively by males as they swim past females while presenting a lateral view (Robertson 1974b); (ii) Sexual signaling, where females respond positively to male courtship advances. This includes the Body-Sigmoid, a static display in which the female sharply curves her body into an S shape, with the belly bulging toward the male, typically as a signal of readiness to spawn (Robertson 1974b); (iii) Coloration differences, as females develop a distinct sexual color pattern during courtship, whereas males do not (Robertson 1974b); and (iv) Spawning posture, where males adopt a superior position during the later phase of courtship, such as the upward spiral, straddling the female and leading the upward rush (Robertson 1974b).

In addition to these qualitative traits, more quantifiable behavioral differences were also used. Males showed greater tolerance of females in proximity, particularly around their feeding areas, and exhibited a higher rate of movement within their territories, frequently visiting females and patrolling territorial boundaries (Robertson 1974b).

Sex identification was further confirmed through spawning patterns. All individuals classified as males were observed spawning with smaller partners, while all females were seen spawning with larger partners. Spawning invariably involved only two individuals, which excludes the existence of sneaker males that would join a spawning event to add their sperm. Over the first year of data collection, 42 individuals were confirmed to have changed sex. While sex change can take up to two weeks to complete physiologically, in the cleaner wrasse, the behavioral expression of reproductive roles can occur immediately (Nakashima et al. 2000). The largest female rapidly adopts male-typical spawning behavior following the disappearance of the dominant male to establish dominance and secure her new position (Robertson 1974b), even while still undergoing gonadal transition (Nakashima et al. 2000). Therefore, the same behavioral traits that reliably distinguish males from females can be used to identify a newly transitioned male. Also, each of these sex changers was observed at least once spawning with a larger partner (as a female) and later with a smaller partner (as a male).

Growth rates

We assessed the growth of each focal fish using a calibrated underwater stereo-photogrammetric system, consisting of two GoPro Hero 8 cameras mounted on a fixed rig, following established protocols for stereo-video measurements (Goetze et al. 2019). Footage was processed using EventMeasure software (Seager 2006) which enables precise three-dimensional measurements based on synchronized stereo images. Before data collection, the system was calibrated using CAL, a dedicated software that ensures accurate geometric alignment between the camera pair (Seager 2006). This stereo setup significantly improves measurement precision over traditional visual estimations (Michael et al. 2011). Individuals were typically revisited approximately once per month (median interval = 28 days, mean = 35 days). Changes in body size between consecutive measurements were generally small (median = 1 mm; mean = 2.5 mm).

The error of this software is known to be around 1-2mm (Euan et al. 2010). To further assess the accuracy of the stereo camera system for our study, a calibration bar with three known distances was used to measure the system's error. Measurement error was ± 1.13mm using the calibration bar and ± 1.81mm of wild cleaner fish due to movement and growth between measurements (See supplementary Materials 6 for more details).

Measurements occasionally indicated that an individual had shrunk since the last assessment. To address this likely consequence of a measurement error, we adopted a standard approach and retained the previous sizing in such instances, adjusting the growth to 0. To evaluate the potential impact of adjusting negative growth values, we ran an additional model (Model 2.3; Supplementary Materials 7) on our raw growth dataset without correcting for shrinkage. The predicted distribution was nearly identical to the predictions from the primary analysis (Model 2.2), indicating that correcting for negative values did not bias the overall pattern (Figure S8).

Survival

Each site was visited at least twice a week, and during each dive, LP systematically surveyed the entire site to maintain an up-to-date record of the presence or absence of focal fish. Survival was assessed strictly within each field period and does not account for intervals between field seasons. At the beginning of each study period, any unmarked adult individual encountered within the study area was captured and tagged, ensuring full control over the composition of each deme from the outset.

Additionally, the sex and life stage of focal individuals were recorded and updated at the beginning of each study period.

When an individual was no longer observed in its territory, we implemented a systematic search protocol across the entire site to confirm true disappearance (i.e., death). Mortality could be reliably distinguished from emigration for several reasons. First, six of the eight study sites consisted of discrete reef patches clearly bounded by unsuitable sandy habitat, effectively limiting movement beyond site boundaries. The remaining two sites (Mermaid West and Watson) were connected to a continuous reef on only one side. At these locations, searches were extended to twice the length of the focal site in the direction of reef continuity to ensure that individuals had not emigrated beyond the study area. Second, the cleaner wrasses are territorial and typically move only over limited distances (Robertson 1974b). Consistent with this, at Lizard Island, most movements occur within 30 m, with only a single individual recorded moving as far as 90m in search of a better harem (Personal observations). Therefore, our search efforts reliably distinguished between a true disappearance and an emigration. Movements between harems were consistently detected in real-time from the beginning of the study, and individuals who shifted harems were continuously tracked. Only in three rare cases were individuals initially considered missing and later rediscovered. These were younger females that had migrated to previously uninhabited peripheral areas, rather than entering existing harems, which later proved to be successful strategies for initiating sex change. These exceptions did not undermine the general approach, as movements within the monitored network were always promptly identified. The appearance of a new cleaner within a previously occupied territory further supported the conclusion that the original individual had disappeared.

Importantly, surveys were not based on short, fixed-duration observations (e.g., transects), but on exhaustive searches specifically targeting known individuals. Each dive involved repeatedly covering the entire site and all cleaning stations until every focal fish had been either located or confidently classified as absent following the extended search protocol. Given this complete coverage and the ability to distinguish disappearance from emigration, detection probability was effectively close to one and was therefore not explicitly modeled in survival analyses.

Cleaner wrasses experience very low predation risk (Bshary and Würth 2001). They provide an obligate cleaning service and flexibly adjust service quality according to client type and contextual factors (Bshary 2002; Bshary and Schäffer 2002; Bshary and Grutter 2006; Johnstone and Bshary 2007; Pinto et al. 2011: 2). In particular, higher-quality service is preferentially provided to predatory clients (Bshary 2001), which in turn refrain from consuming cleaners because the long-term benefits to repeated cleaning interactions outweigh the short-term gain of a single prey item. Therefore, typically, when a fish dies, it is due to natural causes or illness.

Fish census

Cleaner fish density at each study site was initially quantified using 10 replicate 30 m belt transects. In subsequent surveys, a more detailed transect protocol was implemented to estimate both cleaner and client fish densities; however, these latter data were used only for supplementary analyses of client abundance (Supplementary Material 2).

For the present study, cleaner fish density was instead estimated at the population level to capture reef-wide changes across the entire study area. Because all cleaner fish individuals within each study site had been previously identified and repeatedly monitored throughout the study period, and the spatial extent of each site was precisely defined, density estimates could be standardised directly from total population counts. Specifically, at the beginning of each study period, cleaner fish density was calculated as the total number of adult cleaner fish (TL ≥ 5 cm) recorded at a site divided by the corresponding reef area, expressed as individuals per 100 m^2. This approach provided a site-wide estimate of population density that was independent of localized transect variation and, therefore, more appropriate for assessing temporal changes.

Statistical Models

Data analyses were conducted using R version 4.3.1 (RStudio Team 2020). The different research questions were addressed using various statistical models, including Generalised Linear Mixed Effects Models (GLMM), Linear Models (LM), and General Linear Models (GLM). These analyses were performed using the “lme4” (Bates et al. 2015), “nlme” (Pinheiro 2011), “Agricole” (de Mendiburu 2023), and “stats” (R Core Team 2023), packages in R. Diagnostic plots and residual analyses were employed to evaluate the fit of the chosen models. Post-hoc analyses were conducted with Tukey’s adjustment method using the “emmeans” package (Lenth 2023). Full model specifications are available in Supplementary Materials 8. Below, we outline the purpose of each model

Our analyses of cleaner wrasse life history focused on patterns in density, growth, and mortality.

We first examined changes in adult cleaner wrasse density (TL ≥ 5 cm) across years and seasons (Model 1), using standardized fish counts per 100 m^2 at each site. Density values were log-transformed to normalize the distribution. We modeled these data using an LMER with fixed effects for season, year, and their interaction. A random effect for site was included to account for site-specific variability.

To compare growth rates across seasons and years, the cleaner fish population was subdivided into 10 mm size classes to account for ontogenetic differences in growth (younger fish grow faster). The growth rate for each individual was calculated by subtracting the initial size from the final size and then dividing by the number of days between measurements to obtain a per-day growth rate. The mean interval between measurements was 55 days (median = 40 days). The number of growth rate estimates per individual depended on their presence during the sampling period and ranged from one to four (1 = 411 individuals, 2 = 100, 3 = 57, 4 = 26). Only fish in size classes 50 mm, 60 mm, 70 mm, and 80 mm were included in the analysis due to the consistency of sample sizes across seasons.

Growth was analyzed using two complementary modelling approaches. First, we modelled log-transformed growth as a Gaussian response in an LMER (Model 2.1) to assess the effects of size class, season, and year, including their interactions. Random intercepts for site and individual ID were included to account for spatial variability and repeated measures on individuals.

Second, we used a GLMM with a Tweedie distribution (Model 2.2) to model growth rate as a function of sex, year, and season, including their interactions. This model incorporated random intercepts for individual ID and site to account for repeated measurements and spatial heterogeneity, and allowed dispersion to vary by year to accommodate changes in variance over time. The Tweedie distribution was selected to better capture the data's distributional characteristics, including zero inflation and positive continuous values. Both models focused on data where negative growth values had been adjusted.

Mortality patterns were investigated using two complementary modeling approaches designed to address different ecological questions and the structural properties of the data. The first model focused on describing variation in mortality rates between adult males and females across sampling periods using a GLMM (Model 3.1). The response variable was specified as a binomial outcome, with counts of dead and surviving individuals at the end of each period, representing mortality. The fixed effects included sex, study period, and their interaction. To account for unequal duration of sampling periods across sites and seasons (mean duration of 66 days), an offset term was included in the model (offset(log(days)). The site was included as a random intercept to account for repeated measurements.

The second model (Model 3.2) aimed to evaluate whether observed differences in mortality between sexes could be explained by individual body size, given the strong size structuring inherent to the protogynous life history of the study species. Because individuals are born female and transition to male at larger body sizes, sex and size are intrinsically correlated and cannot be fully disentangled at the population level. To address this, we combined the presence-absence survival dataset with the size dataset. For each study period, individuals were assigned a survival score of 1 (survived) or 0 (did not survive), and their initial body size was included. Only individuals with recorded size measurements were used in this analysis. We then fitted an individual-level GLMM with a binomial error distribution and a logit link, in which survival (0/1) was modelled as a function of scaled body size, sex, and their interaction, with a random intercept for individual identity to account for repeated observations. This model allows explicit testing of whether sex effects on survival persist after accounting for body size, thereby evaluating whether apparent sex differences in mortality are driven by size-dependent survival rather than sex per se.

The use of two separate models was necessary due to both biological and statistical constraints. First, the population framework is appropriate for describing variation in aggregated mortality rates across groups and time periods, while the second one provides a mechanistic, individual-level test of size-dependent survival. Second, combining all predictors (sex, size, and sampling period) in a single GLMM resulted in severe estimation issues due to structural confounding and near-complete separation in the data, arising from the biological reality that males are consistently larger than females and that some sex-period combinations contain very few or no mortality events. This prevented reliable estimation of model parameters under a unified framework. The complementary modelling approach, therefore, allows robust inference at both the population and individual levels while respecting the biological structure of the system.

Results

Cleaner wrasse performance

There was a significant decrease in adult cleaner wrasse density in 2024 compared to 2023 (Model 1; Type II, Wald Chi-square Test: Chisq = 8.32, df = 1, p = 0.004). There was no significant seasonal difference (Model 1; TL ≥ 5 cm, Type II, Wald Chi-square Tests: Chisq = 0.34, df = 1, p = 0.56) and no significant interaction between year and season (Model 1; Type II, Wald Chi-Square Test: Chisq = 0.25, df = 1, p = 0.62; Figure 1). On average, cleaner wrasse densities declined by 17.44% in 2024 relative to 2023.

Two years of monitoring marked individuals have shown that adult cleaner fish are highly site-attached, with only a small proportion relocating to neighboring harems. In the first year alone, only 12.7% of females were observed migrating to adjacent harems. These movements were consistently detected in real time and hence were not mistaken for disappearances. Thus, when an individual was no longer observed, it could reliably be interpreted as a mortality event. With this in mind, our analysis revealed significant differences in mortality between sexes and across study periods. Specifically, female cleaner wrasses exhibited a higher overall mortality than males (Figure 2A; Model 3.1, Type II tests, Wald Chi-square Test: Chisq = 22.612, df = 1, p < 0.0001). During the baseline period (2023 Summer) model predictions indicated a mortality probability (on the response scale) of 0.16 (95% CI: 0.11-0.24) for females compared to 0.04 (95% CI: 0.01-0.10) for males. This corresponds to approximately 5 times higher odds of mortality than in males (odds ratio = 5.1; derived from back-transformed log-odds estimates from the model). Mortality also varied significantly across study periods (Model 3.1; Type II tests, Wald Chi-square Test: Chisq = 19.963, df = 3, p = 0.0002), and a significant interaction between sex and study periods indicated that sex differences in mortality were not constant over time (Model 3.1; Type II tests, Wald Chi-square Test: Chisq = 10.788, df = 3, p = 0.013).

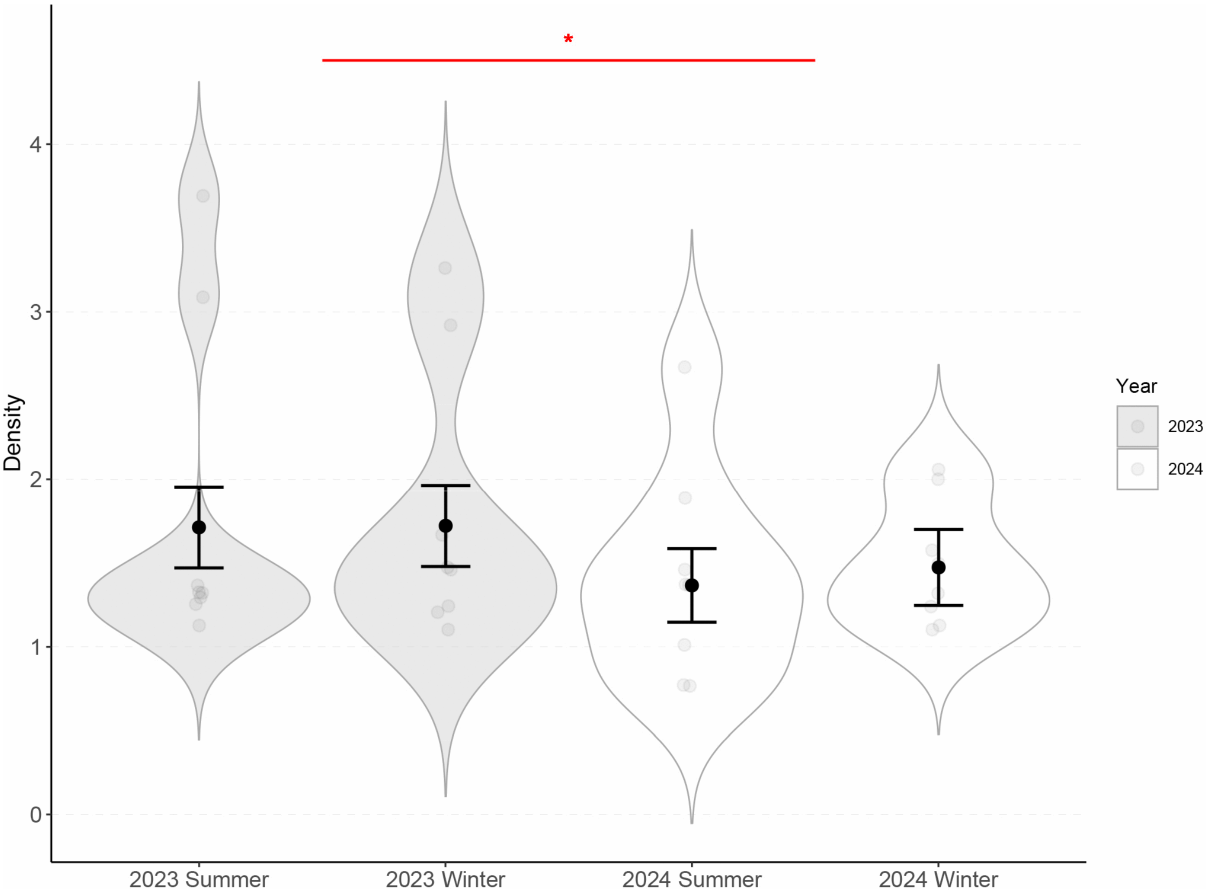

Figure 1: Cleaner fish density before, during, and after the 2024 ENSO event. Distribution of the cleaner wrasse density (individuals per 100 m²) across study periods shown as violins. The jitter represents raw site-level data, while overlaid points and error bars represent model-estimated (Model 1, Gaussian LMM) means ± standard errors (SE). Each one of our 8 sites is represented by a single jitter point for each study period. The line connecting the violins with an asterisk indicates a significant difference between the two groups involved (here, 2023 vs 2024).

Post hoc comparisons confirmed that females had significantly higher odds of mortality than males in Summer 2023 (p = 0.033), Winter 2023 (p = 0.02), and Summer 2024 (p <0.0001), whereas no significant sex difference was observed in Winter 2024 (p = 0.46). In addition, females exhibited a marked increase in mortality in Summer 2024 relative to Summer 2023, corresponding to an approximately 2.7-fold increase in odds of mortality on the response scale (Summer 2023: probability = 0.16, CI = 0.11-0.24; Summer 2024: probability = 0.35, CI = 0.24-0.46).

The second model on survival patterns of the cleaner wrasse confirmed that the effect of sex on survival is independent of body size. The only significant predictor was, in fact, sex (Model 3.2; Analysis of deviance: Chisq = 17.54, df = 1, p-value < 0.0001). Body size was not significant (Model 3.2; Analysis of deviance: Chisq = 0.0003, df = 1, p-value = 0.99) and did not interact with the effect of sex (Model 3.2; Analysis of deviance: Chisq = 0.1, df = 1, p-value = 0.75; Figure 2B).

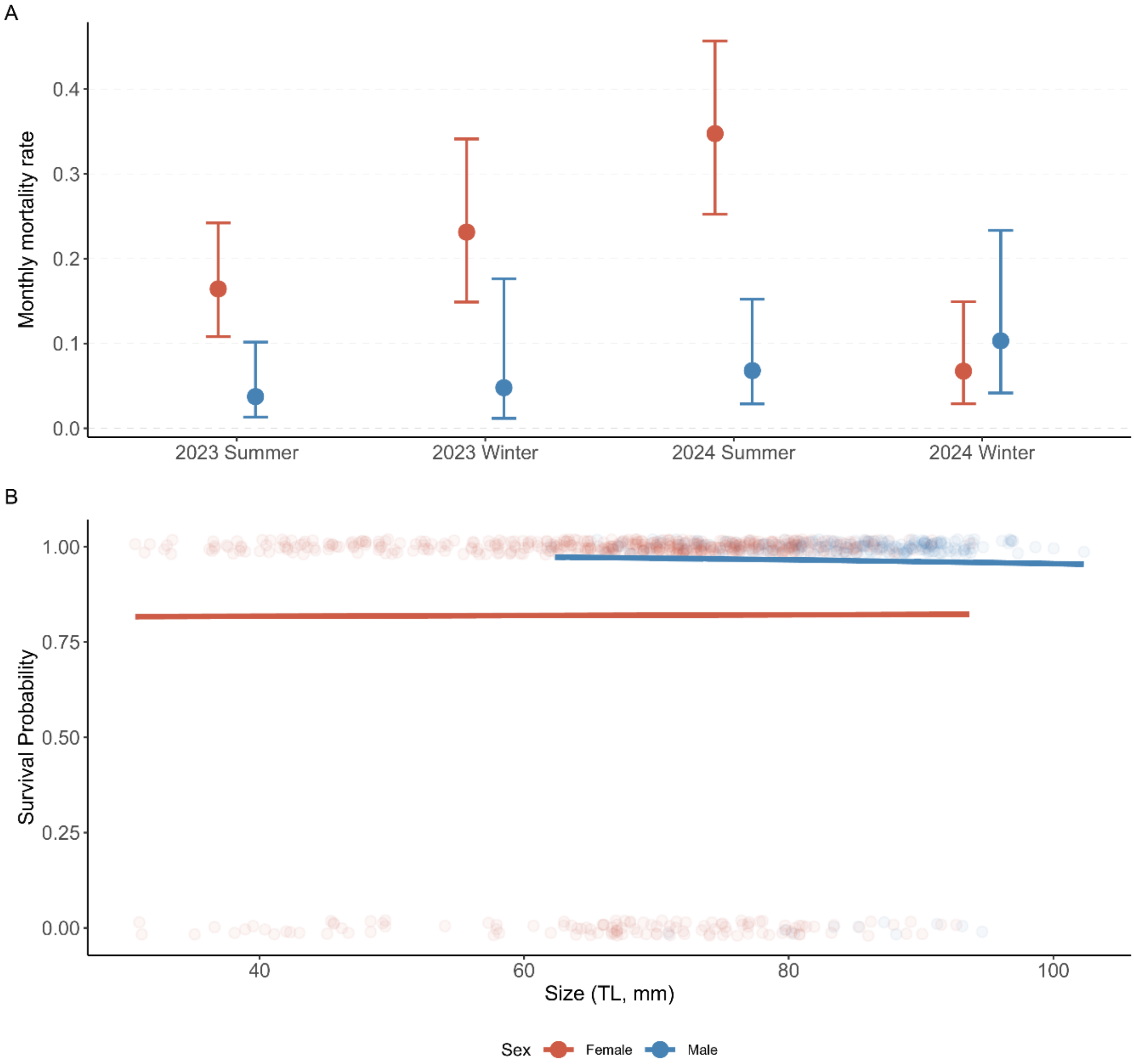

Figure 2: Sex-specific mortality rates of cleaner wrasses. (A) The predicted mortality rates of male and female cleaner wrasse across four study periods: pre-ENSO (2023 Summer, 2023 Winter), ENSO peak (2024 Summer), and post-ENSO (2024 Winter). Points represent the predicted probability of mortality by Model 3.1 (Binomial GLMM). Bars represent uncertainty shown as 95% confidence intervals calculated on the link scale and back-transformed to the response scale. Mortality levels were estimated for each sex at each site. (B) The effect of sex and size on the survival of the cleaner wrasse. The jitter point shows survival (0,1) of the fish, while the lines represent model predictions (Model 3.2, Binomial GLM) for both males (blue) and females (red).

The growth rate of cleaner wrasse varied significantly between seasons (Model 2.1; Type II F-Wald Tests: F = 58.59, df = 1, p < 0.001) but also as an interaction between season and year (Model 2.1; Type II F-Wald Tests: F = 33.96, df = 1, p < 0.001; Figure 3A). Post hoc analyses revealed that growth rates during the ENSO summer 2024 were significantly lower than in all three other seasons (all $p < 0.001$). The only other significant difference was that fish grew more slowly in summer 2023 than in winter 2024 ($p = 0.005$).

As expected in a species where growth declines with age, growth rates differed significantly across size classes (Model 2.1; Type II F-Wald Tests: $F = 12.85$, $df = 3$, $p < 0.001$; Figure 3B). The effect of size class on growth was also year-dependent (Model 2.1; Type II F-Wald Tests: $F = 4.11$, $df = 3$, $p = 0.009$). Post hoc analyses indicated that the reduced growth during summer 2024 was most pronounced in individuals from the 50 mm and 70 mm size classes, while the increased growth observed in winter 2024 was primarily driven by individuals in the 60 mm size class.

A second model assessed the role of sex in cleaner wrasse growth rates. This model revealed a significant main effect of sex, with females generally exhibiting faster growth than males (Model 2.2; Type II Wald-Chisq Tests: $Chisq = 19.8$, $df = 1$, $p < 0.001$). However, this sex effect varied significantly between years (Model 2.2; Type II Wald-Chisq Tests: $Chisq = 5.71$, $df = 1$, $p = 0.02$, Figure 4). Post hoc comparisons revealed a complex pattern. In 2023, a non-bleaching year, females grew significantly more (+45.6%) during winter than during summer ($p = 0.03$), whereas males did not show a seasonal difference ($p = 0.16$). When comparing sexes, females grew approximately 44.1% faster than males in summer and 100.2% faster in winter ($p < 0.0001$ for both), indicating a pronounced and seasonally variable sex-based difference in growth patterns under normal environmental conditions. In contrast, in 2024, both males and females exhibited significantly lower growth rates in summer compared to winter ($p < 0.0001$). Specifically, in summer 2024, the growth rates for females and males were approximately 74% and 61% lower, respectively, compared to winter 2024. Moreover, no significant sex differences were observed in either season ($p > 0.1$), suggesting that environmental stress during bleaching suppressed growth and erased typical sex-based growth differences, potentially due to shared energetic constraints or altered resource availability. Yearly comparisons revealed opposing trends for males and females. For females, growth in summer 2024 was significantly lower than in summer 2023 ($p = 0.0001$), while there was no difference between winters ($p = 0.07$). For males, growth rates were similar across summers ($p = 0.997$), but growth was significantly higher in winter 2024 compared to winter 2023 ($p = 0.01$; Figure 4).

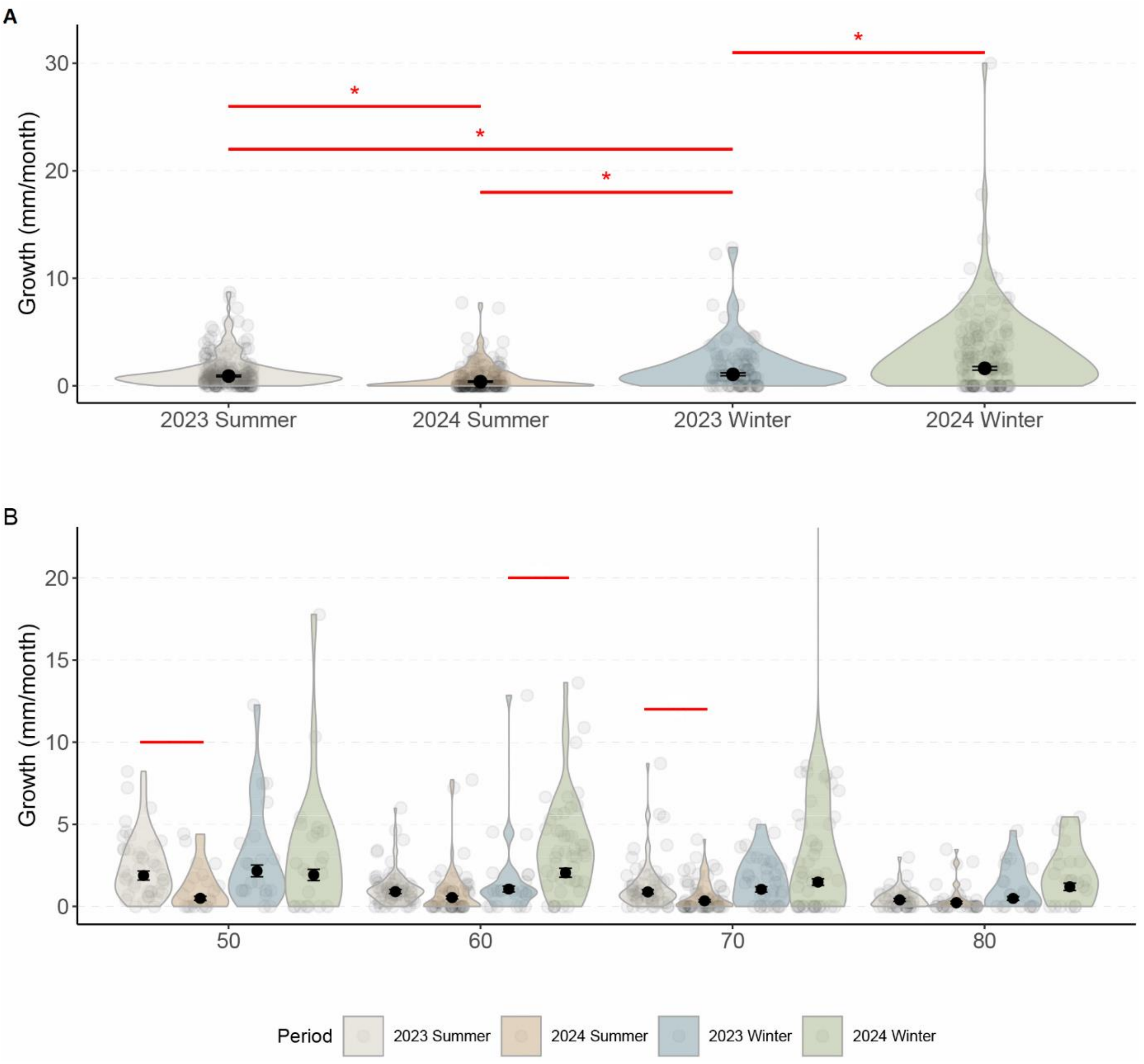

Figure 3: Growth rate variation in cleaner wrasses before, during, and after the 2024 ENSO. Distribution of the cleaner wrasse's growth rates across time periods (A), for adult individuals (TL ≥ 50 mm), and (B), for all size classes shown as violins (Model 2.1, Gaussian LMM). The jitter represents raw individual-level growth rates, while the overlaid points and error bars represent model-estimated means ± standard errors (SE). The line connecting the violins with an asterisk indicates a significant difference between the two groups involved.

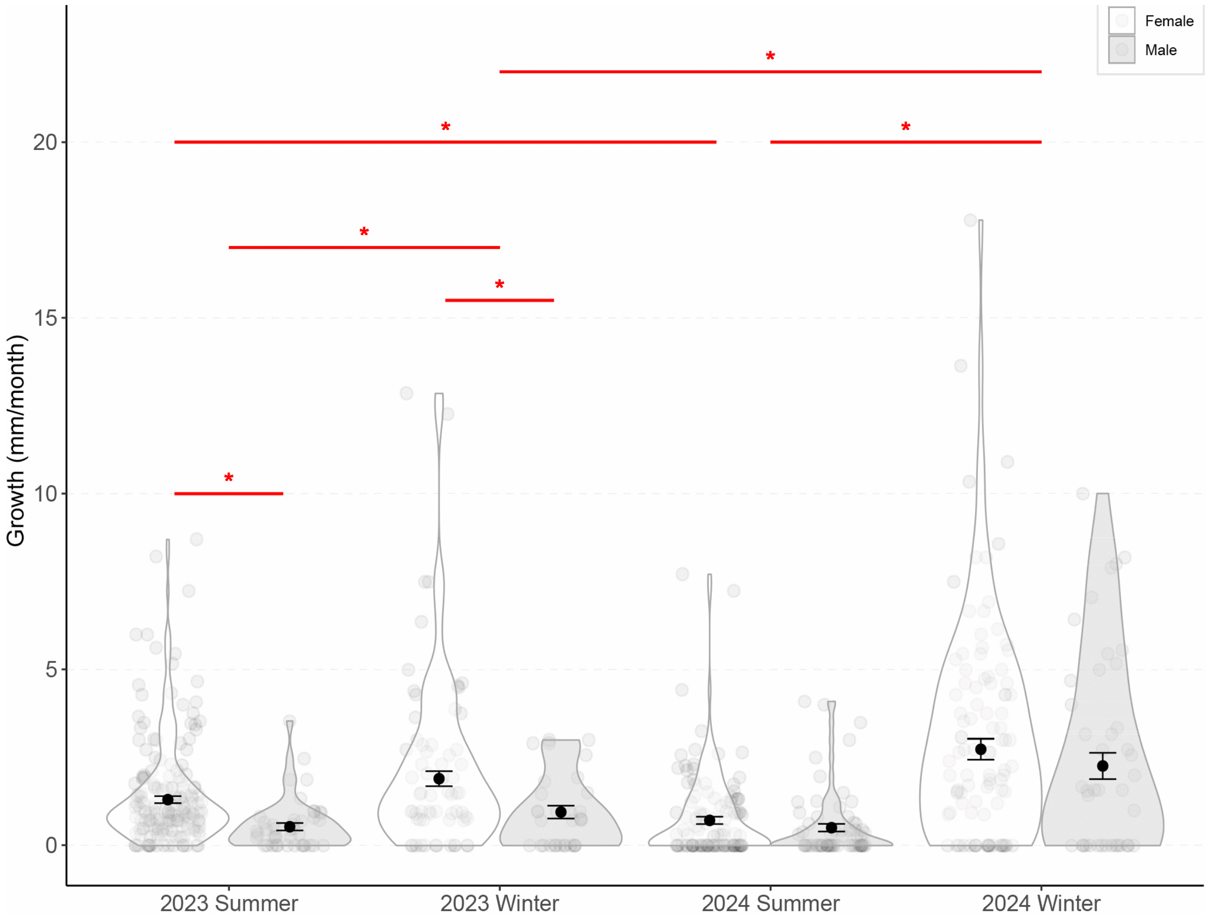

Figure 4: Sex-specific growth rates of cleaner wrasses before, during, and after the 2024 ENSO. Distribution of Male and Female Cleaner wrasse's growth rates across study periods shown as violins. The jitter represents observed individual-level growth rates, while the overlaid points and error bars represent model-estimated means ± standard errors (SE) from Model 2.2 (Tweedie GLMM). The line connecting the violins with an asterisk indicates a significant difference between the two groups involved.

Discussion

In dioecious polygynous systems, sex-specific differences in life-history traits and associated trade-offs have led to the expectation that males should have higher mortality rates than females do, which becomes even more pronounced during prolonged extreme weather events. Contrary to this assumption, our dataset revealed the opposite pattern in a protogynous coral reef fish, the cleaner wrasse *Labroides dimidiatus*. This is particularly remarkable as sex change theory predicts its evolution when the two sexes differ strongly with respect to the relationship between age and reproductive output, with the terminal sex having higher mean reproductive outputs (Ghiselin 1969; Warner 1988; Munday et al. 2006). Thus, cleaner fish males have not only higher fitness gains but also higher survival rates than females do, both under normal and under extreme weather conditions.

The 2024 ENSO event, marked by intense thermal stress on the Great Barrier Reef (NOAA 2019; Australian Institute of Marine Science 2025), clearly counted as a major disturbance to the cleaner fish population around Lizard Island, as growth was significantly reduced in both sexes compared to other time periods. However, male mortality did not increase, in stark contrast to about two times increased mortality in females compared to the previous Australian summer. Previous studies on other species suggest that thermal sensitivity can vary across life stages, with younger individuals often showing greater resilience than larger, older ones (Peck et al. 2009; Clark et al. 2013; Peck et al. 2013; Messmer et al. 2017). This has been attributed to a mismatch between oxygen demand and supply at higher temperatures: warming increases metabolic demand while reducing oxygen solubility, which disproportionately affects larger individuals with lower aerobic scope (Peck et al. 2013). By contrast, juveniles tend to have relatively greater aerobic capacity and may better maintain physiological function under thermal stress. Interestingly, the logic does not appear to apply to our study species. Instead, a potential explanation for the increased female mortality during the ENSO event is that they are more vulnerable to direct physiological impacts of elevated temperature (Neuheimer et al. 2011). However, high temperatures not only affect corals and fish populations but also gnathiid isopods, the main ectoparasites of coral reef fishes in the Indo-Pacific (Sikkel et al. 2019). Thus, it is a non-mutually exclusive possibility that cleaner fish faced a reduced amount of food availability, despite the stable populations of other reef fish species (See Supplementary Materials 2), and that female cleaner fish suffered more than males from that reduction.

The combination of the two factors is consistent with known effects of warming on metabolic rate: elevated temperatures increase standard metabolic rate (SMR), which, if not offset by higher energy intake (Gillooly et al. 2001), leads to slower growth and higher mortality (Gillooly et al. 2001; Sheridan and Bickford 2011). Nevertheless, the question arises why females are more vulnerable than males in protogynous species. We propose two hypotheses. First, females may consistently have higher energy demands compared to males because they need to invest in egg production for current reproductive success, as well as in growth, to eventually transition into the sex with the higher mean reproductive rate. The inevitable trade-off with survival may have been particularly severe during the ENSO event. Personal observations by the main diver can confirm that females did not entirely abandon spawning activities during the ENSO. Second, we hypothesize that relatively higher male survival in protogynous species may be due to males being on average of higher quality, as they all survived the challenges associated with the female phase. Future studies should investigate candidate quality components that may differ between the sexes, contrasting physiological features such as immune function with behavioral and cognitive aspects. Sex differences in cognition have been observed in a variety of species (Geary 1995), including cleaner fish (Triki and Bshary 2021 Jul 14), but are typically linked to niche separation and reproduction (Vinogradov et al. 2025) rather than to differences in survival.

Survival during winter 2024 exceeded typical seasonal levels, potentially reflecting delayed benefits of increased per-capita access to clients (see Supplementary Material 2) and/or reduced intraspecific aggression following the summer decline in cleaner density. Prior studies on the impacts of multiple cyclones and the 2016 ENSO event reported more severe declines in both cleaner and client densities at Lizard Island compared to 2024 (Triki et al. 2018; Triki and Bshary 2019). Differences in bleaching severity or the absence of cyclone-driven physical reef damage during the 2024 event may help explain this discrepancy. However, our current dataset does not include 2016, limiting the strength of any direct comparison.

Coral reefs are among the most climate-sensitive habitats (Walther et al. 2002; Hughes et al. 2003; Parmesan and Yohe 2003; Hoegh-Guldberg 2009; Hughes et al. 2017; Laufkötter et al. 2020; Malhi et al. 2020; Wernberg et al. 2024), already experiencing marked changes in fish distribution, diversity and community structure due to repeated extreme events (Sylvester 1972; Kim et al. 2001; Jones et al. 2004; Brierley and Kingsford 2009; Eliason et al. 2011; Ferrari et al. 2011; Pearce et al. 2011; Tedesco et al. 2013; Ceccarelli et al. 2024; González-Barrios et al. 2025). Cleaner fish are a keystone species in coral reefs, positively affecting client health (Ros et al. 2011; Triki et al. 2016), growth (Waldie et al. 2011), density and diversity (Bshary 2003; Grutter et al. 2003). But also other protogynous hermaphrodites are of major importance for coral reef functioning (Bonaldo et al. 2014; Kuwamura et al. 2020) or represent commercially important species (Zhou and Gui 2010; Kuwamura et al. 2020). Protogynous species are known to suffer disproportionately from fishing pressure, which targets large individuals (Easter et al. 2020). Thus, pending confirmation from studies on additional species, our results are encouraging in that they suggest males of protogynous species may exhibit high resilience to extreme weather events and climate change in general. Furthermore, sex ratios in protogynous species will very quickly return to equilibrium because all new reproductive individuals will be females and because sex change is socially controlled. More generally, our findings contribute to a growing body of evidence that climate change will not affect all individuals equally (Peck et al. 2009; Clark et al. 2013; Peck et al. 2013; Messmer et al. 2017), emphasizing that species with unusual reproductive strategies may exhibit unexpected demographic responses to environmental stress.

Ethical note

Our research adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, and the manipulations were approved by the Australian Animal Ethics Committee (AEC; permit numbers CA 2024/06/1865 and CA 2022-04-1601). We acknowledge that catching and marking are stressful events for fish. To minimize stress and handling time, tagging was performed directly underwater at the point of capture, with the fish being kept in a hand net to maintain normal seawater flow. Fish were then released immediately within their home territory, close to the substrate. The entire capture-tag-release process lasted less than 2 minutes per individual, and all fish resumed normal behaviour immediately after release. Additionally, a previous study has shown that cleaner fish can be followed immediately after capture and injection to collect data on intra- and interspecific interactions (Soares et al. 2012). According to this study, there is no evidence that the short manipulation would increase mortality. To minimize the bycatch of non-target species, barrier nets were positioned away from areas with high densities of small reef fishes (e.g., damselfish aggregations near coral heads). Additionally, barrier nets were never left unsupervised. If any non-target species entered the net, they would be immediately released with care.

All subsequent data collection involved only non-invasive methodologies. Growth was measured using an underwater stereo-camera system that required only a brief, close-range pass to film each fish. All other behavioural and life-history data were collected through direct underwater observations, with the diver maintaining a distance of at least 2-3 m, which does not affect their behaviour. Indeed, cleaners often swim closer to the observers, forcing them to retreat and increase distance, so as not to hinder the potential clients from approaching the cleaners.

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Supplementary Materials for Chapter 1

Supplement 1: Temperature figure

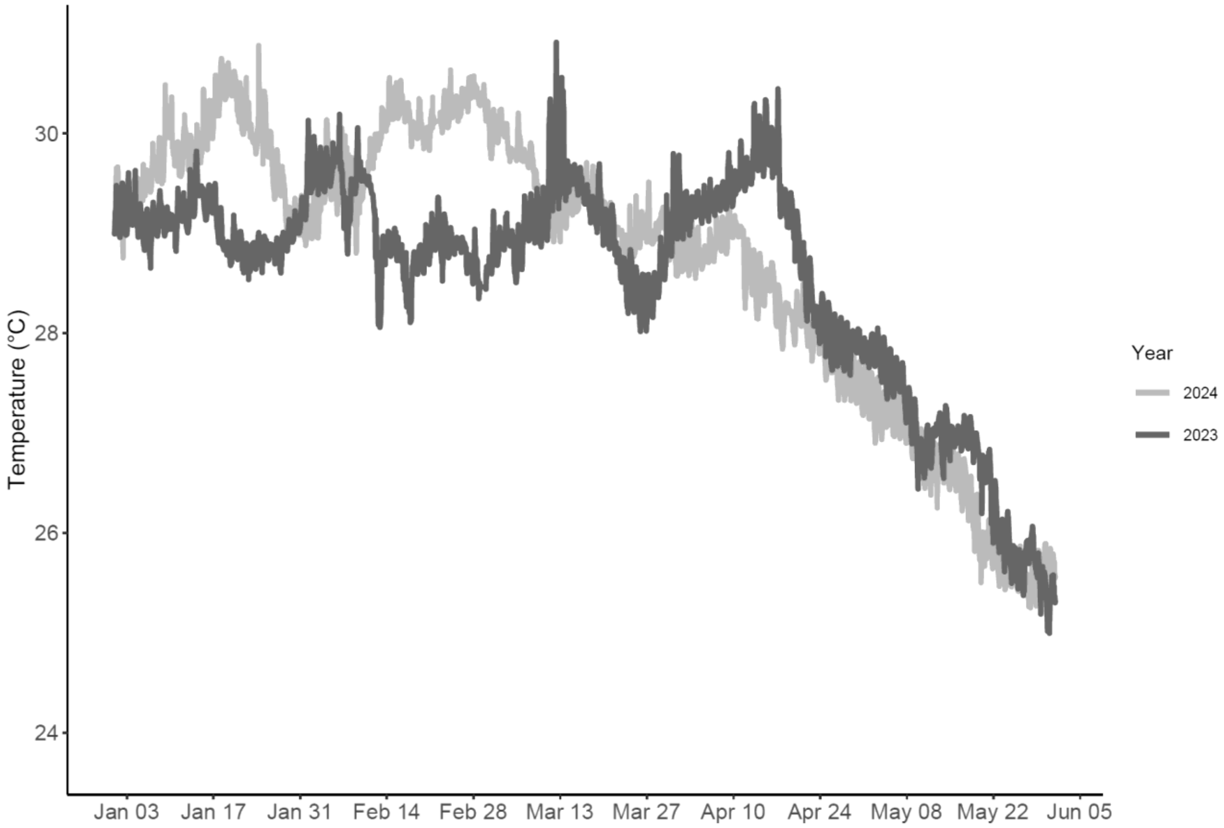

Figure S1: Lagoon shallow water temperature at Lizard Island for the years 2023 and 2024**.** Temperature (°C) is shown for both years over the same calendar period (January–June) to allow direct comparison of interannual thermal conditions. Blue and red lines represent 2023 and 2024, respectively. Data are derived from AIMS in situ buoy measurements (Australian Institute of Marine Science (AIMS) 2020).

Supplement 2: Coral and fish analysis

While not central to the core of the manuscript, we regularly collected information on coral bleaching and on fish densities and diversity at our eight study sites. Such information may be of particular interest to colleagues studying climate change, and it provides more context to the conditions that cleaner fish faced during the 2-year study period.

Methods

Fish counts included all reef fish, except for nocturnal and cryptic species. Fish censuses were conducted in the Australian summers and winters of 2023 and 2024. Counts were stratified into the two habitats of the reef in which our focal cleaner resided: The reef crest and the reef base. The reef crest is defined as the seaward edge of the reef flat (Green 1994), and the reef base as the bottom of the reef slope, where it joins the sand flat (Green 1994). Each fish census involved five 30-meter transects, spaced 2 meters apart, running parallel to the reef edge within each habitat for each site. Counts were conducted during three swims: i) the first swim was used to count large fish swimming above the reef within a 5m belt, ii) the second to count medium-sized fish swimming on the reef within a 3m belt, iii) and the last one to count fish species of the family Pomacentridae within a belt of 2m. The 3m belt width for medium-sized fish was selected based on a previous study demonstrating its effectiveness in counting wrasses(Green 1994). Each transect swim was preceded by a 2-minute wait to reduce the impact of diver disturbance from the previous count. Each transect was swum at a constant speed and performed in approximately 10 minutes. Only individuals larger/equal to 4cm were considered in our counts. Fish were identified at the species level, following the WORMS nomenclature, whenever possible. A total of 343 species and 51 families were encountered over the years.

We took advantage of our Fish census methodology to concurrently collect an additional low key dataset on the conditions of corals at our study Sites. A fourth swim was performed along each fish transect to document the reef's condition. Photographs were taken every 2 m using an Olympus TG-6 camera and a 1 m^2 quadrat frame, resulting in 15 images per 30 m transect. Photo-quadrats were taken at both the reef crest and reef base habitats at each study site during the austral summers and winters of 2023 and 2024.

To assess bleaching and coral mortality over time, we scored photographic quadrats taken at each site. Each photograph was evaluated independently for the presence of bleaching and coral mortality, resulting in two binary variables indicating whether the respective condition was observed (1) or not (0). These binary observations were aggregated per sampling period and habitat type (reef crest vs. slope) to calculate proportions of photos showing bleaching (Model 5) and coral mortality (Model 6).

Model 4 analyzed the proportion of bleached photos using an LMER with an arcsine-square-root transformation to stabilize variance and approximate normality. Fixed effects included sampling period and habitat, while random intercepts accounted for site-level variation. Variance heterogeneity across sampling years was modelled using a variance-identity structure, allowing residual variance to differ by sampling period and improving model fit.

Model 5 modelled coral mortality as a binomial response using a GLMM. Fixed effects included the sampling period and habitat, while the random effects structure was nested to capture repeated measures across transects, sites, habitats, and Dates.

For client fish densities, we first modelled total fish abundance across years and seasons using an LMER, following a Gaussian distribution (Model 6.1). Fish density was log-transformed to normalize the distribution and stabilize variance, as exploratory data revealed positive skewness. Fixed effects included year, season, and their interaction to capture temporal variability in fish abundance. To account for spatial structures and repeated measures, random intercepts were included for site nested within habitat, reflecting the hierarchical sampling design across the 8 sites.

In Model 6.2, we further examine the differences between small (total length ≤ 10 cm) and large clients (total length > 10 cm) using another LMER. Client density was again log-transformed to improve normality. Fixed effects included the sampling period, the client type and their interaction, with the same nested random effects structure as Model 1. Client density was calculated as the number of individuals per 100m^2.

Results

From our own data collection, the proportion of pictures of 1 m^2 sections containing bleached corals varied significantly across sampling periods (Type II, Wald Chi-square tests: Chisq = 2244.51, df = 2, $p < 0.0001$); Figure S2A). Specifically, bleaching was lower in summer 2023 and significantly increased in all subsequent periods (all $p < 0.0011$), peaking in summer 2024 ($p < 0.0001$). Bleaching was also more pronounced on the reef crest than on the slope (Type II, Wald Chi-square tests: Chisq = 7.6, df = 1, p = 0.006). Coral mortality followed a similar pattern, with the proportion of pictures showing dead coral increasing progressively over time (Type II, Wald Chi-square tests: Chisq = 118.6, df = 2, $p < 0.0001$). However, mortality did not differ significantly between reef crests and slopes (Type II, Chi-square tests: Chisq = 0.29, df = 1, p = 0.59). Post hoc comparisons revealed significant differences between all sampling periods (Figure S2B).

Despite the negative impact on corals, there was no evidence that overall fish populations at our sites experienced increased mortality during the El Niño event compared to the previous year. Instead, total fish density increased markedly from 2023 to 2024 (Type II, F-Wald test: F = 86.1539, df = 1, $p < 0.0001$), and it was significantly higher in summer than in winter (Type II, F-Wald test: F = 7.9278 df = 1, p = 0.005185), showing no significant interaction between year and season (Analysis of deviance type II F-Wald test: F = 0.0824, df = 1, p = 0.774209; Figure S3A).

Fish density patterns differed between client types with a significant interaction between sampling period and client category (Type II, F-Wald tests: F = 12.719, df = 3, $p < 0.0001$; Figure S3B). This was primarily driven by an increase in the densities of small fish species (<10 cm maximum total length) in both summer and winter 2024 compared to the same seasons in 2023 (all $p < 0.0001$). In contrast, densities of larger fish species (≥ 10 cm max body length) remained stable across years (summer: p =

0.89; Winter: p = 0.99). Small species were consistently more abundant than large species across all periods (Type II, F-Wald tests, F = 536.92, df = 1, p < 0.0001).

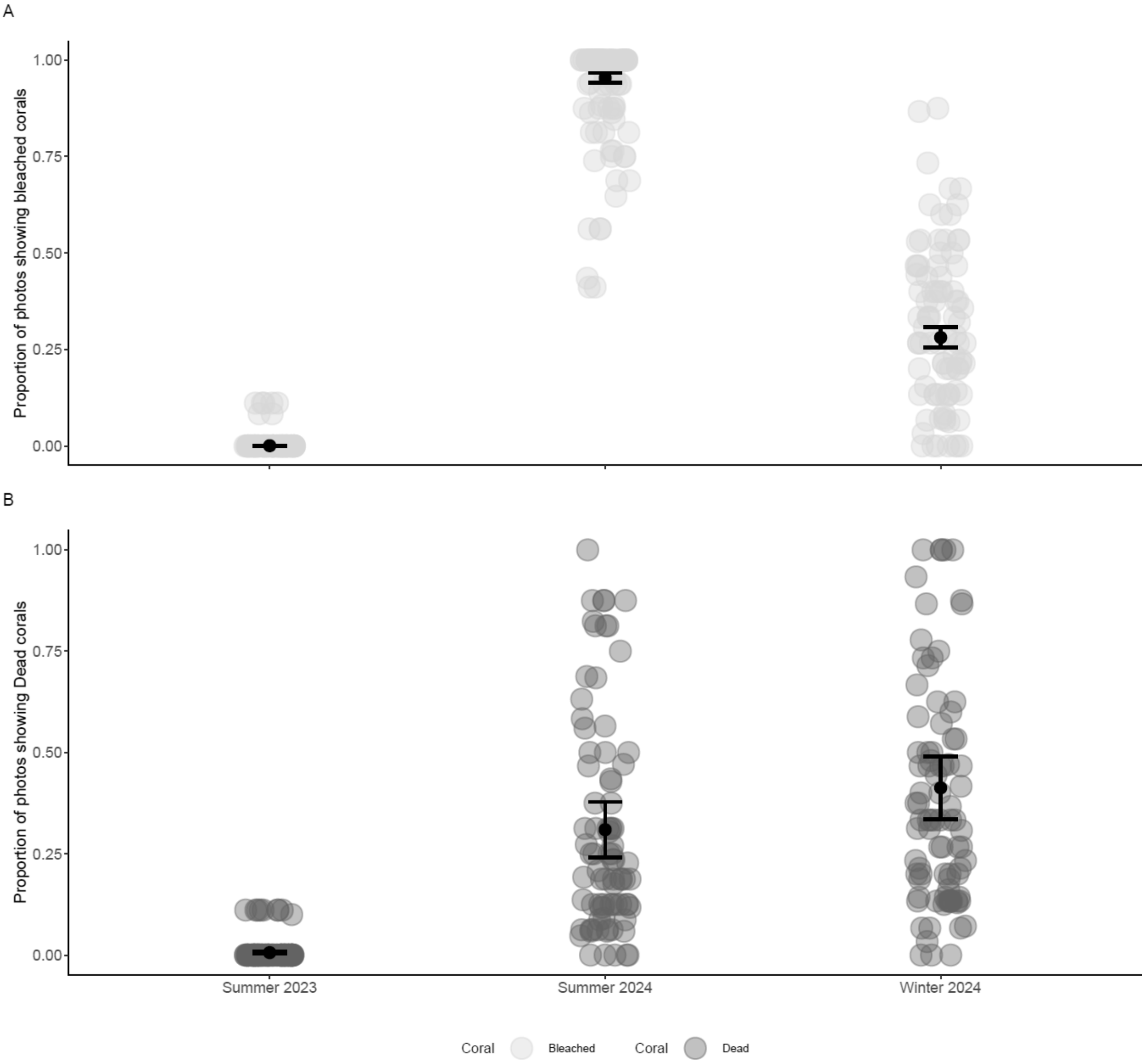

Figure S2: Proportion of coral bleaching and mortality. Proportion of coral bleaching and mortality before, during, and after the 2024 ENSO event. Jittered point data of the proportion of transect photos showing visible coral bleaching (A), and hard coral mortality (B). Overlaid points and error bars represent model-estimated means ± standard error (SE). Individual points represent individual Transects at each study site.

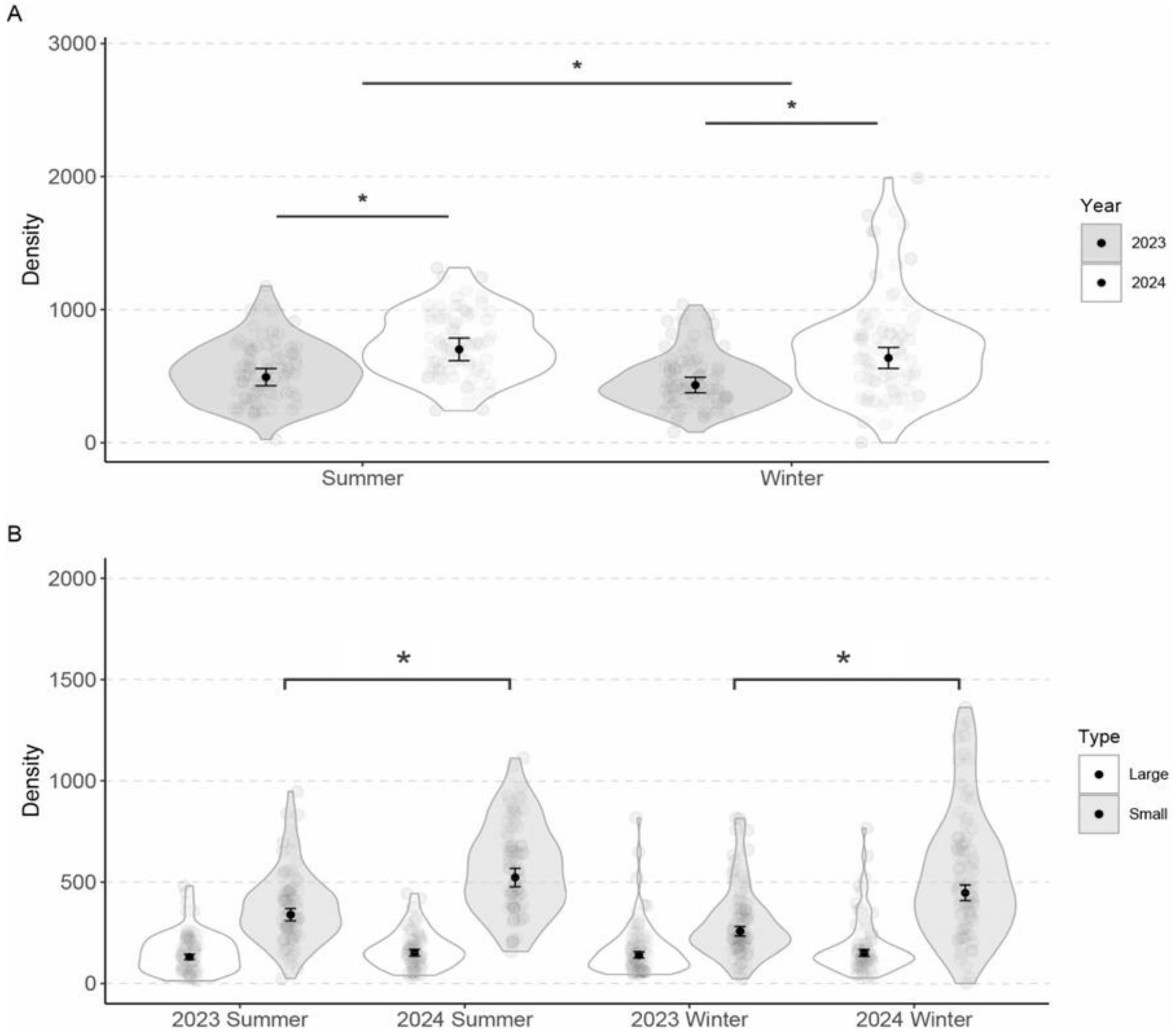

Figure S3: Fish community response before, during, and after the 2024 ENSO event. Distribution of (A), general fish density (individuals per 150 m^2) and (B), large and small reef fish species density across time periods shown as violins and jitter of the raw transect-level observations at each study site. The overlaid points and error bars represent model-estimated means ± standard errors (SE).

Supplement 3: Island figure

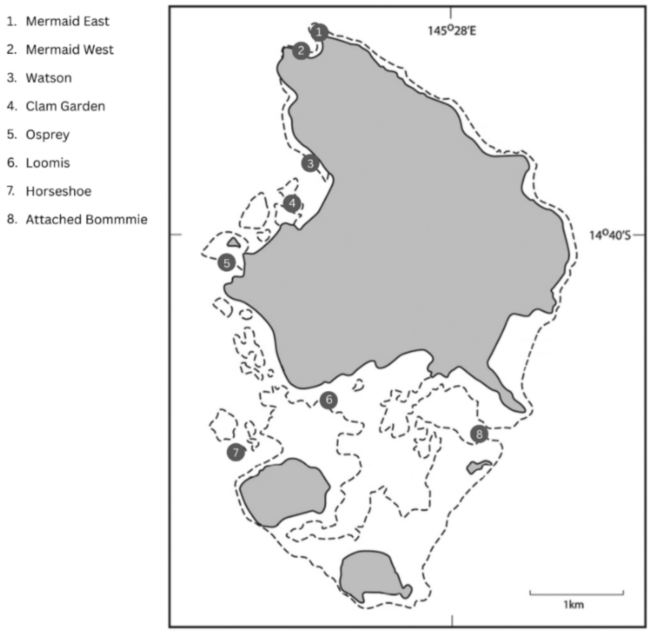

Figure S4: Lizard Island study sites. Grey represents the land, and blue dots represent the reef sites studied.

Supplement 4: Tagging figure

Figure S5: Illustration of the four locations for VIE. Two dots are shown at each location, since colors can be injected in sequence in the same area.

Supplement 5: VIE figure

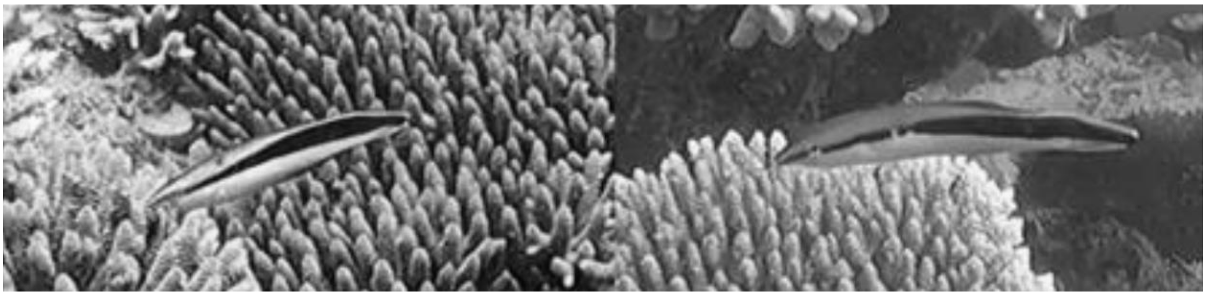

Figure S6: Examples of two individuals that can be recognized without VIE. On the left, the fish has a natural black marking on its beige body band. On the right, the fish shows a natural white interruption of the black band.

Supplement 6: Size error analyses

We assessed the growth of each focal fish using a calibrated underwater stereo-photogrammetric system, consisting of two GoPro Hero 8 cameras mounted on a fixed rig (Seager 2006). Footage was processed with EventMeasure (Seager 2006) which enables precise three-dimensional measurements based on synchronized stereo images. Before data collection, the system was calibrated using CAL, a dedicated software that ensures accurate geometric alignment between the camera pair (Seager 2006). This stereo setup significantly improves measurement precision over traditional visual estimations (Michael et al. 2011). In the first three seasons, size measurements were taken every two weeks, whereas in winter 2024, they were collected at a reduced frequency of once a month.

The error of this software is known to be around 1-2mm (Euan et al. 2010). To further assess the accuracy of the stereo camera system for our study, a calibration bar with three known distances was used to measure the system's error. Measurement error was ± 1.13mm using the calibration bar and ± 1.81mm of wild cleaner fish due to movement and growth between measurements (Figure S7, Table S1).

Because measuring a moving object is more challenging, the software's accuracy was then investigated by comparing the stereo camera measurements of fish longer than 70cm with manual size measurements taken less than 30 days prior. This method provided an average error of ± 1.81mm. Attempts were made to obtain size measurements using the stereo system less than one week after the fish were manually measured post-capture. However, this proved challenging as the fish required more time to re-acclimate to the presence of humans and often swam too quickly or attempted to escape, making accurate measurements difficult within this short time frame. Nevertheless, errors associated with our fish measurements did not show a significant increase in variance (variance = 2.324) compared to the error observed with the calibration toolbar (variance = 2.264). This suggests that the software's measurement error remains consistent when applied to real fish. The positive shift in the median error for the fish measurements (median = 1.48 mm) reflects the natural growth of the fish over the 30-day period between the two measurements. This consistency in error variance across both methods indicates that the software performs reliably for measuring wild fish.

Table S1: Stereo camera system's error. Error in (mm) of the stereo camera system obtained using tool bars of different sizes (small, medium, large), with measurements of fish in the water (Fish), and as an overall mean from the various tool bars.

Method	Mean Error (mm)
Small	± 0.981
Medium	± 1.08
Large	± 1.37
General Tool	± 1.13
Fish	± 1.81

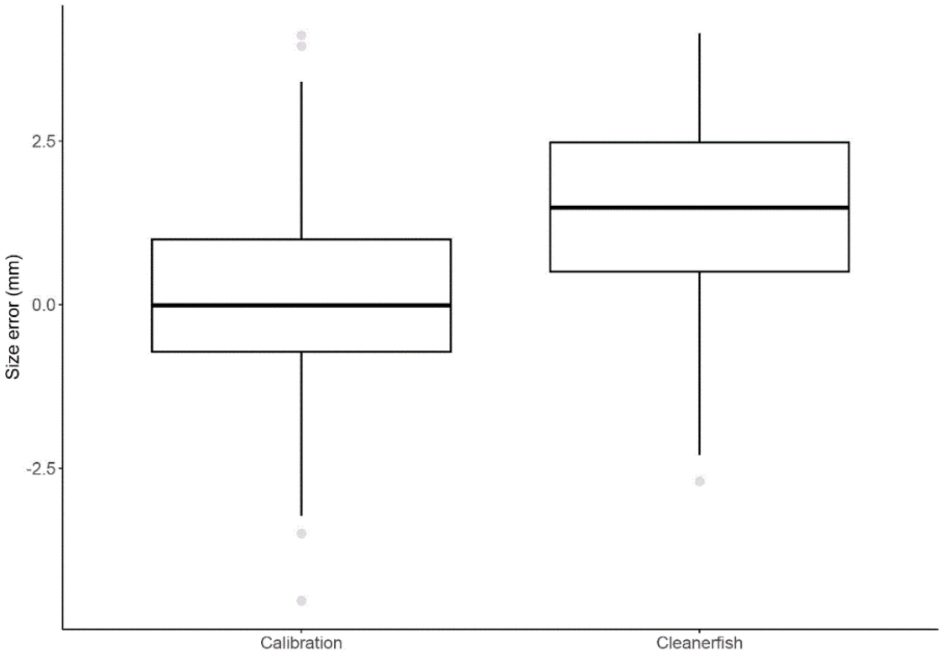

Figure S7: Size error of the software. The size error of the software obtained using size measurements of focal cleaners ("Cleanerfish") obtained 30 days from their manual sizing, and using the objects of known size ("Calibration"). Boxplots show medians (center line), interquartile ranges (boxes), and 95% data range.

Supplement 7: Growth model

To evaluate if this correction affected our interpretation of growth dynamics, we ran an additional model (Model 3.3) using the unadjusted, raw growth data. This model was not used for hypothesis testing, but rather to extract estimates and prediction distributions, verifying that adjusting negative values in the main models did not introduce substantial bias. Because this exploratory model was intended for comparisons rather than inference, strict adherence to model assumptions was not required and was not entirely achievable given the structure of the raw data. This supplementary model was an LMER using the logarithm of growth as the response and year, sex, and season as fixed effects. Random intercepts were included for individual ID nested within site to account for repeated measures and site-level variation. Each observation was weighted by the inverse of the squared daily measurement error ($1/DE^2$), implemented through a fixed variance structure (varFixed), to give greater weight to more precise measurements. Additionally, we included a variance identity function (varIdent) to allow residual variances to differ across levels of the grouping variable (including year, sex and season). These two variance structures were combined using varComb() to simultaneously address both observation-level and group-level heteroscedasticity.

The error associated with growth measurements obtained from the sizing software was calculated by combining the errors of the initial and final size measurements (attributed to be ± 0.981, the error calculated for small lengths). Specifically, growth error was computed as the square root of the sum of the squared size errors at both time points using equation (2).

$$\text{growth error} = \sqrt{(\text{size error}_{\text{initial}})^2 + (\text{size error}_{\text{final}})^2} \qquad (2)$$

This growth error was then standardized dividing it by the number of days between measurements to account for varying measurement intervals, resulting in the daily error (DE).

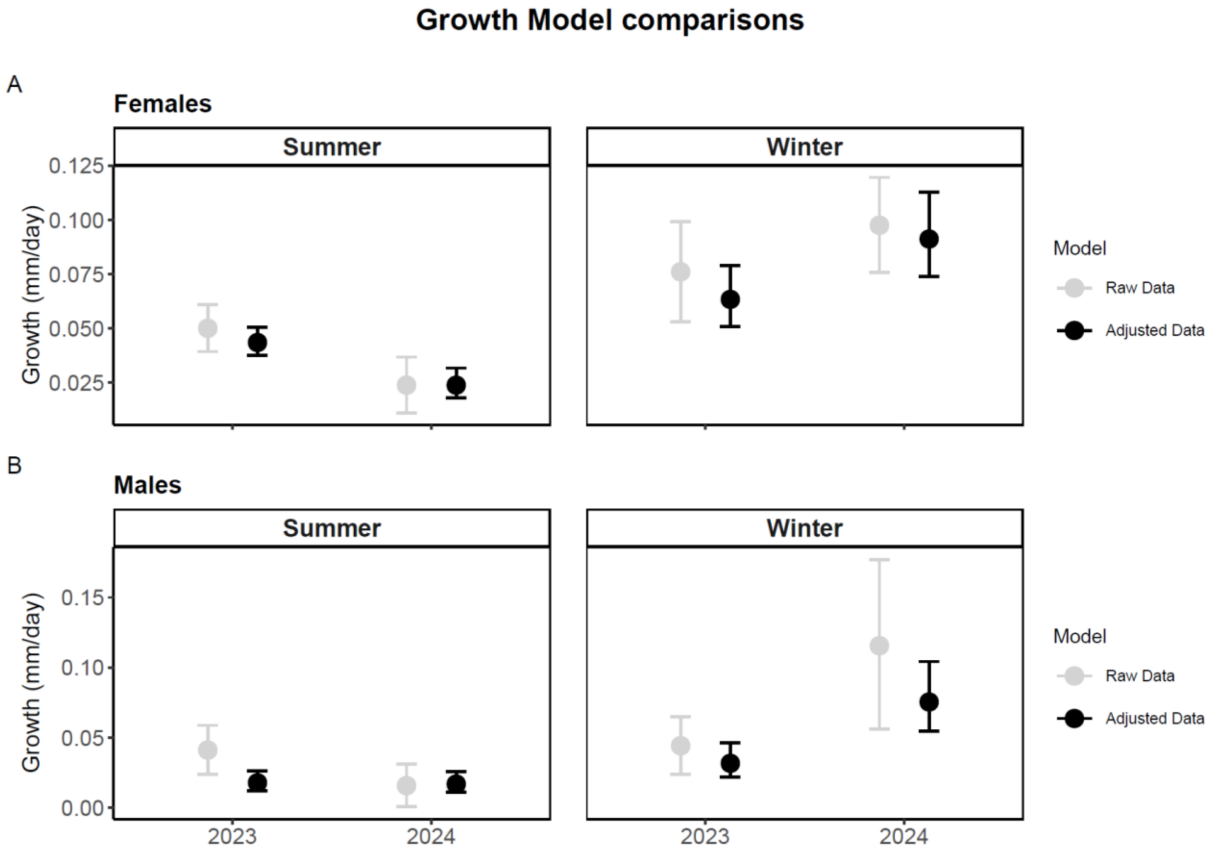

Figure S8: Comparison of predicted growth rate between the raw and adjusted dataset. The (A), Predicted growth rates for female and (B), male cleaner fish across years and seasons, based on models using raw (with negative values) vs adjusted (negative values were adjusted) growth data. Points show median predictions, and error bars show 95% confidence intervals.

Supplement 8: Model information

Table S2: Glossary for Table S3.

Term	Definition
Class	Size class (TL: 60-69mm, 70-79mm, 80-90mm)
Days	Number of days in between first and last survival assessment (to take into account differences among sites and study periods)
DE	Error of the Sizing Software (see Daily error in the method section)
Density	Adult cleaner fish reef density within a deme, standardized by 100m^2
Fish-Density	Client densities counted during transects were standardized per 100m^2
Growth	Growth rate (mm/day)
ID	Cleaner ID used as a random factor to control for repeated measures
	Summer 2023, summer 2024, winter 2023, and winter 2024.
Type	Large or small clients
Season	Summer or winter
Habitat	Reef Crest or Slope.

Table S3: Details about the models.

<table>
<tr><th>Model</th><th>Type</th><th>Family</th><th>Sample Size</th><th>Formula</th></tr>
<tr><td>1</td><td>LMER</td><td>Gaussian</td><td>32 obs</td><td>log(Density+2) ~ Season * Year +(1|Site)</td></tr>
<tr><td>2.1</td><td>LMER</td><td>Gaussian</td><td>617 obs
402 ID</td><td>log(growth+0.01)~(Class+Season)*Year+(1|Site)+(1|ID)</td></tr>
<tr><td>2.2</td><td>GLMER</td><td>Tweedie(log)</td><td>621 obs, 406 ID,
447 Females,
174 Males</td><td>growth~ Sex * Year *Season +(1|ID) + (1|Site), dispformula =~0+Year</td></tr>
<tr><td>2.3</td><td>LME</td><td>Gausian</td><td>621 obs, 406 ID,
447 Females,
174 Males</td><td>Log(growth+1.61) ~ Sex * Year * Season, random = ~1|Cleaner_ID/Site, weights = varComb(varFixed(~I|DE^2)), WarTdent(form =~1|mix)</td></tr>
<tr><td>3.1</td><td>GLMM</td><td>Binomial</td><td>64 obs</td><td>Cbind(dead, alive) ~ Period * Sex + offset(log(Days) +(1|Site)</td></tr>
<tr><td>3.2</td><td>GLM</td><td>Binomial</td><td>827 obs, 451 ID,
364 Females,
93 Males</td><td>Survival ~ Size scaled*Sex +(1|ID)</td></tr>
<tr><td>4</td><td>LMER</td><td>Gaussian</td><td>260 obs</td><td>asin(sqrt(bleached/total)) ~ MY + Habitat, random = ~1|Site, weights = varIdent(form=~1|MY)</td></tr>
<tr><td>5</td><td>GLMM</td><td>binomial</td><td>260 obs</td><td>cbind(dead, tot) ~ MY + Habitat + (Transect/Site/Habitat/Date)</td></tr>
<tr><td>6.1</td><td>LMER</td><td>Gaussian</td><td>324 obs</td><td>Log(Fish Density+160) ~ Year * Season +(1| Habitat/Site)</td></tr>
<tr><td>6.2</td><td>LMER</td><td>Gaussian</td><td>646 obs</td><td>Log(Fish Density+40) ~ Period * Type +(1|Habitat/Site)</td></tr>
</table>

Supplement 9: Details of the Models

Table S4: Analysis of Deviance, Type II Chi-Square Tests for Model 1.

Term	Chisq	Df	Pr (> F)
Season	0.3428	1	0.558205
Year	8.3222	1	0.003916 **
Season:Year	0.2489	1	0.617821

Supplement 10: Details for Model 2.1

Table S5: Emmeans Contrasts by Class for Model 2.1.

Contrast	Estimate	SE	Df	T ratio	p-value
Class = 50					
Summer 2023 – Winter 2023	-0.009370	0.01950	368	-0.482	0.9631
Summer 2023 – Summer 2024	0.040703	0.01190	368	3.419	0.0039
Summer 2023 – Winter 2024	0.015277	0.01540	368	0.993	0.7534
Winter 2023 – Summer 2024	0.050073	0.01780	469	2.811	0.0263
Winter 2023 – Winter 2024	0.024646	0.02030	446	1.214	0.6186
Summer 2024 – Winter 2024	-0.025426	0.01300	446	-1.954	0.2073
Class = 60					
Summer 2023 – Winter 2023	0.000274	0.00867	196	0.032	1.0000
Summer 2023 – Summer 2024	0.016997	0.00534	196	3.183	0.0091
Summer 2023 – Winter 2024	-0.050370	0.01350	196	-3.729	0.0014
Winter 2023 – Summer 2024	0.016724	0.00822	285	2.036	0.1774
Winter 2023 – Winter 2024	-0.050644	0.01480	271	-3.421	0.0040
Summer 2024 – Winter 2024	-0.067368	0.01310	271	-5.156	<.0001
Class = 70					
Summer 2023 – Winter 2023	-0.004397	0.00813	244	-0.541	0.9490
Summer 2023 – Summer 2024	0.017896	0.00522	244	3.425	0.0040
Summer 2023 – Winter 2024	-0.016719	0.00896	244	-1.865	0.2458
Winter 2023 – Summer 2024	0.022294	0.00740	262	3.011	0.0151
Winter 2023 – Winter 2024	-0.012321	0.01040	321	-1.188	0.6347
Summer 2024 – Winter 2024	-0.034615	0.00812	262	-4.265	0.0002
Class = 80					
Summer 2023 – Winter 2023	-0.008854	0.00693	336	-1.277	0.5783
Summer 2023 – Summer 2024	0.003945	0.00418	336	0.944	0.7809
Summer 2023 – Winter 2024	-0.027795	0.01020	336	-2.726	0.0339
Winter 2023 – Summer 2024	0.012799	0.00699	423	1.831	0.2602
Winter 2023 – Winter 2024	-0.018942	0.01160	490	-1.636	0.3593
Summer 2024 – Winter 2024	-0.031741	0.01010	423	-3.149	0.0095

Table S6: Analysis of Deviance, Type II Wald F Tests for Model 2.1.

Term	F	Df	Pr (> F)
Class	12.4499	3	1.018-07 ***
Season	60.0548	1	5.78e-14 ***
Year	7.7467	1	0.005570 **
Class:Year	3.9789	3	0.008031 **
Season:Year	34.9361	1	6.450e-09 ***

Supplement 11: Details for Model 2.2

Table S7: Analysis of Deviance, Chi-square Tests for Model 2.2.

Term	Chisq	Df	Pr (> F)
Sex	19.7634	1	8.764e-06 ***
Year	0.3071	1	0.57948
Season	79.3319	1	< 2.2e-16 ***
Sex:Year	5.7258	1	0.01672 *
Sex:Season	0.7057	1	0.40088
Year:Season	27.2558	1	1.1782e-07 ***
Sex:Year:Season	0.0113	1	0.91549

Table S8: Emmeans Contrasts by Year for Model 2.2.

Contrast	Estimate	SE	Z ratio	p-value
Year = 2023				
Female Summer - Male Summer	0.02568	0.00477	5.380	<.0001
Female Summer - Female Winter	-0.01986	0.00728	-2.729	0.0322
Female Summer - Male Winter	0.01186	0.00678	1.748	0.2990
Male Summer - Female Winter	-0.04553	0.00788	5.777	<.0001
Male Summer - Male Winter	-0.01382	0.00669	2.066	0.1642
Female Winter - Male Winter	0.03171	0.00934	3.396	0.0038
Year = 2024				
Female Summer - Male Summer	0.00698	0.00493	1.416	0.4892
Female Summer - Female Winter	-0.06747	0.01010	-6.688	<.0001
Female Summer - Male Winter	-0.04945	0.01270	-3.895	0.0006
Male Summer - Female Winter	-0.07445	0.01040	-7.180	<.0001
Male Summer - Male Winter	-0.05643	0.01250	-4.508	<.0001
Female Winter - Male Winter	0.01801	0.01540	1.167	0.6479

Table S9: Emmeans Contrasts by sex for Model 2.2.

Contrast	Estimate	SE	Z ratio	p-value
Sex = Female				
2023 Summer - 2024 Summer	0.019637	0.00454	4.330	0.0001
2023 Summer - 2023 Winter	-0.019855	0.00728	-2.729	0.0322
2023 Summer - 2024 Winter	-0.047829	0.01010	-4.747	<.0001
2024 Summer - 2023 Winter	-0.039492	0.00759	-5.206	<.0001
2024 Summer - 2024 Winter	-0.067466	0.01010	-0.04155	<.0001
2023 Winter - 2024 Winter	-0.027974	0.01150	-2.424	0.0725
Sex = Male				
2023 Summer - 2024 Summer	0.000938	0.00489	0.192	0.9975
2023 Summer - 2023 Winter	-0.013822	0.00669	0.00336	0.1642
2023 Summer - 2024 Winter	-0.055496	0.01260	-0.02306	0.0001
2024 Summer - 2023 Winter	-0.014760	0.00687	0.00290	0.0001
2024 Summer - 2024 Winter	-0.056434	0.01250	-0.02427	<.0001

Supplement 12: Details for Model 3.1

Table S10: Analysis of Deviance, Chi-square Tests for Model 3.1.

Term	Chisq	Df	Pr (> F)
MY	22.612	1	1.982e-06***
Sex	19.963	3	0.0001728***
MY:Sex	10.788	3	0.0129290*

Table S11: Emmeans Contrasts by Period for Model 3.1.

Contrast		Estimate	SE	Df	T ratio	p-value
2023 Summer	Female - Male	1.622	0.551	Inf	2.941	0.0033
2023 Winter	Female - Male	1.790	0.754	Inf	2.374	0.0176
2024 Summer	Female - Male	1.988	0.461	Inf	4.316	<. 0001
2024 Winter	Female - Male	-0.464	0.630	Inf	-0.737	0.4614
Results are on the log odds scale (no the response one)						

Table S12: Emmeans Contrasts by Sex for Model 3.1.

Contrast	Estimate	SE	Df	T ratio	p-value
Sex = Female					
Summer 2023 – Winter 2023	-0.425	0.289	Inf	-1.472	0.4547
Summer 2023 - Summer 2024	-0.996	0.250	Inf	-3.980	0.0004
Summer 2023 – Winter 2024	1.001	0.460	Inf	2.176	0.1300
Winter 2023 – Summer 2024	-0.571	0.279	Inf	-2.046	0.1711
Winter 2023 – Winter 2024	1.426	0.476	Inf	2.996	0.0145
Summer 2024 – Winter 2024	1.997	0.454	Inf	4.401	0.0001
Sex = Male					
Summer 2023 – Winter 2023	-0.257	0.889	Inf	-0.289	0.9916
Summer 2023 – Summer 2024	-0.630	0.674	Inf	-0.935	0.7862
Summer 2023 – Winter 2024	-1.085	0.700	Inf	-1.551	0.4069
Winter 2023 – Summer 2024	-0.373	0.839	Inf	-0.444	0.9707
Winter 2023 – Winter 2024	-0.828	0.860	Inf	-0.963	0.7702
Summer 2024 – Winter 2024	-0.455	0.635	Inf	-0.717	0.8902
Results are given on the log odds ratio scale (not the response)					

Supplement 13: Details for Model 3.2

Table S13: Analysis of Deviance, Chi-square Tests for Model 3.2.

Term	Chisq	Df	Pr (> F)
Size scaled	0.0003	1	0.9862
Sex	17.5368	1	2.818-e05***
Size scaled : Sex	0.0976	1	0.7548.

Supplement 14: Details for Model 4

Table S14: Analysis of Deviance, Type II Chi-Square Tests for Model 4.

Term	Chisq	Df	Pr (> F)
MY	2244.5070	2	< 2.2e-16 ***
Habitat	7.5992	1	0.005839 **

Table S15: Emmeans Contrasts for Model 4.

	Estimate	SE	Df	T ratio	p-value
Summer 2023-Summer 2024	-1.327	0.0294	249	-45.096	<.0001
Summer 2023-Winter 2024	-0.5329	0.0285	249	-18.756	<.0001
Summer 2024-Winter 2024	0.7945	0.0386	249	20.430	<.0001

Results averaged over the levels of Scenario, Degrees of freedom method: Kenward-Roger. Results are given on the log scale (not the response one).

Supplement 15: Details for Model 5

Table S16: Analysis of Deviance, Type II Chi-Square Tests for Model 5.

Term	Chisq	Df	Pr (> F)
MY	118.5869	2	< 2.2e-16 ***
Habitat	0.2924	1	0.5887

Table S17: Emmeans Contrasts for Model 5.

	Odds ratio	SE	Df	Z ratio	p-value
Summer 2023-Summer 2024	0.01366	0.00596	1	-9.833	<.0001
Summer 2023-Winter 2024	0.00871	0.00380	1	-10.884	<.0001
Summer 2024-Winter 2024	0.63788	0.11400	1	-2.515	0.0319

Results averaged over the levels of Scenario, Degrees of freedom method : Kenward-Roger. Results are given on the log scale (not the response one).

Supplement 16: Details for Model 6.1

Table S18: Analysis of Deviance, Type II Wald F Tests for Model 6.1.

Term	F ratio	Df	Pr (> F)
Year	86.1539	1	< 2.2e-16 ***
Season	7.9278	1	0.005185 **
Year:Season	0.0824	1	0.774209

Supplement 17: Details for Model 6.2

Table S19: Analysis of Deviance, Type II Wald F Tests for Model 6.2.

Term	F ratio	Df	Pr (> F)
MY	20.752	3	7.953e-13 ***
Type	536.920	1	< 2.2e-16 ***
MY:Type	12.719	3	4.459e-08 ***

Table S20: Emmeans Contrasts for model 6.2.

Contrast	Estimate	SE	T ratio	p-value
Type Resident				
Summer 2023 – Summer 2024	-0.39461	0.0708	-5.577	<.0001
Summer 2023 – Winter 2023	0.24255	0.0693	3.498	0.0028
Summer 2023 – Winter 2024	-0.25050	0.0703	-3.563	0.0022
Summer 2024 – Winter 2023	0.63716	0.0700	9.101	<.0001
Summer 2024 – Winter 2024	0.14411	0.0710	2.031	0.1778
Winter 2023 – Winter 2024	-0.49304	0.0695	-7.091	<.0001
Type Visitor				
Summer 2023 – Summer 2024	-0.11380	0.0710	-1.604	0.3773
Summer 2023 – Winter 2023	-0.05626	0.0695	-0.809	0.8503
Summer 2023 – Winter 2024	0.10741	0.0707	-1.518	0.4271
Summer 2024 – Winter 2023	0.05754	0.0700	0.822	0.8441
Summer 2024 – Winter 2024	0.00639	0.0712	0.090	0.9997
Winter 2023 – Winter 2024	-0.05115	0.0697	-0.733	0.8336

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Chapter 2: Flexible sex change in cleaner wrasse: effects of social control, strategy, and population density

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Manuscript information

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Author contributions

All authors contributed to the project design. LP conducted the fieldwork, performed data and statistical analyses, and led manuscript writing. RB supervised the project and contributed to conceptual development and revision of the manuscript.

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Abstract

Protogynous sex change, where individuals first function as females and later as males, is a key life-history strategy among polygynous reef fishes. In haremic systems, sex change is typically socially regulated, with dominants suppressing subordinates' sex change through aggression. Females within a harem form a size-based hierarchy that can remain stable in most species through the threat of eviction. We studied a different situation in the cleaner wrasse, *Labroides dimidiatus*, where larger females have incomplete control because they spend most of their time alone in their own cleaning territory. We tracked over 400 individuals for 12 months, recording growth, behavior, social organization, and sex change. We confirm that cleaner wrasse hierarchies exhibit key features of size-based systems, including selective aggression toward adjacent subordinates and strategic growth following rank upgrade. However, social control was incomplete: we observed frequent rank reversals and found that 42.9% of sex changers occurred in the presence of the male, often in non-top-ranked females. Early sex change was more common in branching social systems, where male attention is divided, and female territories do not overlap, limiting both male and female control. Strategies to increase the likelihood of sex change include rapid growth and movement between harems. Local population densities further shaped these dynamics, with individuals in high-density demes growing faster and changing sex at larger sizes. Our findings demonstrate that sex change in *L. dimidiatus* is more flexible than classical models predict and is shaped by the interaction between incomplete social control, individual strategies, and ecological conditions.

Keywords

Cleaner wrasse, *Labroides dimidiatus*, Protogyny, Sex change, Size-based hierarchy, Strategic growth.

Introduction

Protogyny, a form of sequential hermaphroditism in which individuals first function as females and then as males (Ghiselin 1969; Sadovy and Shapiro 1987; Ross 1990; Munday et al. 2006), is common among fish, particularly wrasses (Kuwamura et al. 2020). Generally, polygynous mating systems, where large males monopolize mating opportunities, favor female-to-male sex change (Munday et al. 2006; Kuwamura et al. 2020). Among protogynous wrasses with a known mating system, haremic and lek-like polygyny are the most prevalent (Kuwamura et al. 2020). However, the mating system, the occurrence of sex change, and the proportions of primary (male-born) and secondary (sex-changed) males in diandric species can depend on population density (Warner 1982; Wernerus and Tessari 1991; Kuwamura et al. 2020). These patterns suggest that sex change is not a fixed endpoint, but a flexible strategy through which individuals can maximize lifetime reproductive success under specific social and ecological circumstances. For instance, males of some fish species adopt alternative reproductive tactics such as early sex change, occurring before the disappearance of the male (Munday et al. 2006), or parasitic tactics, including sneakers and satellites, that allow smaller individuals to exploit the mating opportunities of dominant males (Taborsky 1998; Alonzo et al. 2000; Sato et al. 2004; Oliveira et al. 2008).

Building on this framework, haremic systems offer a particularly interesting context in which to investigate how such flexibility manifests within size-based hierarchies that are presumed to leave little room to alternative strategies. In these systems, a dominant male controls a group of females (Warner and Robertson 1978), and social rank is based on size, with the largest female holding the highest rank below the male (Moyer and Nakazono 1978; Warner 1978; Warner and Robertson 1978; Shapiro 1979; Sadovy and Shapiro 1987; Ross 1990; Devlin and Nagahama 2002; Nelson et al. 2016; Kuwamura et al. 2020). Following the size advantage hypothesis (SAH), which posits that individuals benefit from adopting a sex changing life history when there is a clear difference in the rate at which fitness increases with size for the two sexes (Ghiselin 1969; Warner 1988; Munday et al. 2006), large individuals would optimize their reproductive value by being males that monopolize several females for reproduction (Munday et al. 2006). Importantly, sex change dynamics in a haremic protogynous system are primarily governed by males suppressing sex change in their female harem members (Warner 1975; Ross 1990). Under these conditions, sex change is expected to be tightly regulated, with dominant males suppressing transitions in subordinate females and thereby constraining the timing of sex change to specific social conditions.

The dynamics of a size-based hierarchy and sex change in haremic protogynous hermaphrodites can be understood within the broader context of strategic growth within size-structured groups, where few individuals have privileged access to reproduction. This also includes protandrous sex changers and cooperatively breeding species. Within these systems, conflicts over resources, breeding opportunities, and social rank are most pronounced among individuals of similar size (Enquist et al. 1987; Jennions and Backwell 1996; Cant and Johnstone 2000; Nathan et al. 2001; Bender et al. 2005). This results in selective aggression, where individuals control those directly below them in the hierarchy through aggressive display in order to maintain the size advantage (Hattori 1991). In return, individuals socially queue and strategically adjust their size and growth rate in relation to those directly above in rank (Hofmann et al. 1999; Kokko and Johnstone 1999; Buston 2003; Heg et al. 2004; Russell et al. 2004; Buston and Cant 2006; Dengler-Crish and Catania 2007; Wong et al. 2007; Young and Bennett 2010; Dubuc and Clutton-Brock 2019), thereby reducing risk of conflict and, in more extreme cases, eviction from the social group (Taborsky 1985; Reeve 1992; Reeve and Nonacs 1997; Reeve et al. 1998; Buston 2003; Buston and Cant 2006; Wong et al. 2007). Similarly, in a protogynous haremic social system, sex change and growth of subordinate individuals are actively suppressed by individuals directly above in rank, with the male primarily focusing on the largest female (Robertson 1972; Moyer and Zaiser 1984; Aldenhoven 1986). These dynamics predict a highly stable hierarchy in which only the top-ranking female changes sex following the disappearance of the dominant male, a pattern commonly referred to as standard sex change (Robertson 1972; Robertson 1974a; Robertson 1974b; Warner 1975; Kuwamura 1984; Ross 1990).

Research and conceptual thinking on strategic growth have focused on species that live in cohesive groups. Under these circumstances, subordinates are always in the vicinity of dominants that can hence regularly aggress against them, and the threat of eviction is credible. However, these predictions rely on the assumption that dominants can effectively monitor and control subordinates, which is most plausible in cohesive social groups. In systems characterized by female territoriality, where individuals occupy separate core areas and rarely aggregate as a group, such control may be substantially reduced. This spatial structure limits opportunities for repeated aggression and weakens the threat of eviction, potentially allowing subordinates to deviate from the expected growth trajectories. As a consequence, females may grow faster than predicted or even initiate sex change before the disappearance of the dominant male, hereafter referred to as early sex change. This suggests that sex change in such systems may be more flexible and less strictly controlled than classical models predict. This raises a key question: to what extent is sex change in such systems constrained by social control versus shaped by individual strategies and local ecological conditions?

The cleaner wrasse, *Labroides dimidiatus*, provides an ideal model for investigating these dynamics. This species is well known for its complex interspecific social interactions with other reef fishes (Randall 1958; Trivers 1971; Potts 1973; Grutter 1995; Bshary 2001; Grutter 2001; Bshary 2002; Bshary and Grutter 2002a; Bshary and Grutter 2002b; Grutter and Bshary 2003; Bshary and Grutter 2005; Grutter et al. 2005; Bshary and Grutter 2006; Johnstone and Bshary 2007; Pinto et al. 2011), and its social organization has been extensively studied. The cleaner wrasse is a monoandric protogynous hermaphrodite (meaning that all individuals are initially females; there are no initial males) with a size-based hierarchy (Robertson 1972; Robertson 1974a; Robertson 1974b; Kuwamura 1984; Nakashima et al. 2000). Parasitic alternative reproductive tactics are not present as neither males nor females tolerate additional males within their territory (Kuwamura 1984), and spawning occurs exclusively between one male and one female (Robertson and Choat 1974). Bi-directional sex change has been observed (Kuwamura et al. 2020), but it appears to be entirely governed by social status (Kuwamura et al. 2011). Each female cleaner wrasse maintains her own territory within the range of a dominant male. Female territories can overlap to varying degrees, resulting in either linear or branching social structures, depending on the size differences among females (Robertson 1972; Robertson 1974a; Robertson 1974b; Kuwamura 1984). In branching systems, several groups of females (branches) hold non-overlapping territories, allowing the coexistence of codominant females, defined as individuals of similar size that avoid interactions with each other (Kuwamura 1984). In contrast, linear systems consist of a single group of females of different sizes with overlapping territories (Kuwamura 1984). Hereafter, we refer to these two configurations as the linear and branching systems. Migration between harems was suggested as a strategy used by lower-ranking females to enhance their opportunities for sex change (Sakai et al. 2001). Classic studies demonstrated sex change suppression and hierarchical control within harems, resulting in standard sex change (Robertson 1972; Robertson 1974a; Kuwamura 1984).

Despite extensive work on this system, it remains unclear how social structure, individual strategies, and ecological conditions jointly determine when and under which circumstances individuals change sex. Detailed individual-level data on growth trajectories, early sex change, and potential effects of local density are still lacking, leaving the drivers of sex change timing in this species largely unresolved. A focus on individual life histories is of particular interest in light of recent evidence that male cleaner wrasse do not only have higher reproductive rates but also higher survival rates compared to females (Pessina and Bshary 2026) , making sex change a particularly advantageous goal for females.

Here, we conducted a 12-month observational study at Lizard Island on the Great Barrier Reef, Australia, to investigate the social and ecological determinants of sex change in the cleaner wrasse. We marked over 400 individuals and collected detailed data on growth, behavior, and social organization to identify the conditions under which individuals transition from female to male.

To provide an integrated understanding of sex change, we address three key components. First, we characterize the social hierarchy of the cleaner wrasse by testing whether this species forms a strictly size-based hierarchy, in which individuals primarily regulate those directly below them in rank. Second, we assess the extent to which this system deviates from the classical model of strict social control. Specifically, we quantify how often subordinate females outgrow higher-ranking individuals and how frequently sex change occurs while the dominant male is still present (early sex change). We further examine the social conditions that may facilitate such early transitions, including reduced male control and variation in harem structure (linear versus branching systems). Third, we investigate the individual strategies that may facilitate sex change, testing whether rapid growth or movement between harems increases the likelihood of becoming male. Finally, we investigate how these processes vary across ecological contexts by examining whether local population density influences growth patterns and the timing of sex change.

Together, these analyses provide an integrated understanding of how social structure, individual behavior, and ecological conditions interact to shape the timing and occurrence of sex change in a protogynous fish with reduced social control.

Methods

Site and study demes

This study was conducted between July 2022 and September 2023 as part of a long-term observational project at Lizard Island on the Great Barrier Reef, Australia. We selected eight reefs (Figure 1) as study demes to capture variation in cleaner and client fish densities.

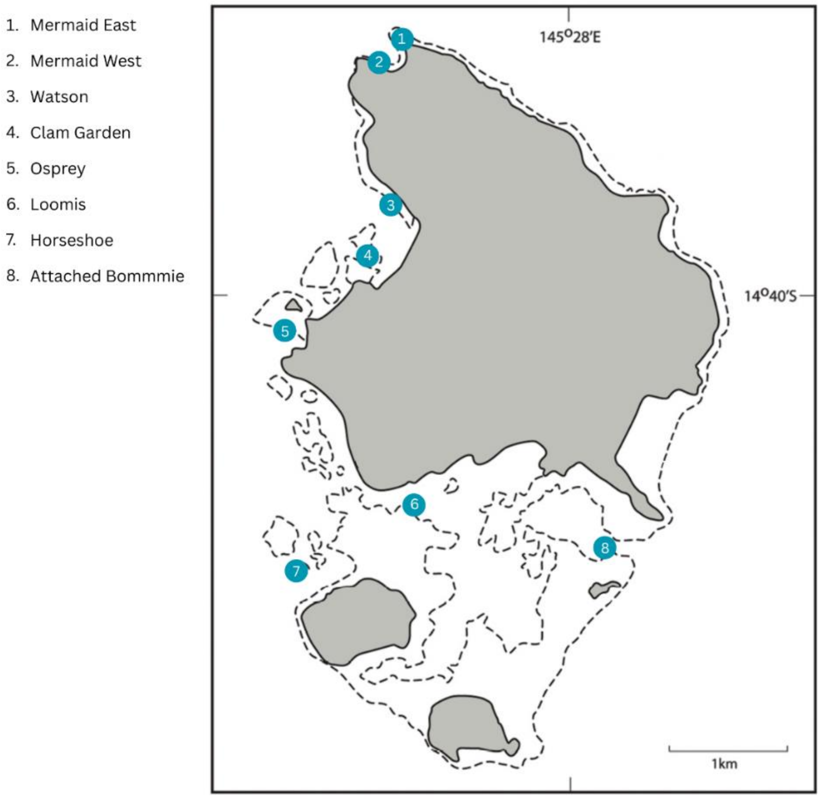

Figure 1: Field observation sites on the coral reefs surrounding Lizard Island, Australia.

Individuals were recognized either by distinctive markings, such as pigmentation patterns or irregularities in the lateral black band (Supplementary Figure S1.2), or by visible implant elastomer

(VIE) tags, a common method for small reef fishes (Jungwirth et al. 2019). Tagging was performed underwater after the fish were caught on SCUBA using hand nets (10 x 15cm) and barrier nets (4.7 x 1.8m with 2mm mesh size for small individuals; 1x1.2m with 5 mm mesh size for fish > 6.5 cm), and they were immediately released at the site of capture.

Each adult was marked with two subcutaneous VIE injections placed at distinct locations among four possible body sites (anterior and posterior regions on both sides; Supplementary Figure S1.1). Injections were applied along the pale band above the black stripe using six color options (red, pink, yellow, green, blue, white). Combining two colors across four positions allowed up to 1296 unique identification codes, or more if color order within the same body location was considered (e.g., yellow followed by green or green followed by yellow). Tag combinations could be reused across isolated reefs, as *Labroides dimidiatus* are highly territorial and do not cross open waters. Unique tag sets were maintained only between the two adjacent Mermaid sites.

The VIE pigment-hardener mix (Northwest Marine Technology, Inc. 2017) was applied without hardener to prevent rapid solidification and material loss during large-scale tagging in warm water. Tags remained visible throughout the study despite minor expansion as the fish grew. Recapture of 34 individuals after 12-20 months confirmed the durability of our VIE tags, exceeding previously reported longevity (Jungwirth et al. 2019).

In total, 280 adults were tagged, and 95 were individually recognized by natural features (Supplement Table S1). From November 2022 onwards, approximately 505 juveniles were included in the monitored populations. For the current study, only 165 juveniles that reached a total length of 40 mm are relevant, as they were tagged at that point and subsequently included in the data set. For marking, we used a single contrasting-color injection (red, pink, or yellow), yielding 108 unique tag codes. Overall, 540 individuals were followed, with site-specific sample sizes ranging from 47 (Loomis) to 88 (Mermaid East).

The primary researcher conducted all fieldwork, totaling ~1,000 dives and ~1,750 hours of underwater observation. Continuous monitoring enabled reliable identification of both tagged and untagged individuals through exceptional familiarity with their appearance and behavior.

Growth

Fish size was measured monthly using a photogrammetric stereo camera system composed of two GoPro Hero 8 cameras (Seager 2006). The system, held by the main diver while swimming through the reef, allowed 3D length measurements from video footage analyzed in EventMeasure (Seager 2006), after calibration in CAL (Seager 2006). Stereo photogrammetry provides higher accuracy than visual estimates (Michael et al. 2011), with reported software errors of 1-2mm (Euan et al. 2010). In our calibration tests, the mean measurement error was ±1.13 mm using a bar of known distances and ±1.81

mm using wild cleaner wrasses, reflecting movement and growth between measurements (See Supplementary Material S2 for full validation details).

When consecutive measurements suggested shrinkage, the previous length was retained as a conservative correction for measurement error. Individuals were typically revisited approximately once per month (median interval = 28 days, mean = 35 days). Changes in body size between consecutive measurements were generally small (median = 1 mm; mean = 2.5 mm). Because the software of the photogrammetric sizing camera records body size as continuous values rather than fixed size classes, measurements did not occur at uniform size intervals among individuals. We therefore used linear interpolation between consecutive measurements to estimate the time required for each fish to reach successive millimeter increments. This procedure reconstructed continuous, evenly spaced size trajectories for each individual, allowing direct comparisons among individuals when constructing deme-level size–age growth curves. To estimate deme-specific growth rates, we calculated the average time required for fish to grow 1 mm at each site and for each body length. These values provided an expected size-age relationship used to approximate individual ages, as direct age data were not available. Growth curves for each deme were then modeled using the Von Bertalanffy Growth Function (VBGF), fitted via non-linear least squares regression using the nlsLM() function from the *minpack.lm* package (Elzhov et al. 2023).

Distinct deme-level growth trajectories allowed classification of individuals as fast, slow, and average growers at each site. Classification was based on each fish's final size relative to its deme-specific curve: sizes exceeding half the upper standard deviation limit were labeled as fast growers, those below half the lower limit as slow growers, and intermediate values as average growers. The use of half upper and lower limits of standard deviation was chosen to ensure a balanced classification, avoiding an overrepresentation of average growers. Growth-type classification was used to compare survival rates and the occurrence of sex change between growth strategies. To assess the influence of local cleaner densities on the proportions of growth strategies, a secondary dataset classified fast, slow, and average growers relative to a population-level growth curve rather than using deme-specific curves.

Social system

Sex changing events and key aspects of the cleaner wrasse social structure and dynamics at Lizard Island, including (i) social hierarchies, (ii) formation of linear and branching social systems, and (iii) effects of individual migration, were documented through extensive direct underwater observations. Data were collected bi-weekly via scuba observations and recorded on underwater notebooks.

All individuals within study harems were identifiable through VIE tags or unique morphological features, allowing accurate determination of harem composition, size, and social rank. Changes were tracked by regularly updating individual presence/absence records. An individual was considered absent if no longer seen in the territory, and absence was confirmed after thorough searches in adjacent harems and surrounding reefs. Movements between harems or to peripheral areas were consistently detected and not mistaken for disappearances. To identify the type of social system (branching or linear) in which early and standard sex change occurs, the harem spatial structure was mapped using 2D reef maps generated from DJI Mini 3 Aerial drone footage. Most spatial reconstructions were based on monthly focal videos, with the focal cleaner wrasse's position plotted every 30 seconds. For some individuals, spatial positions were obtained through direct underwater observations instead. Only the territory of the male, the sex changing female, and her potential competitors in the harem was mapped. All maps were generated in Adobe Photoshop (Adobe 2019). Full details and maps of the social system are available in Supplementary Material S15.

Reliable sex identification was essential to describe sex-change dynamics. Although cleaner wrasses show limited sexual dimorphism, sex was determined from well-established behavioral cues previously validated by Robertson (1974a) through gonadal inspections. This approach enabled long-term, non-invasive monitoring without disrupting social dynamics.

Sex-specific behaviors used for identification included: (i) Flutter-run, an exclusively male display involving tail fluttering and fin spreading while swimming past females; (ii) Body-Sigmoid, a female sexual signal where females display an S-shaped posture; (iii) Female-specific sexual coloration during courtship; and (iv) males occupying the superior position during the final phase of the spawning rush. In addition, quantitatively males showed greater tolerance toward nearby females, higher movement within territories, and more frequent visits to females. Sex classifications were further validated through spawning observations: males spawned only with smaller partners, females only with larger ones. These behaviors were used solely to determine the sex of the focal individuals and were not included as variables in the behavioral analysis described below.

During the first year, 42 individuals were confirmed to have changed sex, first spawning as females with larger partners and later as males with smaller partners. Consistent with previous findings (Robertson 1974a), following male loss the largest female rapidly displayed male-typical behaviors, signaling an ongoing sex change prior to full physiological transition.

Intraspecific behavior observations

Behavioral data was collected for 464 cleaner wrasses across sexes and life stages. Each focal individual was observed at least once per month, yielding 1–13 videos per fish (mean = 4). Among the 42 sex-changing individuals, 0–13 videos were obtained per fish (mean = 7). Only 23 of these were retained for analysis, as others lacked recordings from their female phase.

Each behavioral observation consisted of a 20-minute video filmed with a GoPro Hero 9 by a scuba diver positioned 2-3m from the focal fish. Videos were then analyzed to quantify the number and duration of intraspecific interactions. For each partner, we recorded sex, relative size to the focal individual, and identity (when possible). Absences of interactions were treated as zero values and added during analyses in R Studio (RStudio Team 2020). Social rank for both focal and partner individuals was assigned using the monthly-updated social hierarchy dataset.

To define social rank, individuals within each group were ordered strictly by body size (TL). Labroides dimidiatus is known to form a simple, stable, size-based dominance hierarchy governed by a "size principle" where aggression flows almost exclusively down the size gradient (Robertson 1972; Robertson 1974a; Robertson 1974b; Kuwamura 1984; Nakashima et al. 2000). We empirically validated this for our study population by analyzing 1,147 aggressive interactions across 537 videos, including male and alpha, beta, gamma, and delta focal fish interacting with partners of known rank. In 87% of these interactions (n=996), a larger individual aggressed a smaller one. Because relative body size so reliably dictates intra-group aggressive interactions, using additional ranking algorithms based on behavioral matrices was unnecessary.

Behavioral data were used to quantify both male–female interaction time prior to sex change and patterns of size-based dominance. For analyses of male–female interactions before sex change (Model 5), we quantified the total duration of time males spent interacting with focal females, irrespective of interaction type, thereby integrating neutral, positive, and aggressive interactions into a single measure of association time.

In contrast, analyses of social hierarchy maintenance (Models 1.1-1.2) were restricted to interactions in which the focal individual aggressed their partner through various-intensity chasing behaviors (low: nipping; medium: rushing; high: chase). While preliminary analyses revealed frequent aggression toward small, untagged juveniles without defined rank, only interactions involving individually recognized (tagged or untagged) adults and juveniles with established rank positions were retained. To ensure comparability, only interactions involving individuals with established rank positions were retained, and focal individuals were required to have at least 10 video observations and the opportunity to interact with both adjacent and non-adjacent subordinates. The final dataset for hierarchy analyses included 120 individuals (47 males and 73 females), with behavioral metrics averaged per individual.

Cleaner fish density

To examine whether variation in local population density could influence growth patterns and sex-change dynamics among study sites, we quantified cleaner wrasse density at each site. We obtained cleaner fish density at our study sites by conducting 10 replicates of 30m transects per site. Counts were stratified into the two habitats of the reef in which our focal cleaner resided: The reef crest and the reef base. The reef crest is defined as the seaward edge of the reef flat, and the reef base as the bottom of the reef slope where it joins the sand flat (Green, 1994). Each fish census involved five 30-meter transects, spaced 2 meters apart, running parallel to the reef edge within each habitat for each site. We conducted counts using a 3m belt, a width previously demonstrated to be effective in counting wrasses (Green 1996). We swam each transect at a constant speed and performed it in approximately 10 minutes. For our analyses, we calculated cleaner densities considering only the counts of adult cleaner wrasse, of which the total length is larger than or equal to 50mm. Cleaner fish counts were then standardized to 150 m^2.

Statistical methods

Data analyses were conducted in R version 4.3.1(R Core Team 2023) using RStudio (RStudio Team 2020). Depending on the question, we used Generalized Linear Mixed-Effects Models (GLMM), Linear Mixed-Effects Models (LMM), Linear Models (LM), General Linear Models (GLM), and non-parametric tests (e.g., Wilcoxon signed-rank test and Chi-square tests). Models were fitted using lme4 (Bates et al. 2015), glmmTMB (Mollie et al. 2017), and stats (R Core Team 2023) packages. Model assumptions were verified through residual analyses and visual inspections of model fit. When appropriate, post hoc comparisons were performed with the emmeans package (Lenth 2023). Full model specifications are provided in Supplementary Material S3.

Size-based hierarchy

To test for size-based hierarchical control, we assessed whether aggression was preferentially directed toward the immediately subordinate individual, separating between males and females (Model 1.1 and Model 1.2). For each 20-minute focal observation, all aggressive interactions (nipping, rushing, chasing) were identified and assigned to the target individual. Each target was classified as either adjacent (the individual directly below the focal fish in size rank) or non-adjacent (all other lower-ranking individuals).

For each observation, we calculated the proportion of total aggression directed toward the adjacent individual. We also recorded the number of lower-ranking individuals present (n), allowing us to calculate the expected proportion under a null model of equal allocation of aggression across subordinates (1/n). Observed and expected proportions were then averaged across observations for each focal individual, yielding one pair of values per individual (47 males and 73 females). These were compared using paired Wilcoxon signed-rank tests (Models 1.1–1.2) to determine whether aggression toward the adjacent subordinate exceeded random expectations. Videos lacking aggression were excluded from analysis. Because expected values depend on the number of subordinates (1/n), both observed and expected proportions vary among individuals; reported values represent averages across individuals.

Having investigated the presence of a size-based hierarchy, we then evaluated its effectiveness by testing whether changes in social rank, with and without sex change, influenced individual growth trajectories. To this end, we modeled growth before and after sex change using an LMER model (Model 2), with log-transformed growth rate as the response variable. Sex, sex-change scenario (standard or early), initial size, and their interactions were included as fixed effects. Female growth rate was calculated using the size measurement 30 days before sex change and at sex change, while the male rates were calculated between the size at sex change and the measurement approximately 30 days after. Accordingly, the initial size refers to the size measured approximately 30 days before sex change for females, and the size at sex change for males.

A complementary LMER model examined growth responses to rank upgrade that did not involve sex change (Model 3). Here, we compared growth rates before and after rank upgrade following the loss of a dominant male, using Period (Before vs. After upgrade) as a fixed factor, and the log-transformed growth (ln(GR 0.3)) as the response variable. In both models, Fish ID was included as a random effect to account for repeated measures. Analyses were restricted to individuals with both pre- and post-event data(sex change: n = 33; rank upgrade: n = 19). The estimated uncertainty in detecting the exact day of sex change was three to four days, with a maximum of one week in isolated cases.

Limits of social control

To assess deviations from the classical model of strict social control, we examined both the occurrence of early sex change and the social conditions under which it arises.

We first tested whether the frequency of early versus standard sex change differed between social systems (linear vs. branching), based on direct field observations (Supplementary Material S15). The association between sex change scenario and social system was then evaluated using a Pearson's chi-squared test of independence (Model 4).

We then asked whether reduced social control facilitates early sex change by analyzing interaction patterns prior to transition (Model 5). Using an LMM with repeated measures from 23 sex changers recorded within 300 days before sex change, we modelled log-transformed interaction duration (ln(duration + 0.3)) as the response variable, with sex change scenario, days to sex change, and their interaction as fixed effects. Fish ID was included as a random factor to account for repeated observations of individuals.

Strategies of sex change

We then investigated individual strategies that may increase the likelihood of sex change.

To test whether growth patterns differed between individuals that did or did not change sex, we used binomial GLM (Model 6) to examine the distribution of growth strategies (fast, average, and slow) across sex-change categories. Growth strategy, sex-change status (sex-changing or not), and their interaction were included as predictors, and the model was weighted by the number of individuals in each sex-change category (sex-changing: n = 42; non-sex-changing: n = 334).

We further examined whether migration influenced the timing of sex change by testing with an LM model whether migrants transitioned at smaller sizes than residents (Model 7). Size at sex change was used as the response variable and migration status (migrant or not), sex change scenario, and their interaction as fixed effects.

Ecological context

Finally, we examined how local population density shapes social structure, growth strategies, and sex change.

We first tested whether adult cleaner density and the number of adult females in a harem (TL ≥ 50 mm) predicted social system type (branching vs. linear) using a binomial GLM (Model 8). We then assessed whether cleaner density predicted the number of adult females per harem using a negative binomial GLM (Model 9). To evaluate density-dependent variation in growth strategies, we fitted a binomial GLM (Model 10), testing whether the distribution of growth strategies varied across sites differing in adult cleaner density. Finally, we examined whether size at sex change depended on local cleaner density and sex-change scenario using an LM model (Model 11).

Results

Size-based hierarchy

Cleaners directed a disproportionate amount of aggression toward their immediate subordinate (Figure 2, Models 1.1 and 1.2). On average, females directed 58.3% of their aggression toward the adjacent lower-ranked individual (average expected 36.6%), while males directed 49.5% (average expected = 35.8%). In both sexes, observed values were significantly higher than expected under a scenario in which aggression was evenly distributed across all lower-ranking individuals (Males: V = 730.5, p = 0.038;Females: V = 2121, p < 0.0001). Although the adjacent individual did not always receive the majority of aggression, these results indicate that aggression is preferentially biased toward the closest subordinate rather than evenly distributed across group members.

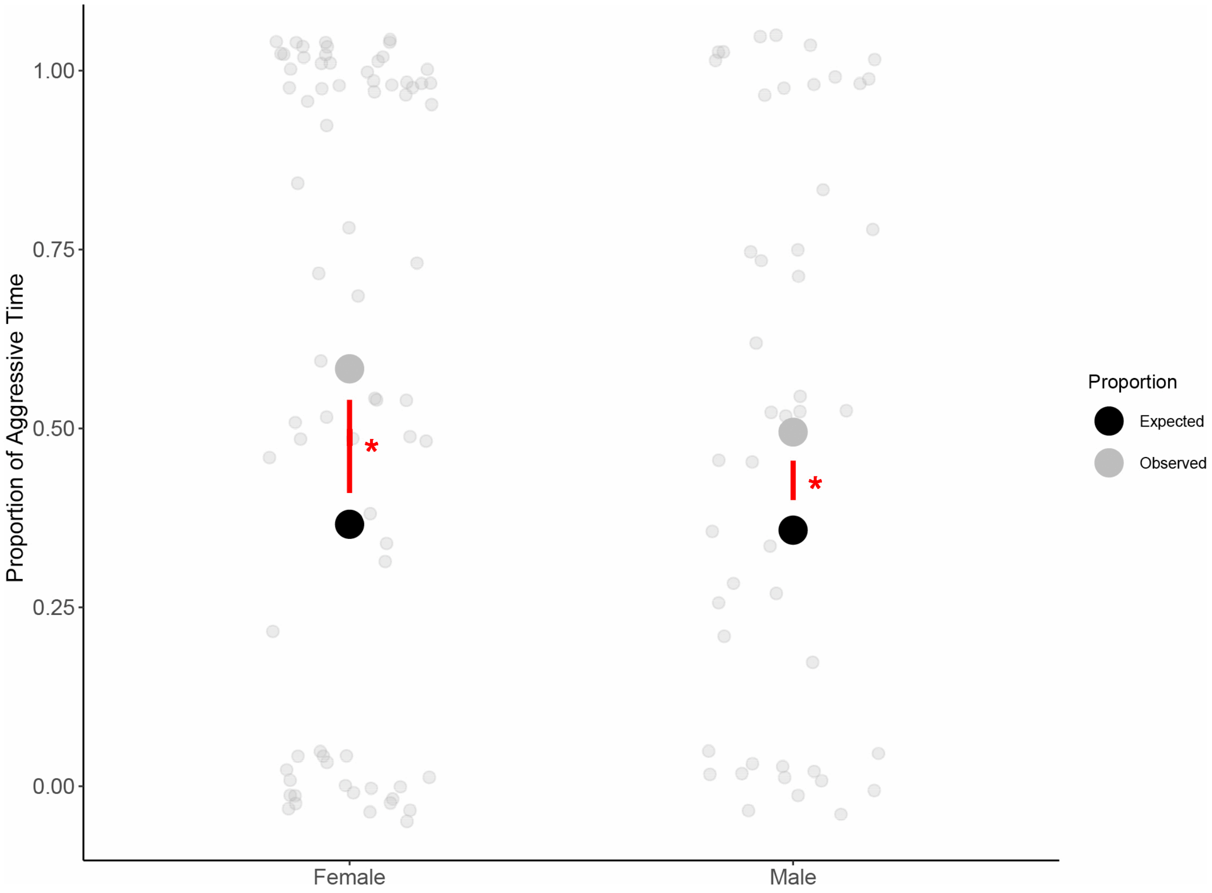

Figure 2: Observed against expected proportion of time spent aggressing adjacent individuals. The distribution of the proportion of time spent aggressing an individual of adjacent rank is shown as a jitter of the raw individual-level observation. Overlayed points show expected (red) and observed (black) mean proportions. These results come from Model 1.1 for males (n = 47) and Model 1.2 for females (n = 69). A line connecting the expected and observed mean proportion with an asterisk indicates a significant difference between the two groups (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$).

Growth rates of sex changers significantly decreased after transition (Model 2; Analysis of deviance: Chisq = 4.99, df = 1, p = 0.025; Figure 3a), independently of whether it was a standard or early sex change (Model 2; Analysis of deviance: Chisq = 0.0781, df = 1, p = 0.78). Initial size did not significantly interact with the effect of sex change on growth rates (Model 2; Analysis of deviance: Chisq = 1.25, df = 1, p = 0.26), but post hoc tests showed that reduced growth was driven by larger individuals (76–80 mm TL; $p < 0.05$), whose male-phase growth was 1.5–1.7 times lower than during their female phase.

In contrast, females who upgraded their rank showed a 48% increase in growth following the upgrade (Model 3; Analysis of deviance: Chisq = 6.83, df = 1, p = 0.009; Estimate = 0.39, SE = 0.15; Figure 3b).

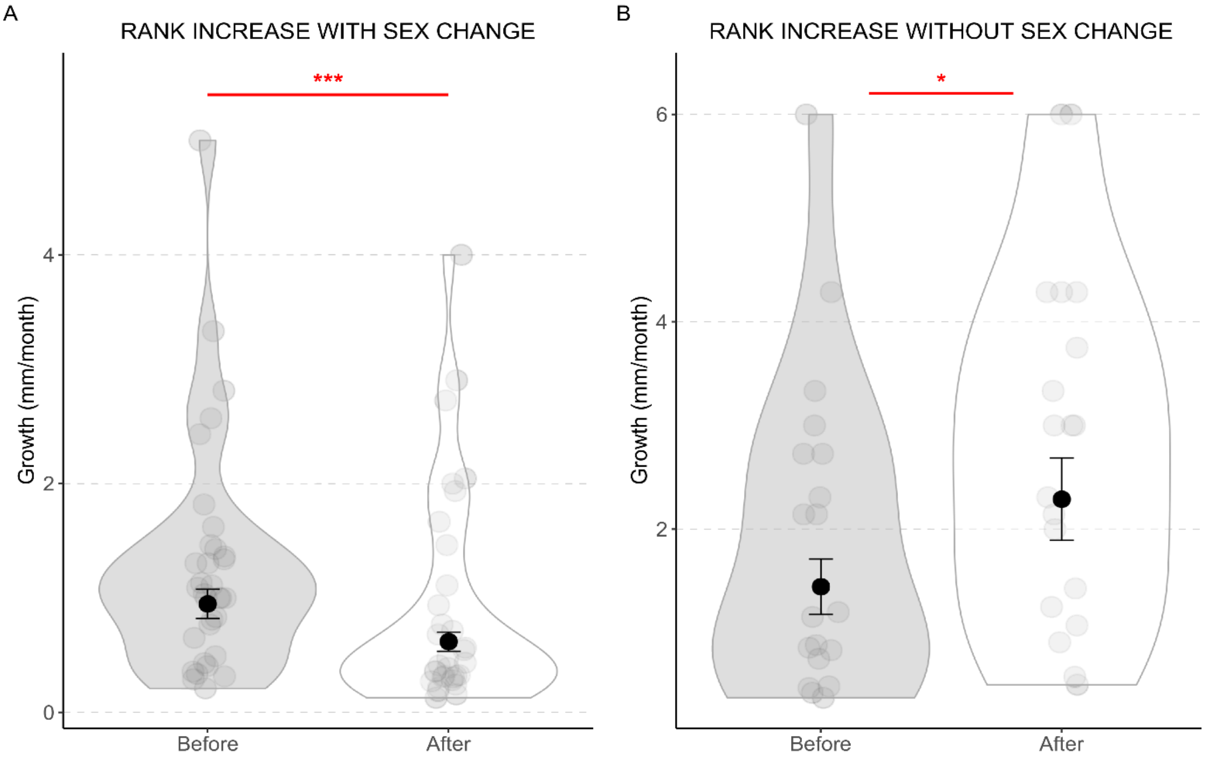

Figure 3: Effects of status upgrade on growth rate. A, Distribution of growth rates (mm/month) before and after upgrading rank position with sex change, shown as violins and jitter of the raw individual level observations. These results are based on Model 2 and include 66 observations, representing before-and-after measurements for 33 cleaner wrasses. B. Distribution of growth rates (mm/month) before and after upgrading rank position as a female, shown as violins and jitter of the war individual level observations. These results are based on Model 3 and include 38 observations, representing the before-and-after measurements for 19 cleaner wrasses. The overlaid points and error bar represent model-estimated means ± standard errors (SE). The line connecting the violins with an asterisk indicates a significant difference between the two groups involved (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$).

Limits to social control

Rank reversals, defined as instances in which an initially smaller female grew larger than the individual directly above her in the size-based hierarchy, occurred in 20 of 63 harems, with 30 females overtaking the individual directly above them.

Among the 196 initial females, 42 underwent sex change between July 2022 and September 2023. Of these, 57.1% (n = 24) and 42.9% (n = 18) were standard and early sex changes, respectively. In total, 88.5% of the standard sex changers were the largest and most dominant females in their harems. In contrast, only half of the early sex changers were dominant, with the remainder being smaller, lower-ranking females. Most standard sex changes occurred in linear social systems (N = 20, 83.3%), whereas most early sex changes occurred in branching social systems (N = 14, 77.8%). A chi-squared test of independence showing a significant association between sex change scenario (early vs standard sex change) and social system (Model 4; Pearson's Chi-squared test with Yates' continuity correction: Chi-square = 14.15, df = 1 p < 0.001). The adult sex ratio remained similar over the study period, with 4.2 females per male at the beginning and 4.4 at the end.

Analyses of male-female interactions before sex change, based on total interaction duration irrespective of interaction type, revealed that males spent significantly more time with standard sex changers than with early sex changers (Model 5; Analysis of deviance: Chisq = 7.92, df = 1, p = 0.005). Interaction time increased significantly as females approached sex change (Model 5; Analysis of deviance: Chisq = 15.24, df = 1, p < 0.001). This was true for both standard and early sex changers (Model 5; Analysis of deviance: Chisq = 0.014, df = 1, p = 0.90; Figure 4). Post hoc comparisons indicated that standard sex changers (emmeans = 1.088, SE = 0.71, on the log-scale) spent almost nine times longer interacting with males than early sex changers (emmeans = 3.16, SE = 0.69, on the log-scale).

Strategies of sex change

We next examined whether individual traits and behaviors influence the likelihood of sex change. Although the average growth strategy was most common across the population (Figure 5a), growth strategy distribution differed significantly between sex-changing and non-sex-changing individuals (Model 6; Analysis of deviance: LR Chisq = 18.17, df = 2, p < 0.001). Post hoc comparisons showed that fast growers were 87.5% more frequent among sex changers (45%) than among non-sex changers (24%; Estimate = -0.972, SE = 0.335, p = 0.0038), whereas slow growers were significantly underrepresented (14% vs. 38%; Estimate = 1.281, SE = 0.455, p = 0.0049) Average growers showed no difference between the two groups (Estimate = -0.075, SE = 0.334, p = 0.8229).

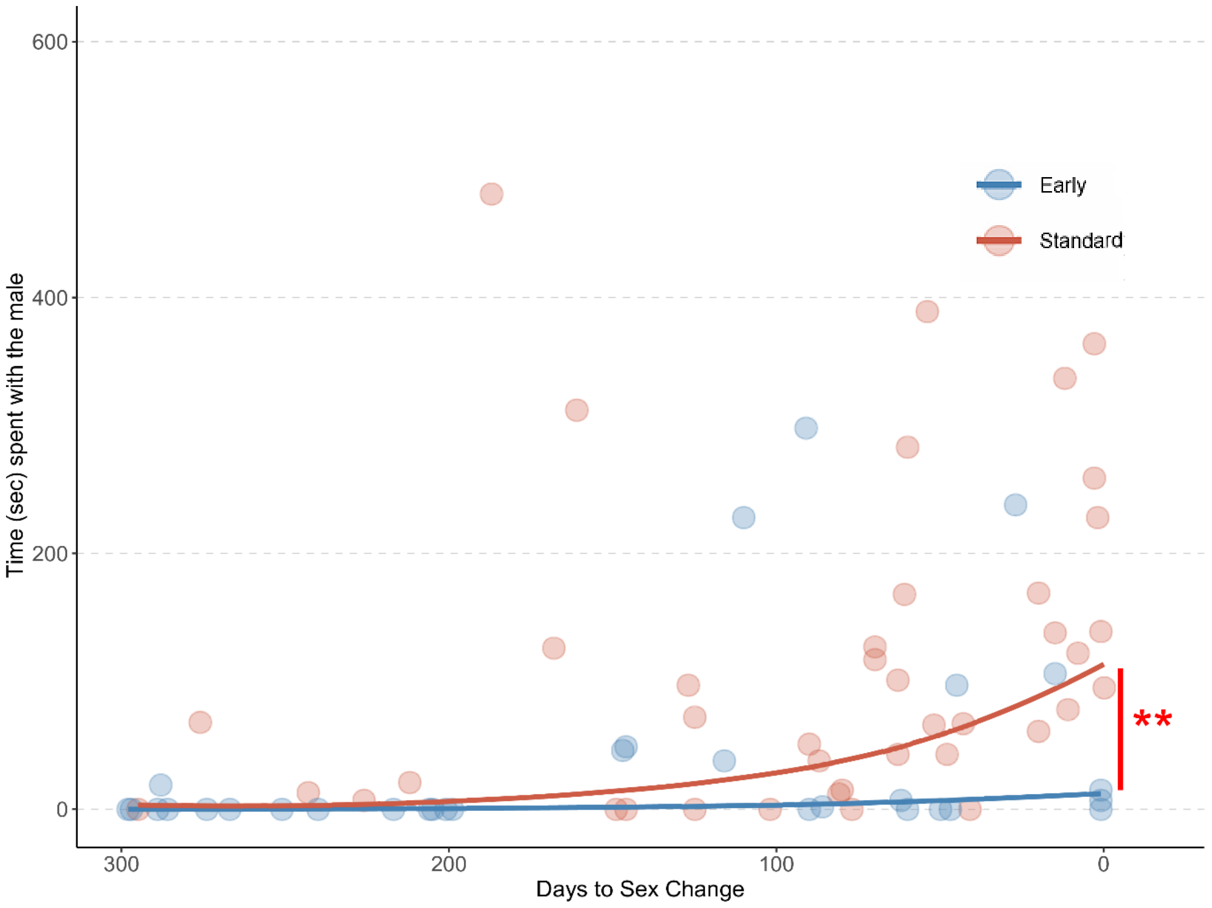

Figure 4: Time males spent with sex-changing females prior to sex change for the two sex change scenarios. Distribution of the time males spent with the sex-changing female during 20-minute video observations taken at different moments prior to their sex change for each sex scenario (standard and early sex change). Raw individual observations are shown as jitter and the overlaid lines represent model predictions. These results are based on Model 5 and comprise 34 observations for early sex change and 38 for standard sex change. The line connecting the two prediction lines, marked with an asterisk, indicates a significant difference between the two groups (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$).

Migration also influenced sex change dynamics. Individuals that moved between harems before transitioning changed sex at significantly smaller sizes than non-migrants (Model 7; Analysis of deviance: $F = 5.33$, $df = 1$, $p = 0.027$; Figure 6a), with no interaction between migration and sex-change scenario (Model 7; Analysis of deviance: $F = 0.95$, $df = 1$, $p = 0.33$). On average, migrants changed sex at 6% smaller body size than non-migrants (early sex change: 73.9 ± 2.23 mm vs. 80.7 ± 1.99 mm; Standard sex change: 76.6 ± 2.23 mm vs. 79.5 ± 1.58 mm).

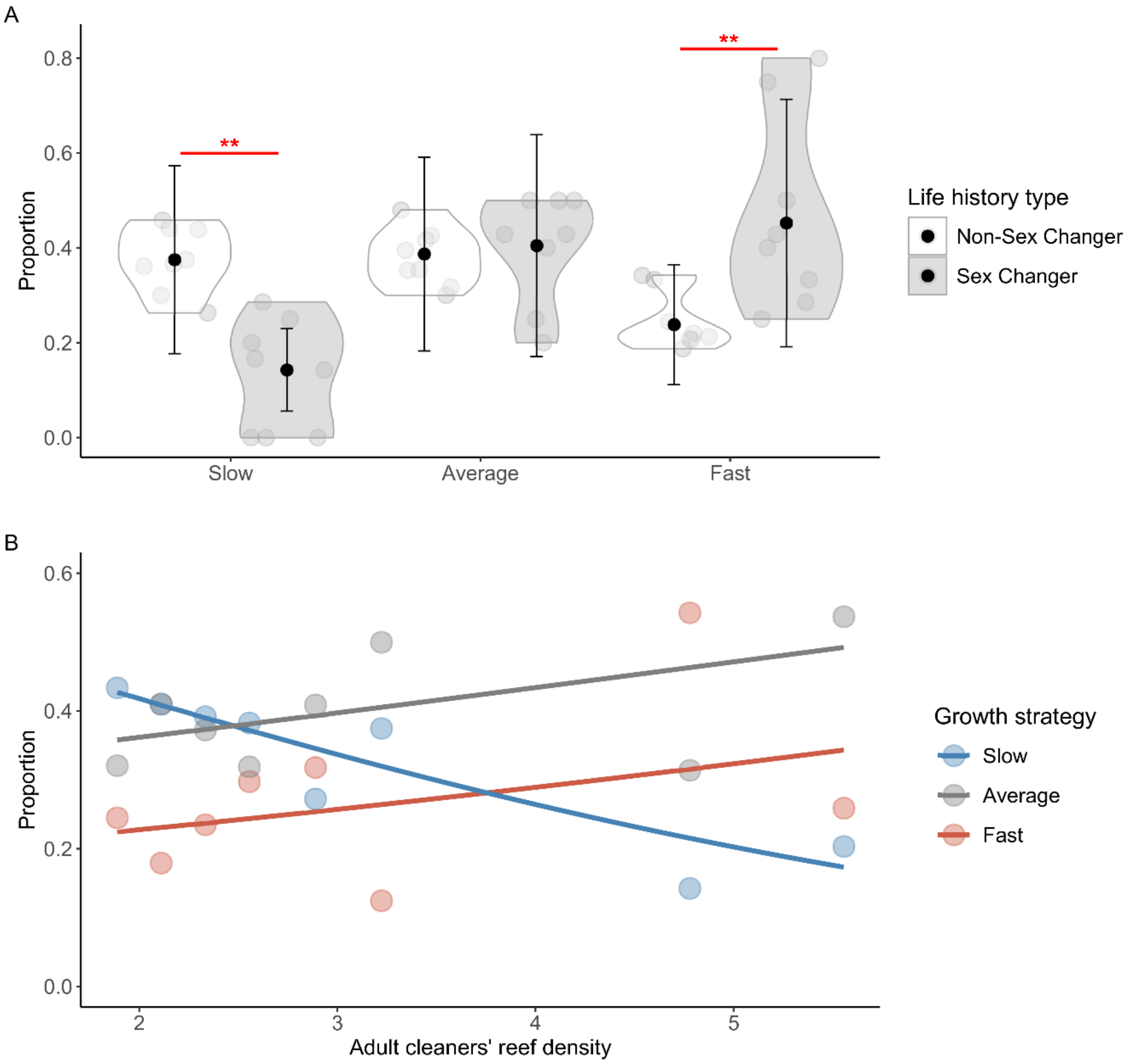

Figure 5: Proportions of fast, slow, and average growers. A. Distribution of the proportions of fast, slow, and average growers within sex and non-sex changers at each site (n = 48), shown as violins and jitter of the war site-level observations. Overlaid points and error bars represent model-estimated means ± standard errors (SE) obtained from Model 6. A line connecting the violins with an asterisk indicates a significant difference between the two groups involved (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$). B. Distribution of the proportion of fast, slow, and average growers across different adult cleaner wrasse reef densities (n = 24) shown as a jitter of the site-level raw observation overlayed by model predictions (Model 10).

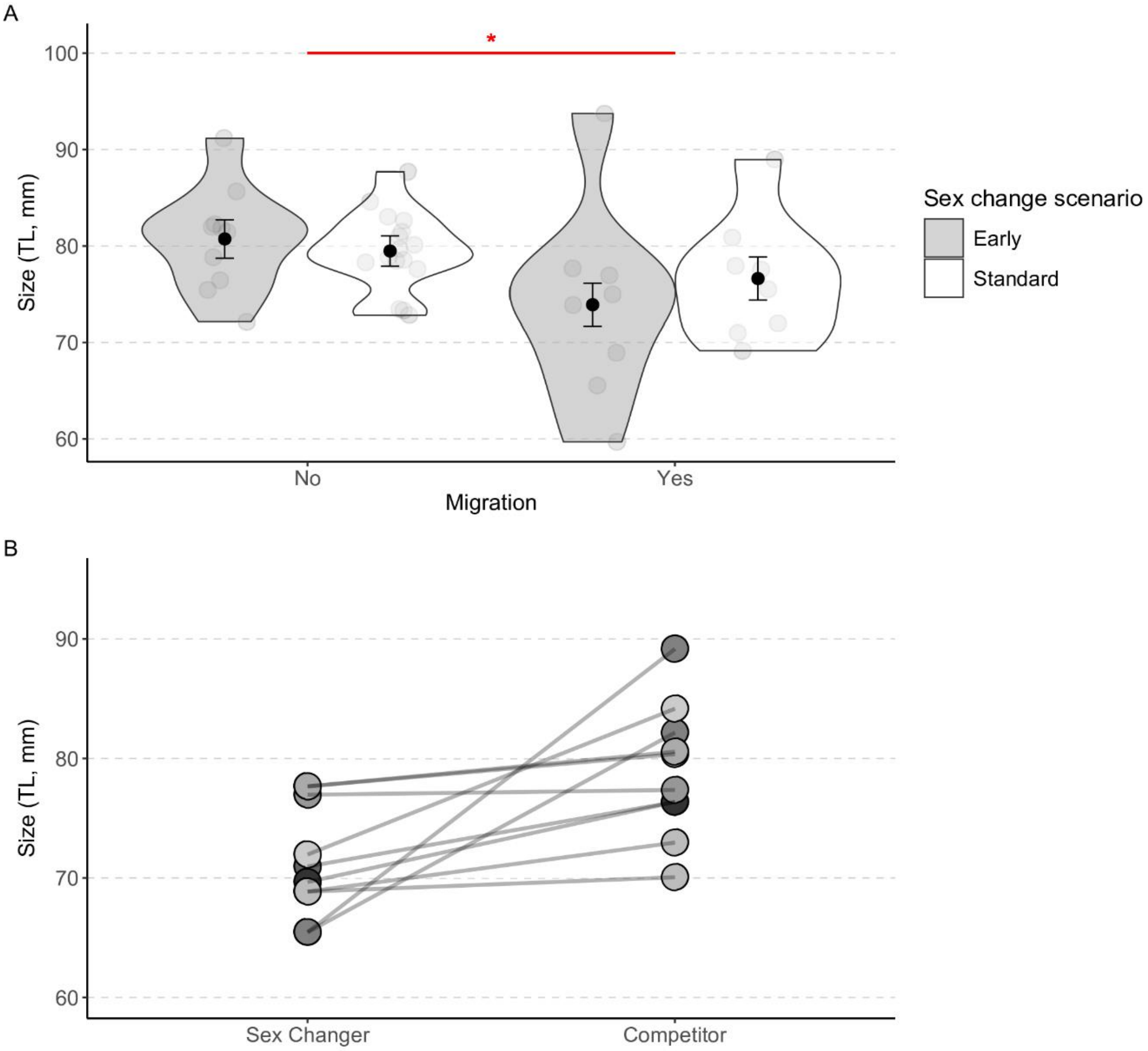

Figure 6: Effects of migrating. A. Distribution of size at sex change (TL, mm) for migrant and non-migrant females in the two sex change scenarios, shown as a jitter and violins of the raw individual-level observations. The overlaid points and error bar represent model-estimated means ± standard errors (SE) obtained from Model 7. These results include one data point for each sex changer (n = 42). A line connecting the violins with an asterisk indicates a significant difference between the two groups involved (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$). B. Size at sex change (TL, mm) of seven migrant females compared to the size of their competitors in the original harem at the time of sex change.

Consistent with this pattern, 38.1% (16 of 42) of the sex changers were migrants at a certain point in their life, compared with a 12.7% migration rate in the general population (37 of 291), corresponding to a 43.2% probability of sex change in migrant versus 10.2% in non-migrant female population. Excluding the four individuals for whom we have no information before their migration, 91.7% (11 of 12) migrant sex changers were low-ranking females in their previous harem. For seven migrant sex changers, we have additional information about their original harem (Figure 6b). All of them would not have had the opportunity of changing sex in their original harem at the time of their sex change, as they would still be occupying a low rank position (either Beta or lower, Figure 6b).

Most migrants transitioned within linear systems (68.75%). The number of migrant standard sex changers (n = 8) was similar to the number of migrant early sex changers (n = 7). Of the 8 migrant early sex changers, four transitioned after the male abandoned a branch within a branching system, one after the male left his linear harem, and three after moving to peripheral territories to establish new branches.

Finally, six individuals changed sex at sizes smaller than 75mm, raising the question whether sex change was beneficial or rather the product of a mechanism ('change sex if not regularly visited by a male') wrongly triggered. Three of these small individuals migrated to the periphery of their social group and formed new harems with only one to three juveniles and hence reduced current reproductive rates, whereas the remaining three gained adult females as subordinates. The 10 larger sex changing females (≥ 75 mm) typically obtained one to five adult females and up to four juveniles after transitioning (see Supplement S16).

Ecological context

We finally examined how variation in local ecological conditions shapes social structure and sex change dynamics.

Branching systems were always associated with the presence of codominant females, defined as large individuals of similar size in the male's territory. Codominant females were not present in any of the linear systems (see Supplementary tables S15.1.1 and S15.2.1). In the four cases of standard sex change that occurred in a branching system, two pairs of codominant females changed sex at the same time and split the original harem (see S15.2l, S15.2o). Three of the early sex changers that belonged to a linear system were the largest females that migrated at the periphery of the male's territory and created their own harem instead (see S15.1h, S15.1f). The remaining one was abandoned by its male (see S15.1l).

At the population level, branching systems were harems, characterized by significantly more adult females than linear systems (Model 8; Analysis of Deviance: LR Chisq = 18.59, df =1, $p < 0.0001$, Figure 7). However, cleaner wrasse reef density did not predict the formation of linear or branching systems (Model 8; Analysis of Deviance: LR Chisq = 2.97, df =1, p = 0.08). Also, adult cleaner reef density did not significantly affect adult female harem size (Model 9; Analysis of deviance Type II: Chisq = 0.16, df = 1, p = 0.69).

Growth strategies varied with local cleaner density. Pooling all data to calculate an overall population growth curve revealed that the distribution of growth strategies varied statistically with adult cleaner density (Model 10; Analysis of deviance: LR Chisq = 19.79, df = 2, p = 0.0001; Figure 5b). Both fast and average growers increased in frequency with density (Average trend: estimate = 0.151, SE = 0.123; Fast trend: estimate = 0.161, SE = 0.09), while slow growers declined (trend estimate = -0.346, SE = 0.996).

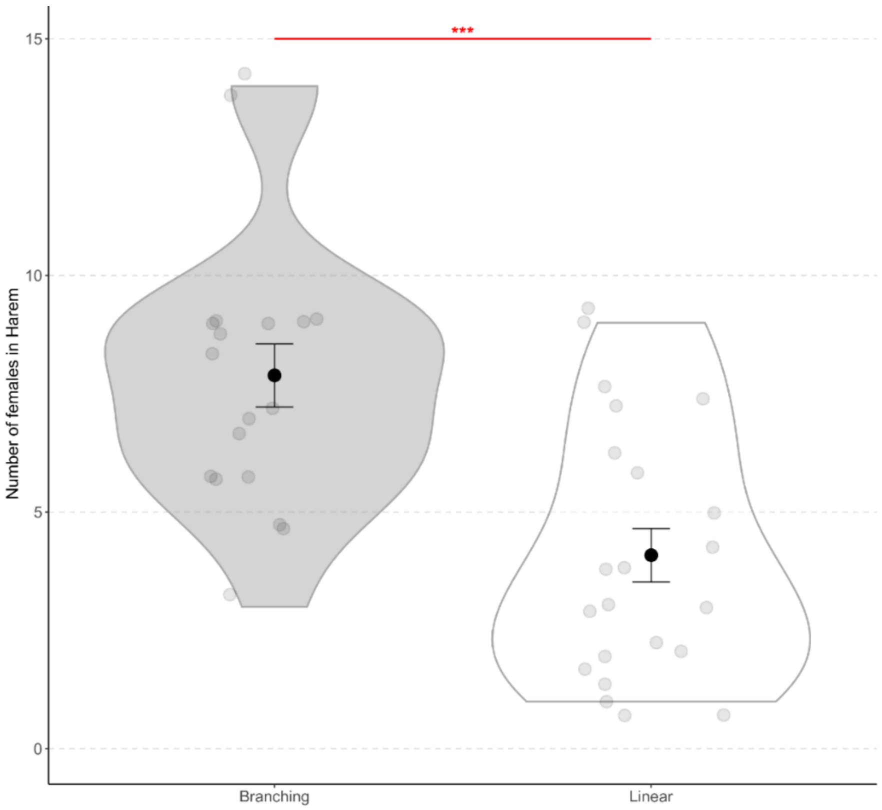

Figure 7: Number of adult female cleaner wrasse in branching and linear social systems. Distribution of the number of adult females (TL ≥ 50mm) within branching and linear shown as violins and jitter of the raw transect-level observations at each study site. The overlaid points and error bars represent model-estimated means ± standard errors (SE) obtained from Model 8.

Finally, size at sex change increased significantly with adult cleaner reef density (Model 11; Analysis of deviance: F = 9.35, df = 1, p = 0.004; Figure 8), while sex change scenario (standard vs. early) had no effect on size at sex change (Model 11; Analysis of deviance: F = 6.71, df = 1, p = 0.66). Across sites, mean size at sex change was 78.35mm TL.

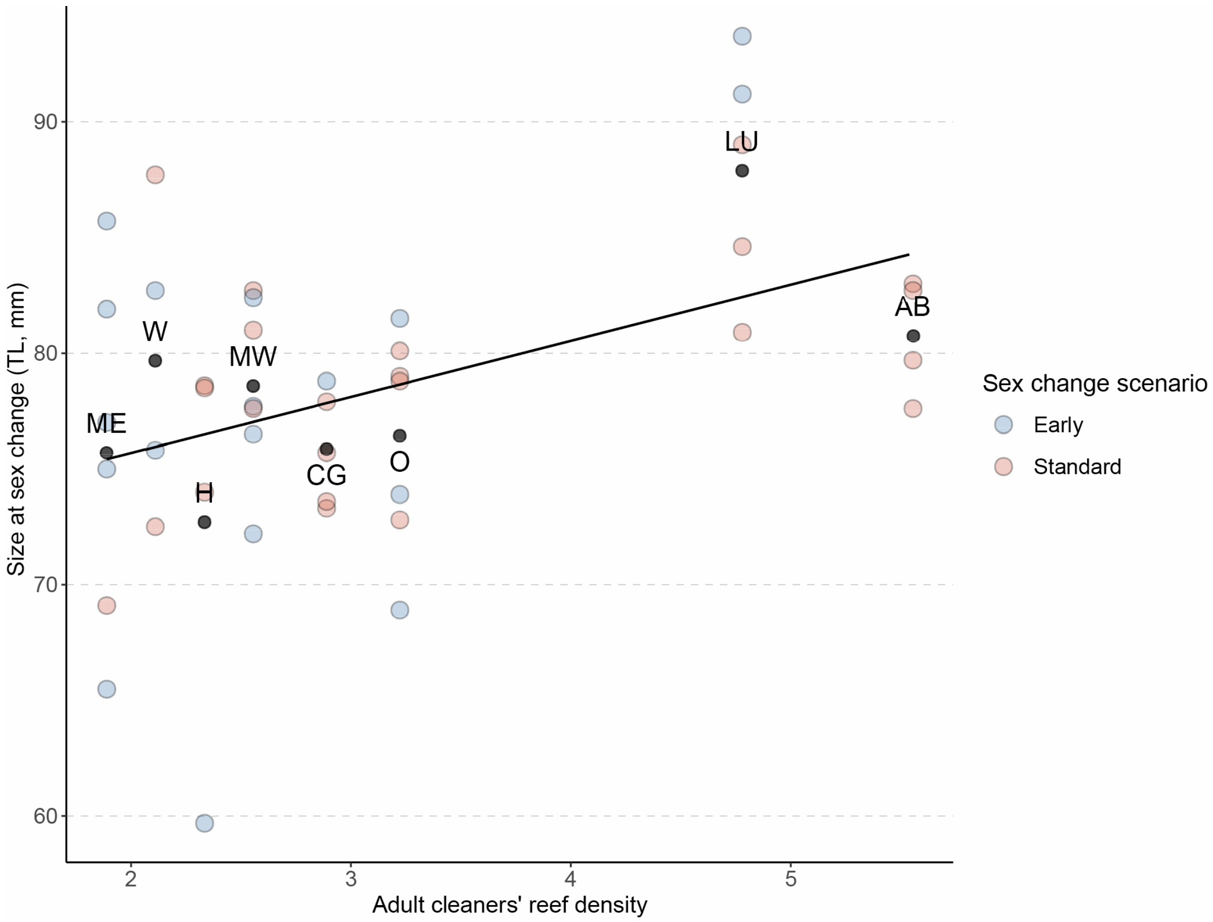

Figure 8: Size at sex change across adult reef cleaner densities. Distribution of size at sex change (TL, mm) for our 42 sex changers, plotted against adult cleaner fish reef density, with jittered raw individual-level observations overlaid on the model predictions (Model 11). Labeled black points represent average size at sex change for each site (ME = Mermaid East, MW = Mermaid West, W = Watson, CG = Clam Garden, O = Osprey, LU = Loomis, H = Horseshoe, AB = Attached Bommie).

Discussion

Our study provides an integrated understanding of the timing and occurrence of sex change in the cleaner wrasse at Lizard Island, showing that while size-based hierarchies structure social interactions, they do not fully constrain individual trajectories. Instead, sex change emerges from the interplay between incomplete social control, individual strategies, and ecological context.

Size-based hierarchy

Our results confirm that the social system of the cleaner wrasse at Lizard Island retains key features of a size-based hierarchy. As predicted, aggression was disproportionately directed towards subordinate individuals, supporting the idea that conflicts are strongest among similarly sized competitors (Enquist et al. 1987; Jennions and Backwell 1996; Cant and Johnstone 2000; Nathan et al. 2001; Bender et al. 2005). This pattern is consistent with selective aggression toward immediate subordinates, a hallmark of size-based systems (Robertson 1972; Moyer and Zaiser 1984; Aldenhoven 1986; Hattori 1991).

We also found evidence for strategic growth. Females that increased in rank without changing sex accelerated their growth following the disappearance of a higher-ranking individual, consistent with theoretical predictions (Hofmann et al. 1999; Kokko and Johnstone 1999; Buston 2003; Heg et al. 2004; Russell et al. 2004; Buston and Cant 2006; Dengler-Crish and Catania 2007; Wong et al. 2007; Young and Bennett 2010; Dubuc and Clutton-Brock 2019). In contrast, individuals that underwent sex change exhibited a reduction in growth rate, likely reflecting additional dynamics associated with sex change, where top dominance position is no longer the primary driver of growth.

Importantly, increased female growth following rank upgrade may not solely reflect intrinsic strategic adjustments. At Lizard Island, females upgrading in rank often occupy the cleaning station previously held by the disappeared individual, potentially gaining access to more profitable client interactions (unpublished data, Pessina et al.). Thus, growth acceleration may result from both adaptive strategic responses and improved access to resources.

Limits to social control

Despite the presence of size-based hierarchical features, our results demonstrated that social control in this system is incomplete. We documented multiple rank reversals, with initially smaller individuals outgrowing and overtaking initially larger ones. To our knowledge, such reversals have not been reported in species where strict control is maintained through the threat of eviction.

Most strikingly, early sex change was common as 42.9% of the sex-changing events happened in the presence of the male, and most of these individuals were not the top-ranking female. This strongly deviates from classical expectations for haremic protogynous systems with a size-based hierarchy, where sex change is assumed to be tightly suppressed and restricted to the largest female (Ross, 1990; Warner, 1975). Although early sex change has previously been reported in this species (Robertson 1972; Robertson 1974a; Kuwamura 1984), its presence has likely been underestimated as most studies relied on experimental male removals that mask its natural frequency.

Our results further show that the breakdown of social control is not random but structured by social organization. Early sex change was more frequent in branching systems, which inherently limit the effectiveness of size-based control. This limitation arises for two main reasons. First, branching systems include more females than linear hierarchies, forcing males to divide their attention among a larger number of harem members. Second, the territories of co-dominant females do not overlap, reducing direct interactions among females and weakening female–female regulation within the hierarchy. Consistent with these constraints, males spent less time with individuals that later underwent early sex change compared to standard sex changers. This suggests that males face a trade-off in allocating attention and may fail to effectively monitor all subordinates, particularly non–top-ranked individuals.

Reduced oversight may therefore create opportunities for these individuals to initiate sex change earlier than predicted by size-based control models.

This dynamic closely resembles predictions from game theory, particularly the three-person duel model, in which the "weakest" individual can prevail over stronger competitors under conditions of indirect competition (Archetti 2012; Dorraki et al. 2019) . In this system, limited male attention and reduced interactions among females may create opportunities for lower-ranking individuals to bypass typical size-based constraints and advance in the hierarchy.

Taken together, these findings challenge the assumption that sex change in protogynous systems with a size-based hierarchy is tightly regulated (Ross, 1990; Warner, 1975). This is particularly striking given that *Labroides dimidiatus* has long been considered a classic example of sex change suppression (Warner 1975; Ross 1990). Instead, our results show that in this model system, social control is limited and context-dependent.

Strategies of sex change

Given the existence of incomplete control, individuals appear to adopt strategies that increase their likelihood of transitioning to male. One key factor is growth rate: fast-growing individuals were more likely to change sex. In principle, fast growers could be individuals of high quality (either as successful cleaners or because of efficient immune function) or they might trade off current reproductive success (egg production) against potential future reproductive success. However, recent evidence that male cleaner wrasse have higher survival rates than females do (Pessina and Bshary 2026) on top of the higher reproductive rate, suggests that any decisions that increase the likelihood of eventually achieving sex change are the best possible options, and that only low-quality individuals would opt out of the general competition and focus on current reproductive success.

Migration to a more suitable harem also emerged as a strategy used by females to improve their chances of sex change. This result aligns with previous observations (Sakai et al., 2001). As harem compositions are outside the control of individuals, switching will always be an opportunistic decision. At this stage, we do not know whether there is inter-individual variation in prospecting neighboring harems or whether all individuals have knowledge about the composition of neighboring harems.

However, our results also indicate that early sex change is not always advantageous. Individuals that transitioned at smaller sizes and inherited harems composed mainly of juveniles reduced their reproductive rate compared to the alternative of having remained a female and have their own eggs fertilized by the male harem owner. Early laboratory experiments on cleaner wrasse suggest that the social control mechanism responsible for sex change suppression may sometimes cause wrong decisions: medium-sized females can be induced to change sex when taken away from the male and paired with a smaller female, but then may reverse back if paired again with a larger male (Kuwamura et al. 2002; Kuwamura et al. 2011). Together, these findings indicate that sex change decisions can be flexible but are not always optimal.

Ecological context

Ecological conditions further modulate the dynamics of growth and sex change. Contrary to expectations, the number of females in a harem and the social structure (linear vs. branching) were not influenced by cleaner density. However, density was positively correlated with growth rates and size at sex change.

Rather than reflecting within-harem competition, this pattern may arise from interactions with neighboring harems. In high-density areas, individuals may face stronger competition from nearby males or transitioning females, requiring them to reach a larger size before successfully changing sex (Robertson 1972). Alternatively, as cleaner density is known to correlate with the density of large client fish (Triki et al. 2019), individuals growing up in high-density sites might simply grow faster because of access to more food resources and shift partly the tradeoff between current egg production and investment in becoming a male.

Both mechanisms are consistent with the observed increase in fast-growing individuals at higher densities. Local population density is hence an important factor affecting growth and sex change decisions in cleaner wrasse. Its importance for strategic growth in species living in cohesive groups with subordinates facing the threat of being evicted remains to be investigated.

Conclusion

In conclusion, sex change in cleaner wrasse emerges from the interaction between social structure, individual strategies, and ecological conditions, rather than being strictly controlled by dominant individuals. The occurrence of rank reversals, frequent early sex change, and context-dependent growth patterns demonstrates that social control is inherently limited in this system, likely due to its spatially structured and non-cohesive nature, as well as to the lack of threat of eviction. These findings call for a revision of classical models of sex change, which typically assume effective and continuous dominant control. Instead, future theoretical frameworks should explicitly incorporate variation in the degree of social control and consider how spatial structure and ecological context constrain the ability of dominants to regulate subordinates.

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Supplementary Materials for Chapter 2

Supplement 1: Specific numbers of cleaner wrasse per site

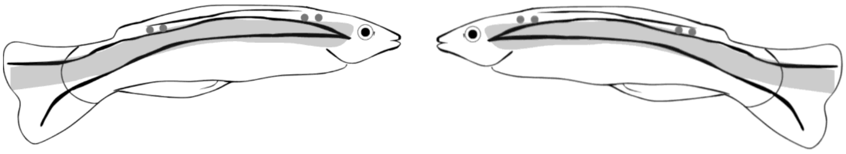


Figure S1.1: Illustration of the four locations for VIE.

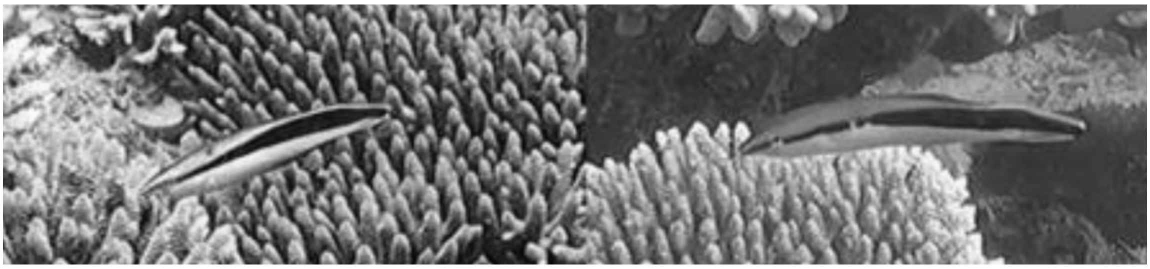


Figure S1.2: Examples of two individuals that can be recognized without VIE.

Table S1: Total number of focal cleaner wrasses at the 8 sites. This table summarizes he total number of tagged (VIE) and non-tagged (No VIE) for the 8 sites: Mermaid East (ME), Mermaid West (MW), Watson (W), Clam Garden (CG), Osprey (O), Horseshoe (H), Loomis (LU), and Attached Bommie (AB).

Site	**Adult Males**		**Adult Females**		**Juveniles**	**Total**	**Sex changers**
	VIE	No VIE	VIE	No VIE	VIE		
ME	3	1	45	5	34	88	6
MW	6	0	29	10	28	73	7
W	3	3	31	8	19	64	4
CG	5	1	31	9	12	58	5
O	2	3	33	10	19	67	7
H	6	0	38	17	18	79	4
LU	3	1	18	9	16	47	5
AB	5	5	22	13	19	64	4
	33	14	247	81	165	540	42
Total	47		328		165	540	42

Supplement 2: Stereo camera sizing error

We measured the size of each focal fish every month, using two GoPro Hero 8 cameras mounted in a photogrammetric underwater stereo camera system (Seager 2006). Sizing footage was analyzed using Event Measure (Seager 2006), a software enabling 3d length measurements. This method relies on prior calibration of the stereo camera system performed by the CAL software (Seager 2006). Utilizing a stereo camera system enhances accuracy and precision compared to visually estimating fish size (Michael et al. 2011). The error of this software is known to be around 1-2mm (Euan et al. 2010). To further assess the accuracy of the stereo camera system for our study, a calibration bar with three known distances was used to measure the system's error. Measurement error was ± 1.13mm using the calibration bar and ± 1.81mm of wild cleaner fish due to movement and growth between measurements (Figure S2, Table S2).

The overall mean error obtained with the toolbar was ± 1.13mm. Because measuring a moving object is more challenging, the software's accuracy was then investigated by comparing the stereo camera measurements of fish longer than 70cm with manual size measurements taken less than 30 days prior. This method provided an average error of ± 1.81mm. Attempts were made to obtain size measurements using the stereo system within 1 week of the fish being manually measured post-capture. However, this proved challenging, as the fish required more time to re-acclimate to human presence and often swam too quickly or attempted to escape, making accurate measurements difficult within this short time frame. Nevertheless, the errors associated with our fish measurements did not show a significant increase in variance (variance = 2.324) compared to those observed with the calibration toolbar (variance = 2.264). This suggests that the software's measurement error remains consistent when applied to real fish. The positive shift in the median error for the fish measurements (median = 1.48 mm) reflects the fish's natural growth over the 30 days between the two measurements. This consistency in error variance across both methods indicates that the software performs reliably for measuring wild fish.

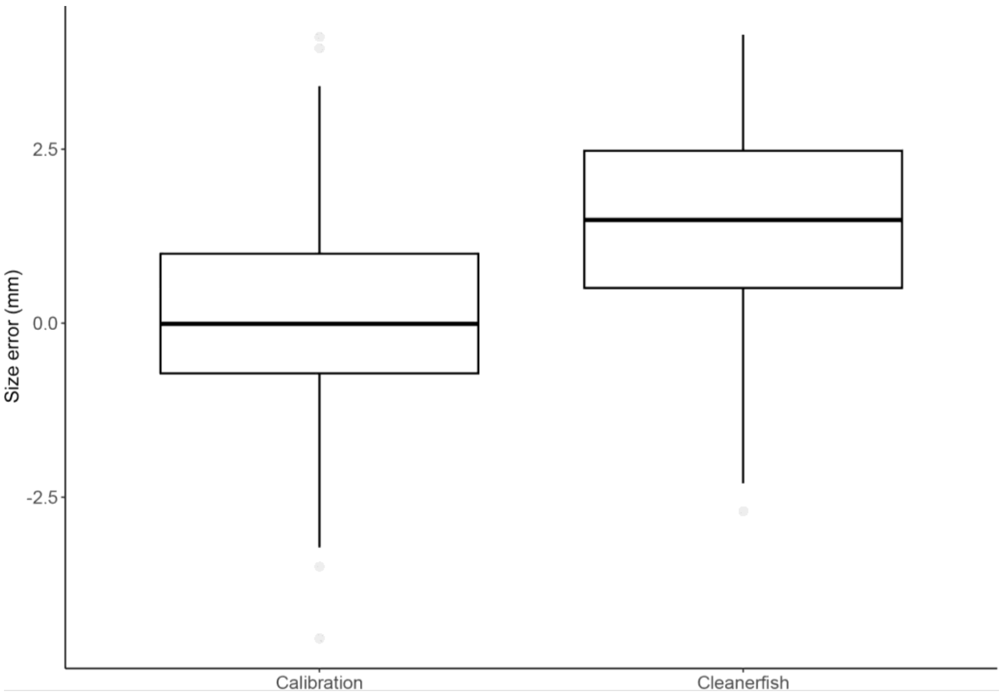


Figure S2: Sizing error using the calibration tool and the focal cleaners. The following figure shows the size error of the software obtained using sizing focal cleaners (“Cleanerfish”) measured 30 days from their manual sizing, and using the objects of known size (“Calibration”).

Table S2: System’s errors obtained with the different methods.

Method	**Mean Error (mm)**
Small	± 0.981
Medium	± 1.08
Large	± 1.37
General Tool	± 1.13
Fish	± 1.81

Supplement 3: Model Details and Assumption Checks

Table S3.1: Glossary for tables 4.2 and 4.3.

Term	Definition
Days	Days to sex change
Density	Adult cleaner fish reef density within a deme (per 150m^2)
Females	Number of adult females in a Harem
GR	Growth rate (mm/month)
ID	Cleaner ID used as a random factor to control for repeated measures
Interaction	Total time spent with the male (in seconds over a 20-minute video)
Initial Size	The size measured approximately 30 days before sex change for the female phase, and the size at sex change for the male phase
LifeHistory	Sex changer or non-sex changer
Migration	If the fish migrated to another harem (yes or no) before their sex change
Period	Before and after upgrading the cleaning station
Prop	Proportion
Scenario	Early or standard sex change
Size	Size of the cleaner fish (TL in mm)

Table S3.2: Model Description.

Model	Description
1.1	Tests differences between observed and expected proportions of aggression directed toward adjacent individuals, taking only males into account
1.2	Tests differences between observed and expected proportions of aggression directed toward adjacent individuals, accounting only for females (Alpha, Beta, and Gamma).
2	Examines the effect of sex change on growth rate.
3	Examines the effect of rank and cleaning station upgrade on growth rate.
4	Examines link between sex change scenario (early, standard) and social system
5	Investigate whether sex change in the presence of the male is associated with a reduction of social interactions (duration in seconds) with the latter.
6	Tests whether a specific growth strategy increases the likelihood of sex change.
7	Investigate the size at sex change in migrants versus non-migrants across sex change scenarios.
8	Examines what determines a linear and branching social system
9	Investigates a correlation between number of females in a harem and adult cleaner reef density
10	Examines whether reef density influences the proportions of different growth strategies.
11	Assesses how reef cleaner density and sex change scenario affect size at sex change.

Table S3.3: Model Summary.

Model	Type	Family	Challenge	Formula	Sample Size
1.1	Wilcoxon test	-	Non-normality	Prop, expected, paired = T	N = 47, Cleaners= 47
1.2	Wilcoxon test	-	Non-normality	Prop, expected, paired = T	N = 73, Cleaners = 69
2	LMER	Gaussian	Right Skew	log(GR)~Sex + Scenario + initial-Size+ Sex:Secnario + Sex:Initial_Size + (1|ID)	N = 66; Cleaners = 33
3	LMER	Gaussian	Right skew	Log(GR+0.3)~Period+(1|ID)	N = 38; Cleaners = 19
4	Chisq test			Chisq.test(table(Scenario,System)	2x2 table
5	LMER	Gaussian	Long tail	log(0.3 +Interaction) ~ Scenario * days + (1|Site/ID)	N = 70 (Alive: 34; Dead: 38); Cleaners = 23
6	GLM	Binomial (logit)	Bounded proportions	Prop ~ Strategy*LifeHistory, weights	N = 48; Sites = 8; Strategy = 3; LifeHistory = 2
7	LM	Gaussian	-	Size ~ Migration * Scenario	N = 42
8	GLM	Binomial (logit)	-	System~Females*Density	N=40
9	GLM	Negative Binomial (log)	-	Females~Density	N=40
10	GLM	Binomial (logit)	Bounded proportions	Prop~ Strategy * Density, weights	N = 24; Sites = 8; Strategy = 3
11	LM	Gaussian	-	Size ~ Density * Scenario	N = 42

Supplement 4: Details for Model 1

Table S4.1: Wilcoxon signed rank test with continuity correction for Model 1.

Model	Sex	V	P value
M1.1	Males	730.5	0.038
M1.2	Females	2109.5	2.845e-05
	Alternative Hypothesis: true location shift is not equal to 0		

Supplement 5: Details for Model 2

Table S5.1: Emmeans Contrasts, for Model 2.

Initial Size	Ratio	SE	Df	T ratio	P value
		Contrast Female / Male			
60	0.903	0.456	1	-0.201	0.8417
61	0.932	0.447	1	-0.146	0.8847
62	0.962	0.436	1	-0.084	0.9332
63	0.993	0.425	1	-0.015	0.9878
64	1.025	0.413	1	0.062	0.9506
65	1.059	0.400	1	0.150	0.8814
66	1.093	0.387	1	0.250	0.8040
67	1.128	0.373	1	0.364	0.7184
68	1.164	0.359	1	0.493	0.6252
69	1.202	0.345	1	0.641	0.5261
70	1.241	0.331	1	0.809	0.4247
71	1.281	0.317	1	0.998	0.3261
72	1.322	0.306	1	1.207	0.2367
73	1.364	0.296	1	1.432	0.1622
74	1.408	0.290	1	1.664	0.1062
75	1.454	0.288	1	1.889	0.0682
76	1.501	0.292	1	2.090	0.0449
77	1.549	0.301	1	2.250	0.0316
78	1.599	0.318	1	2.361	0.0247
79	1.651	0.342	1	2.421	0.0215
80	1.704	0.372	1	2.438	0.0207

Re75sults averaged over the levels of Scenario, Degrees of freedom method: Kenward-Roger. Results are given on the log scale (not the response one).

Table S5.2: Analysis of Deviance – Type II Wald Chi-square Tests, for Model 2.

Term	Chisq	Df	Pr (> Chisq)
Sex	4.9934	1	0.025442 *
Scenario	0.3043	1	0.5811872
Initial-Size	12.2010	1	0.0004777***
Sex : Scenario	0.0781	1	0.7798972
Sex : Initial-Size	1.2521	1	0.2631450

Supplement 6: Details for Model 3

Table S6.1: Analysis of Deviance – Type II Wald Chi-square Tests, for Model 3.

Term	Chisq	Df	Pr (> Chisq)
Period	6.8265	1	0.00891 **

Table S6.2: Emmeans contrasts for Model 3.

Contrast	Estimate	SE	Df	T ratio	P value
Period	0.394	0.151	19	2.613	0.0171

Supplement 7: Details for Model 4

Table S7: Pearson's Chi-squared test with Yate's continuity correction, for Model 4.

X-squared	Df	P value
14.146	1	0.0001692

Supplement 8: Details for Model 5

Table S8.1: Analysis of Deviance – Type II Wald Chi-square Tests, for Model 5.

Term	Chisq	Df	Pr (> Chisq)
Scenario	7.9220	1	0.004884 **
Days	15.2425	1	9.455e-05 ***
Scenario : Days	0.0143	1	0.904960

Table S8.2: Emmeans contrasts, for Model 5.

Scenario	Emmean	Back transformed Emmean	SE	Df
Early	1.088395	2.042953	0.7143962	10.66
Standard	3.156595	23.190463	0.6916696	9.93

Supplement 9: Details for Model 6

Table S9.1: Analysis of Deviance – Type II Wald Chi-square Tests, for Model 6.

Term	LR Chisq	Df	Pr (> Chisq)
Strategy	14.591	2	0.0006786 ***
LifeHistory	0	1	0.9999998
Strategy : LifeHistory	18.171	2	0.0001133 ***

Table S9.2: Emmeans Contrasts for Model 6.

	Estimate	SE	Df	Z ratio	P value
Average	-0.0747	0.334	Inf	-0.224	0.8229
Fast	-0.9721	0.335	Inf	-2.898	0.0038
Slow	1.2809	0.455	inf	2.814	0.0049
Results are given on the log odd ratio scale (not response one)					

Supplement 10: Details for Model 7

Table S10: Analysis of Deviance – Type II Tests, for Model 7.

Term	Sum Sq	Df	F value	Pr (> F)
Migration	211.60	1	5.3264	0.02654 *
Scenario	0.98	1	0.0246	0.87632
Migration : Scenario	37.81	1	0.9517	0.33545
Residuals	1509.58	38		

Supplement 11: Details for Model 8

Table S11: Analysis of Deviance – Type II Wald Chi-square Tests, for Model 8.

Term	LR Chisq	Df	Pr (> Chisq)
Females	18.5853	1	1.625e-05 ***
Density	2.9747	1	0.08458 .
Females:Density	0.1383	1	0.71003

Supplement 12: Details for Model 9

Table S12: Analysis of Deviance – Type II Tests, for Model 9.

Term	LR Chisq	Df	Pr (> Chisq)
Density	0.15478	1	0.694

Supplement 13: Details for Model 10

Table S13.1: Analysis of Deviance – Type II Tests, for Model 10.

Term	LR Chisq	Df	Pr (> Chisq)
Strategy	16.760	2	0.0002294 ***
Density	0	1	0.999999
Strategy : Density	19.787	2	0.05e-05 ***

Table S13.2: Emmtrends for Model 10.

	Density trend	SE	Df	Asymp LCL	Asymp UCL
Average	0.151	0.123	Inf	-0.0131	0.315
Fast	0.161	0.0907	Inf	-0.0168	0.339
Slow	-0.346	0.996	inf	-0.5417	-0.151

Supplement 14: Details for Model 11

Table S14: Analysis of Deviance – Type II Tests, for Model 11.

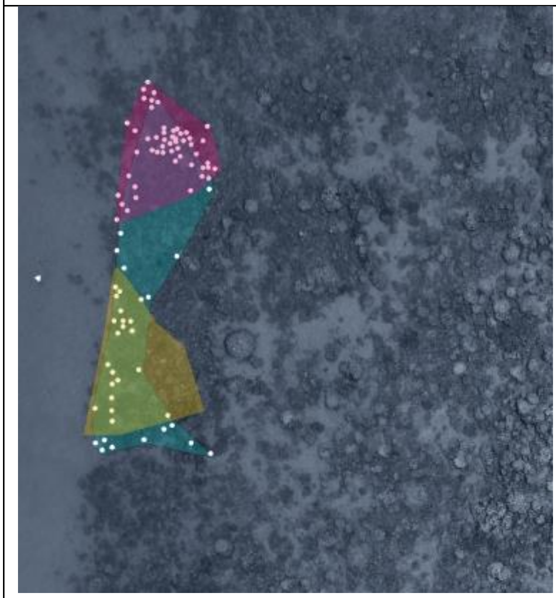
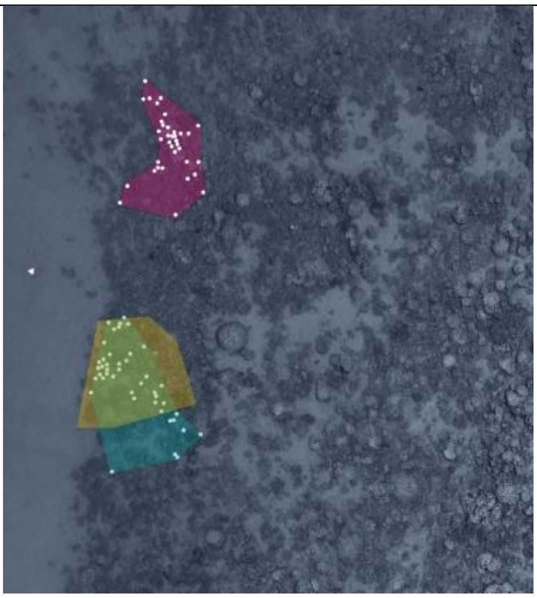
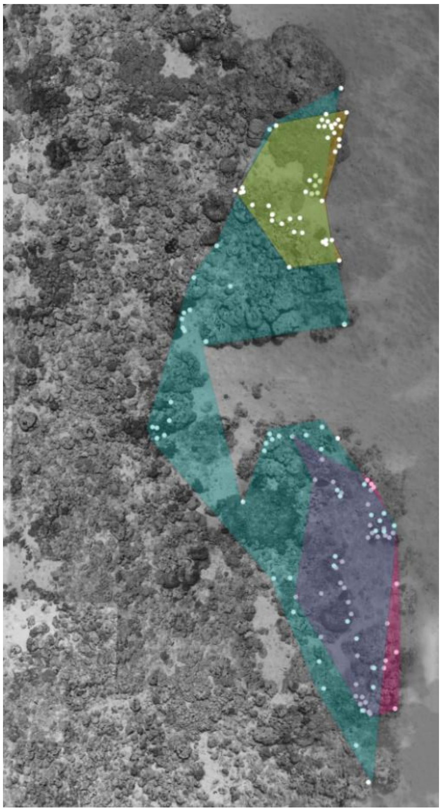
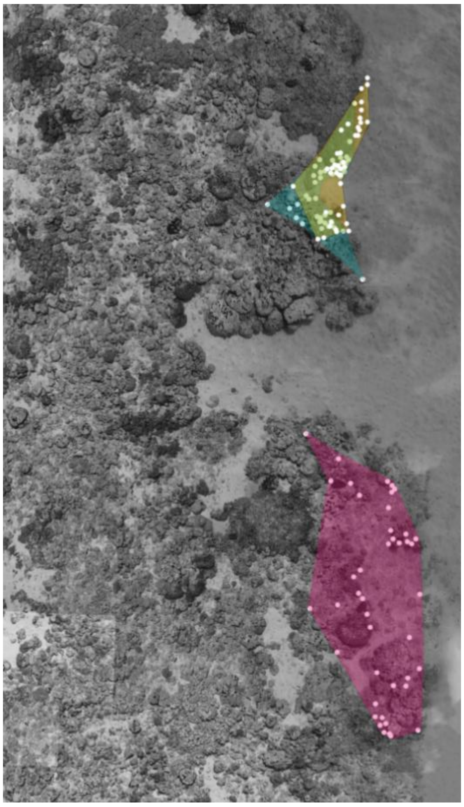
Term	Sum Sq	Df	F value	Pr (> F)
Density	323.95	1	9.3530	0.004065 **
Scenario	6.71	1	0.1937	0.662349
Density : Scenario	90.46	1	2.6117	0.114351
Residuals	1316.15	38		

Supplement 15: Details on sex changers in the alive and dead scenario

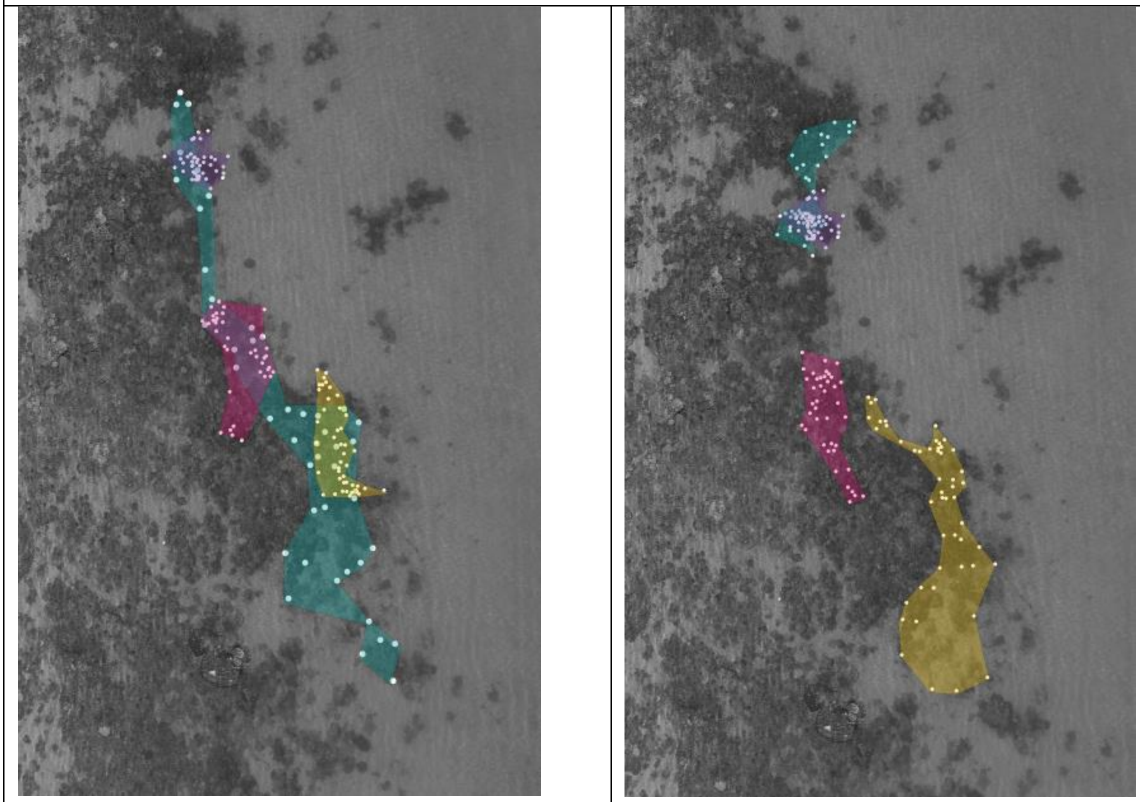
Table S15.1.1: Information on the sex changing females in the alive scenario.

Sex Changer	Social System	Migration to periphery	Codominant females	Map appendix
Alive Scenario				
CGRFYY	Branching	No	2	S15.1a
HLMRR	Linear	Yes	NA	S15.1b
LUAnninuccia	Linear	Yes	0	S15.1c
LUWhiteWoman	Branching	No	2	S15.1d
MLApprentist2	Linear	No	0	S15.1e
MLLFYR	Linear	Yes	0	S15.1f
MLLMP	Branching	No	4	S15.1g
MLNewRFWW	Branching	No	4	S15.1g
MLRMYY	Branching	No	4	S15.1g
MRLMWW	Branching	Yes	2	S15.1h
MRPuntino	Branching	No	3	S15.1i
MRRMGR	Branching	No	3	S15.1i
MRRMRY	Branching	No	3	S15.1j
ONewBBFemale	Branching	No	3	S15.1k
ORFPY	Branching	Yes	3	S15.1k
OWhiteNinja	Branching	No	2	S15.1l
WLMGG	Branching	No	2	S15.1m
WRFYY	Branching	No	3	S15.1m

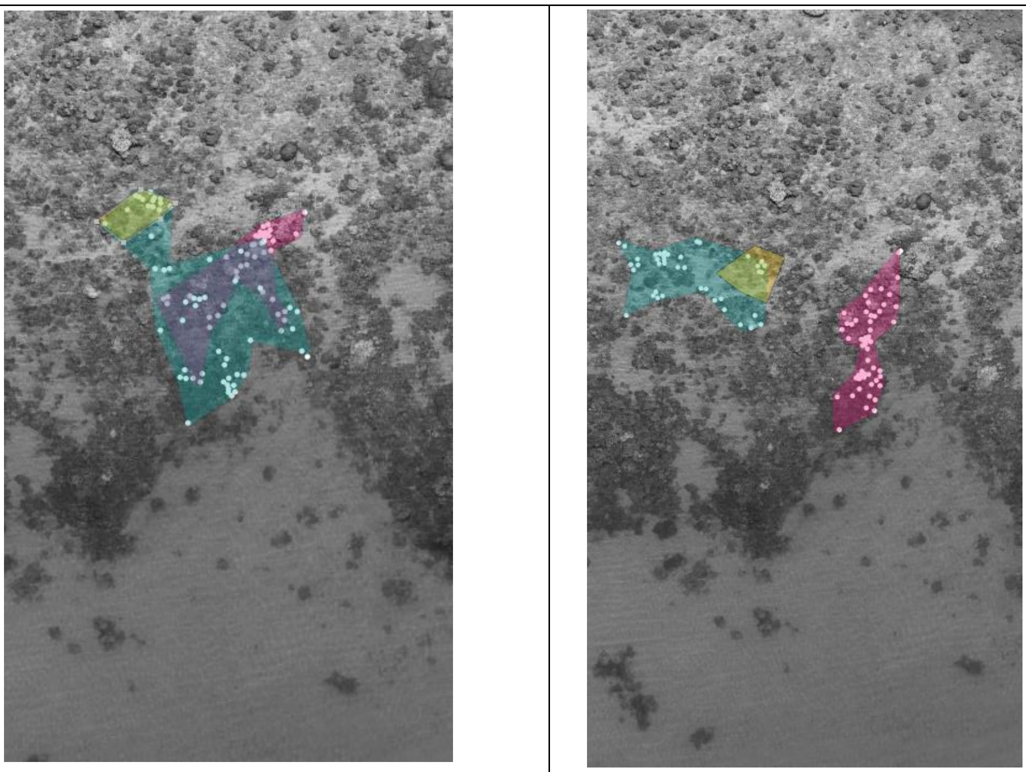
Table S15.1.2: Maps of Sex changing females and their male in the alive scenarios. The table shows the territories of the sex changer (in pink), her male (in blue) and potential co-dominant females (in yellow, purple), before (left side) and after (right side) the sex change event.

BEFORE SEX CHANGE	**AFTER SEX CHANGE**
S15.1a : CGRFYY	
	
S15.1d : LUWhiteWoman	
	

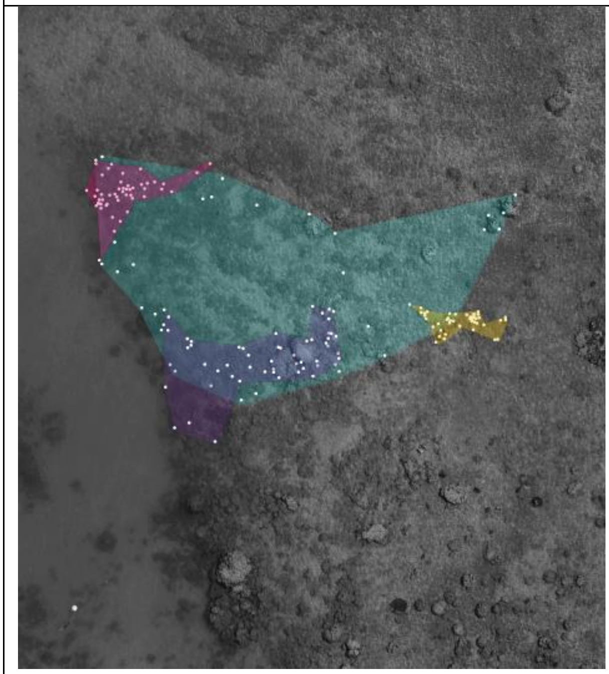
S15.1k : OnewBBFemale, ORFPY

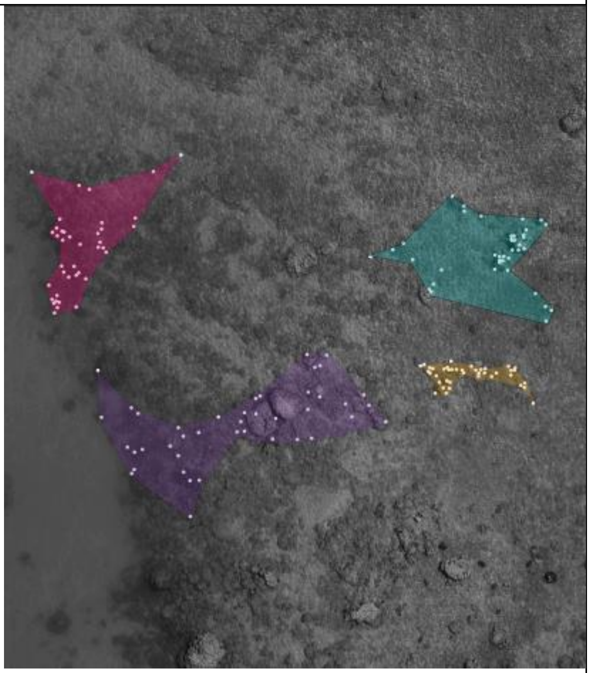


S15.1l : OWhiteNinja

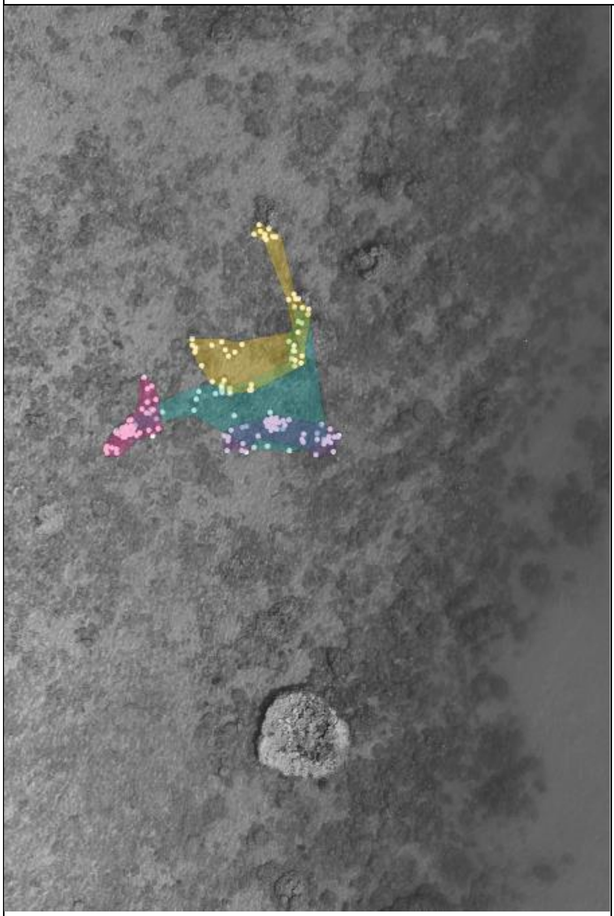


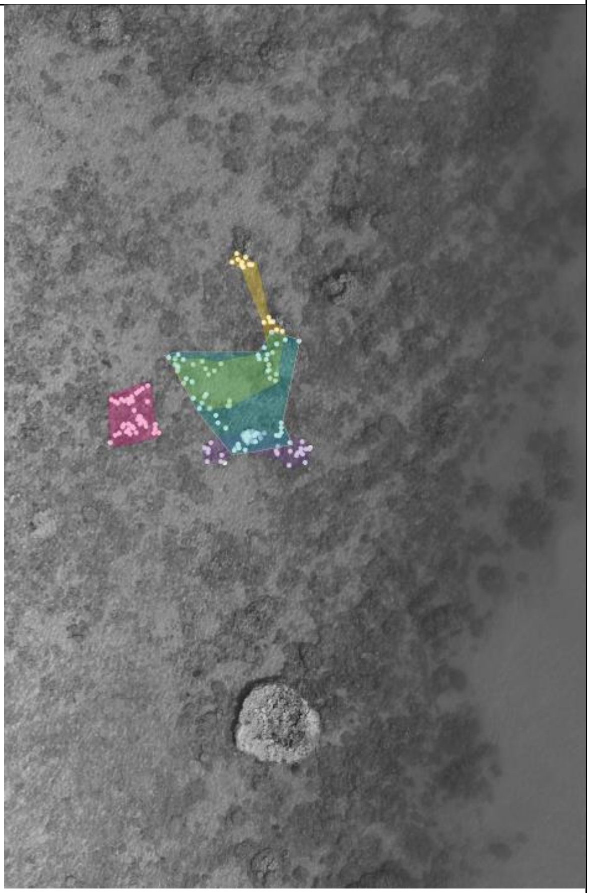
S15.1g: MLRFWW, MLLMP; MLRMYY



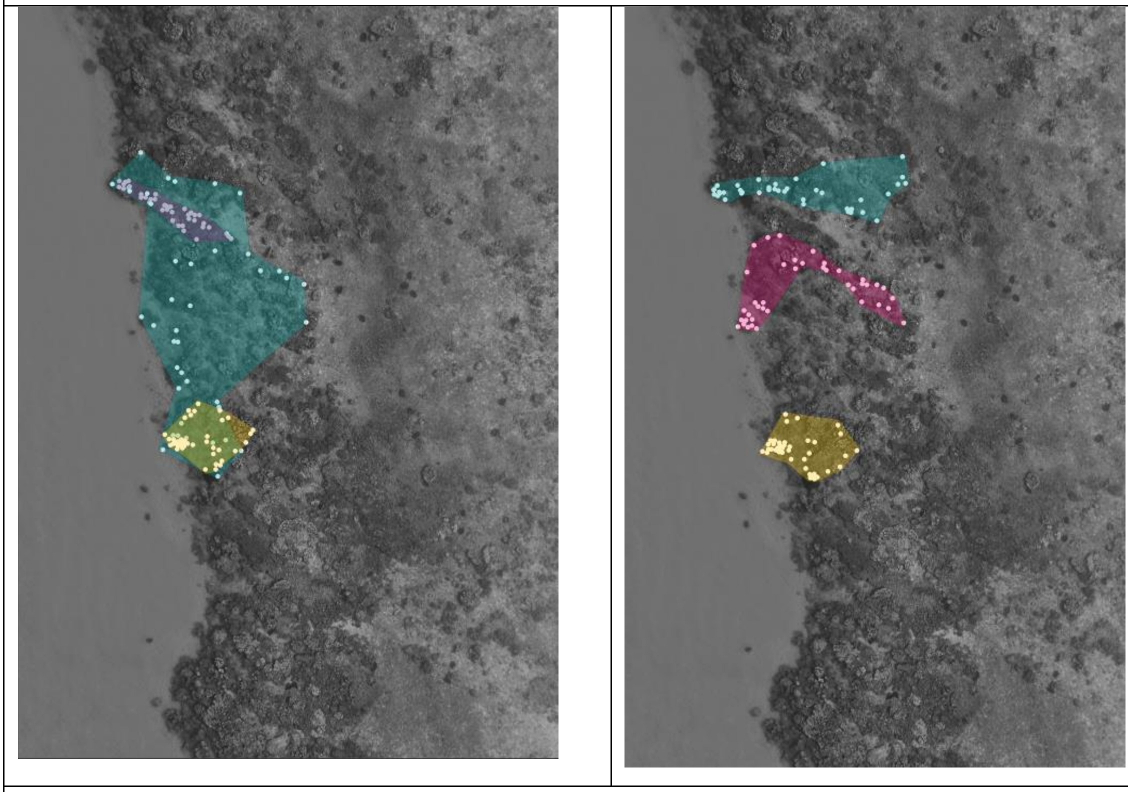


S15.1j: MRRMRY

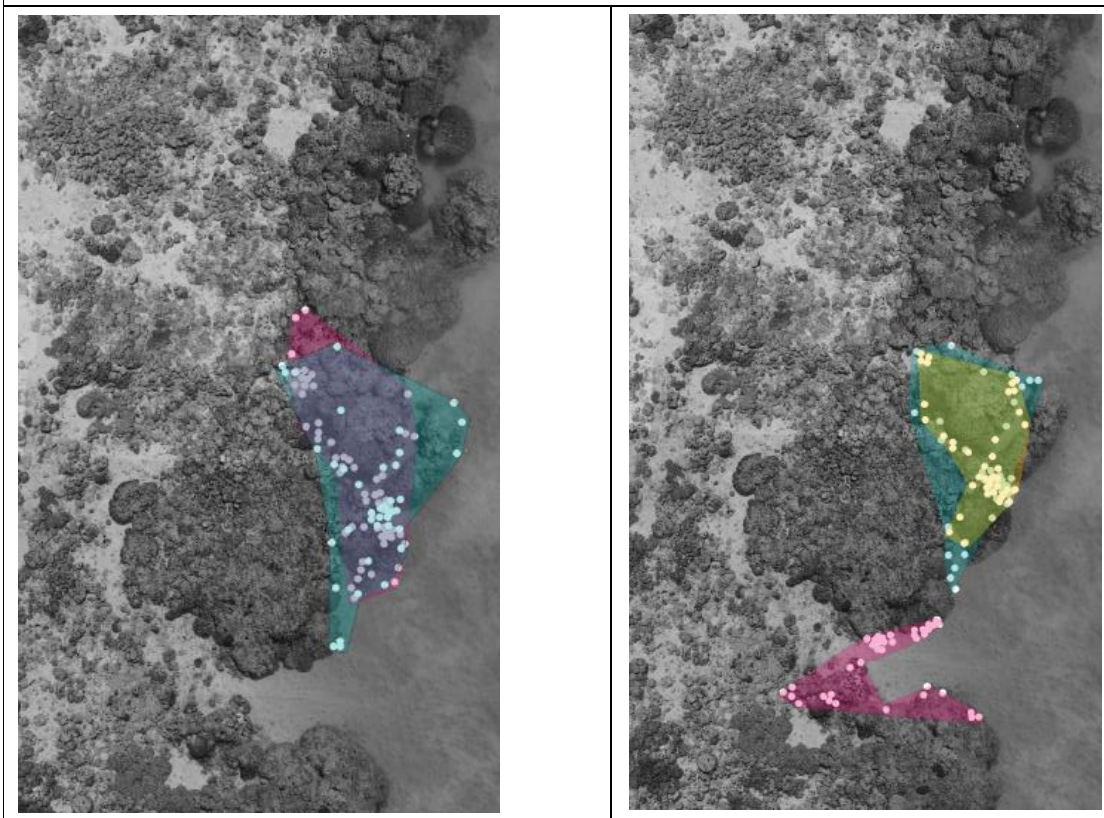




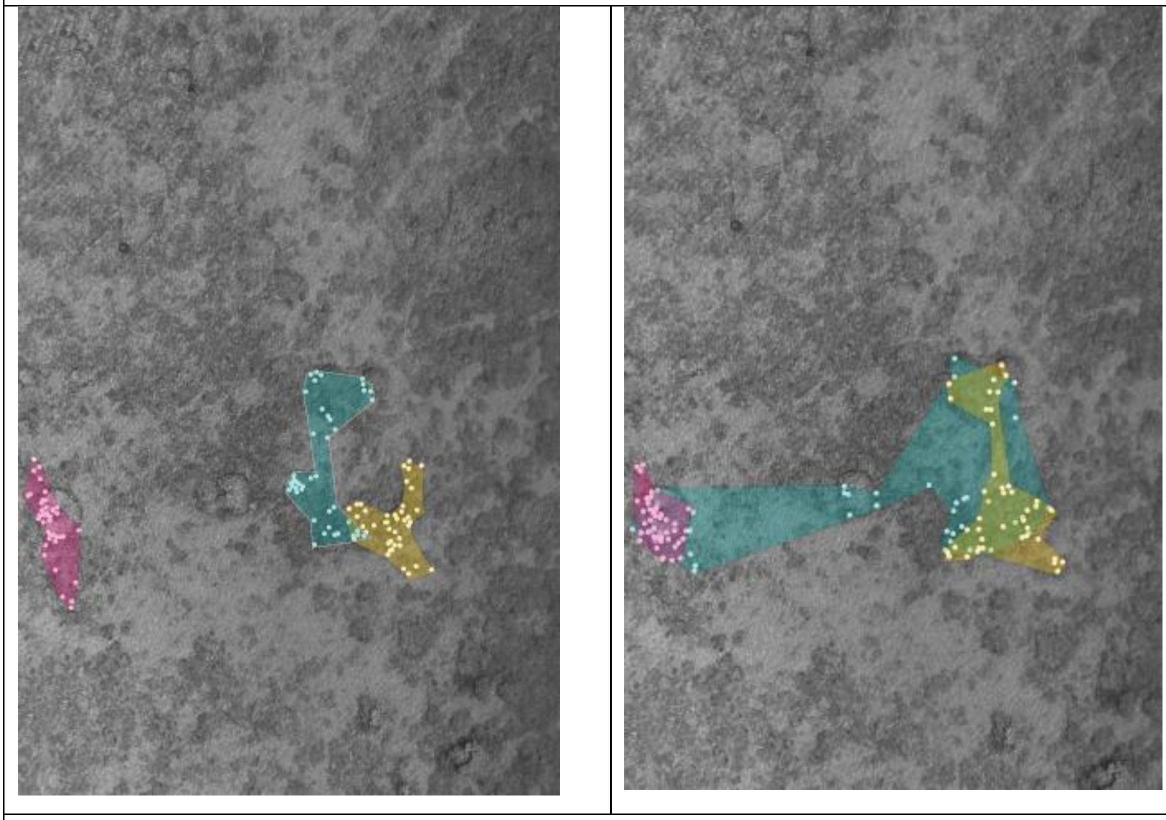
S15.1m: WRFYY, WLMGG



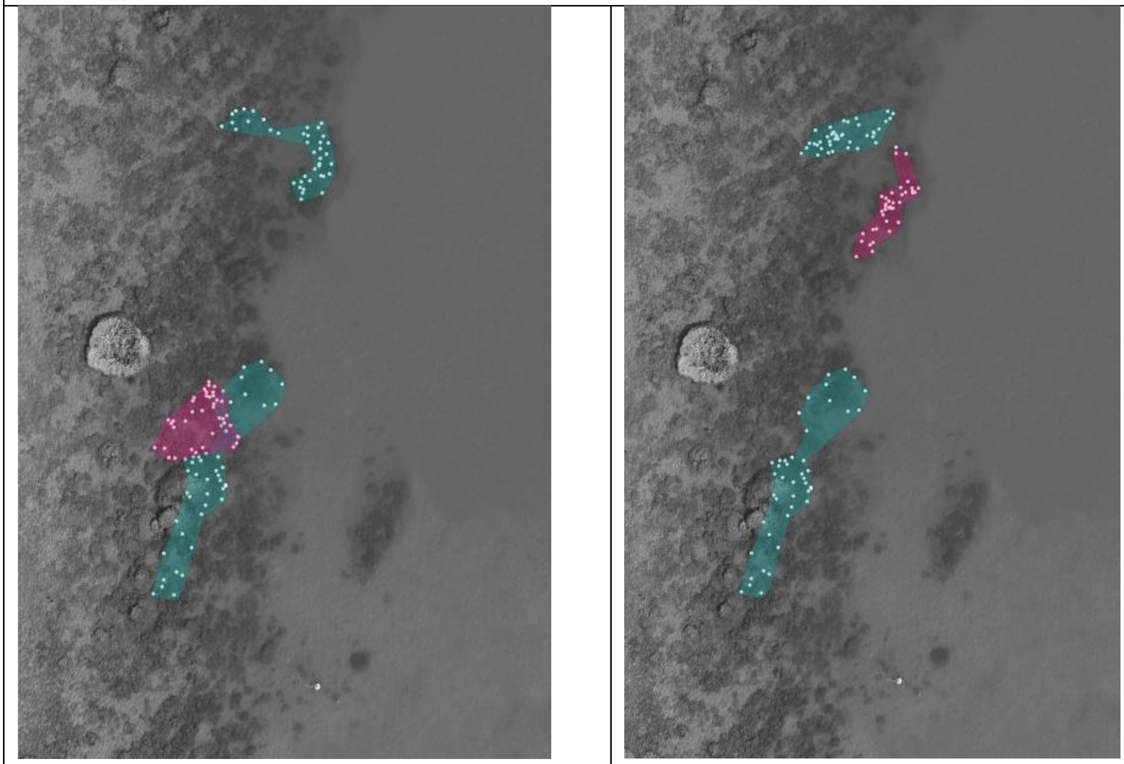
S15.1c: LUAnninuccia



S15.1i: MRPuntino, MRRMGR



S15.1h: MRLMWW



S15.1f: MLLFYR

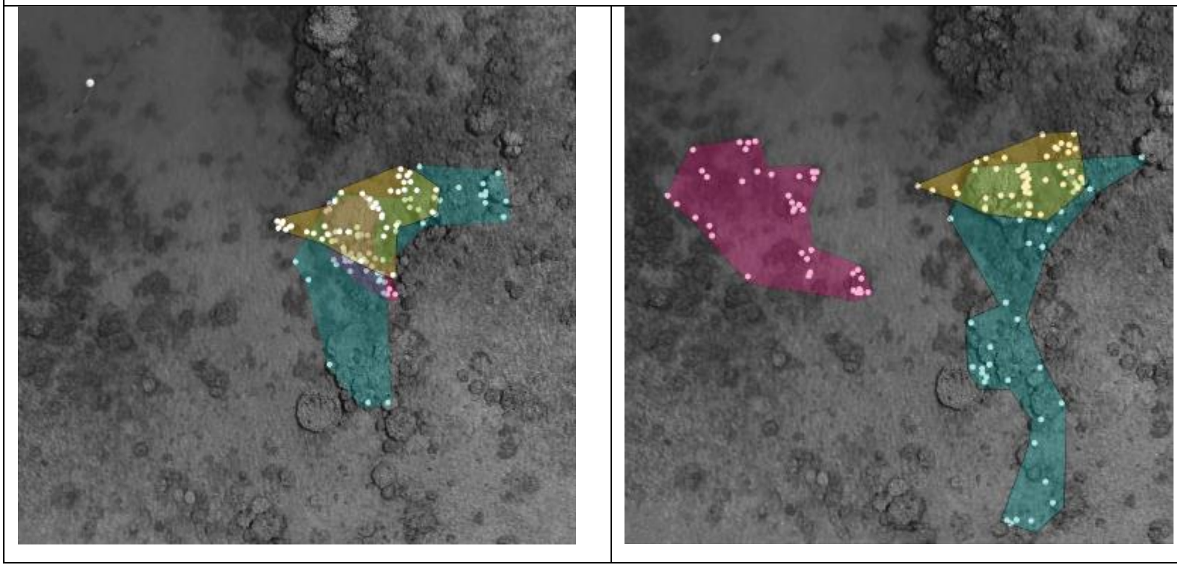
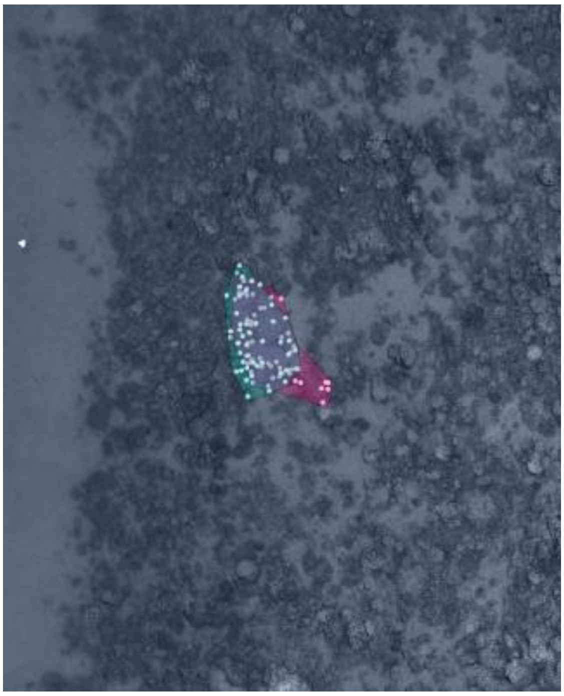
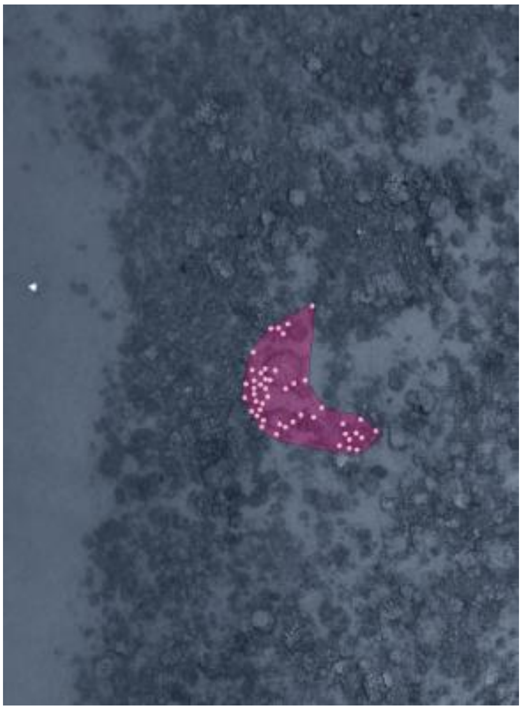


Table S15.2.1: Information on the sex changing females in the dead scenario.

Sex Changer	Social System	Migration to periphery	Codominant females	Map appendix
Dead Scenario				
CGLFGG	Linear	No	0	S15.2a
CGLFPY	Linear	No	0	S15.2b
CGMinnie	Linear	No	0	S15.2c
CGNewLFPP	Linear	No	0	S15.2d
HLFWW	Linear	No	0	S15.2e
HRMYY	Linear	No	0	S15.2f
Hyelcor	Linear	No	0	S15.2g
LUAnnFriend	Linear	No	0	S15.2h
LUBS2	Linear	No	0	S15.2i
LUWhitie	Linear	No	0	S15.2j
MBB2Alpha	Linear	No	0	S15.2k
MBIslGirl	Branching	No	2	S15.2l
MBLMPGFriend	Linear	No	0	S15.2m
MBWierdo	Branching	No	2	S15.2l
MLApprentist	Linear	No	0	S15.2n
MRAlphaRR	Branching	No	2	S15.2o
MRLMRY	Linear	No	0	S15.2p
MRNewLFWW	Branching	No	2	S15.2o
OLMPY	Linear	No	0	S15.2q
ORFGGMP	Linear	No	0	S15.2r
ORFPP	Linear	No	0	S15.2s
ORFWP	Linear	No	0	S15.2t
WLFPY	Linear	No	0	S15.2u
WSaladFemale	Linear	No	0	NA

Table S15.2.2: Maps of Sex changing females and their male in the dead scenario. The table shows the territories of the sex changer (in pink), her male (in blue) and potential co-dominant females (in yellow, purple), before (left side) and after (right side) the sex change event.

<table>
<tr><th>BEFORE SEX CHANGE</th><th>AFTER SEX CHANGE</th></tr>
<tr><td colspan="2">S15.2b : CGLFPY</td></tr>
<tr><td></td><td></td></tr>
<tr><td colspan="2">S15.2c: CGMinnie</td></tr>
<tr><td></td><td></td></tr>
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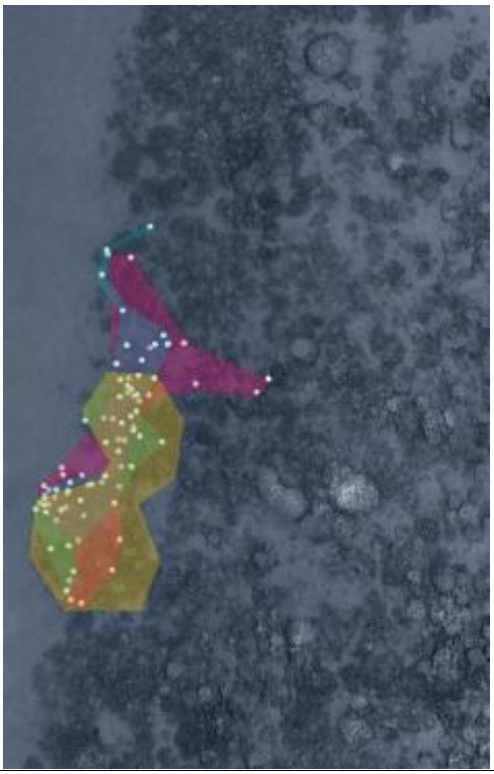
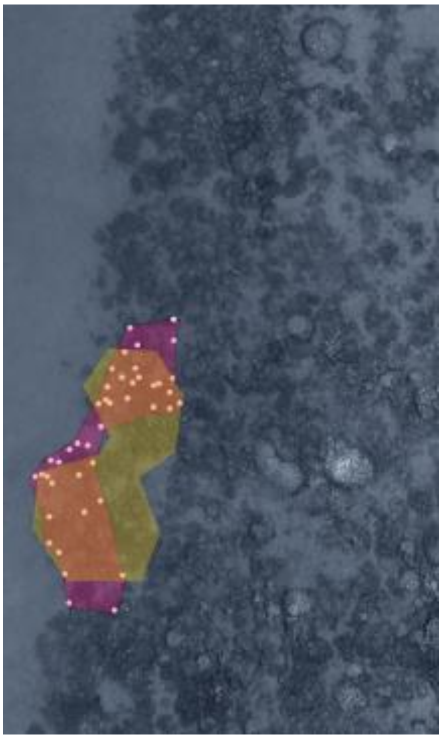
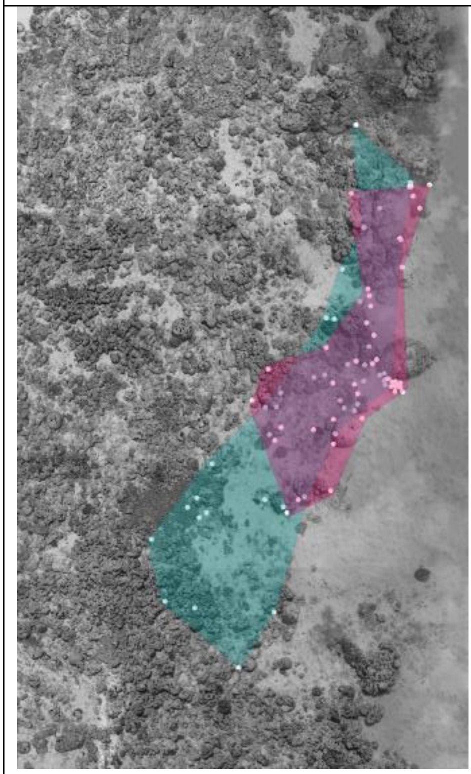
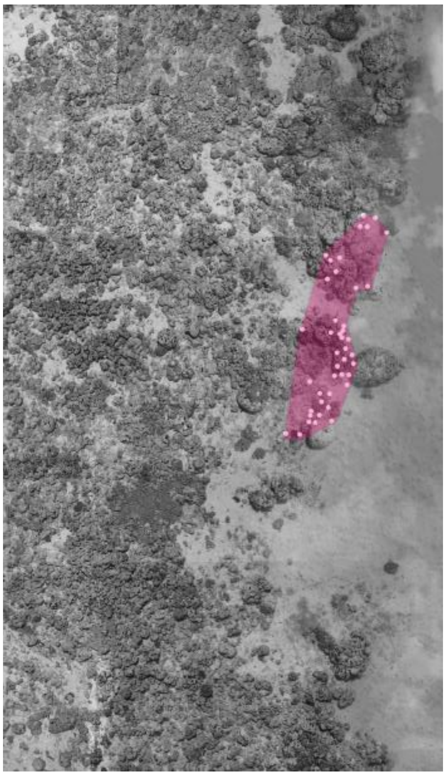
S15.2d: CGNewLFPP

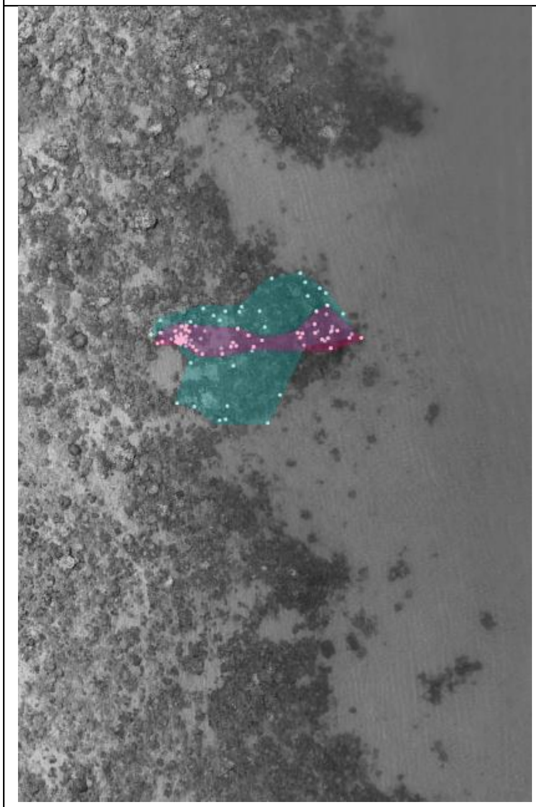
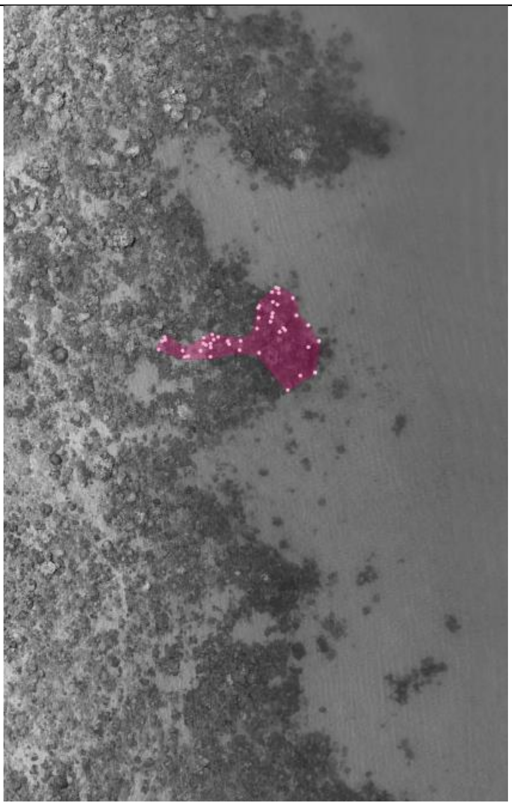
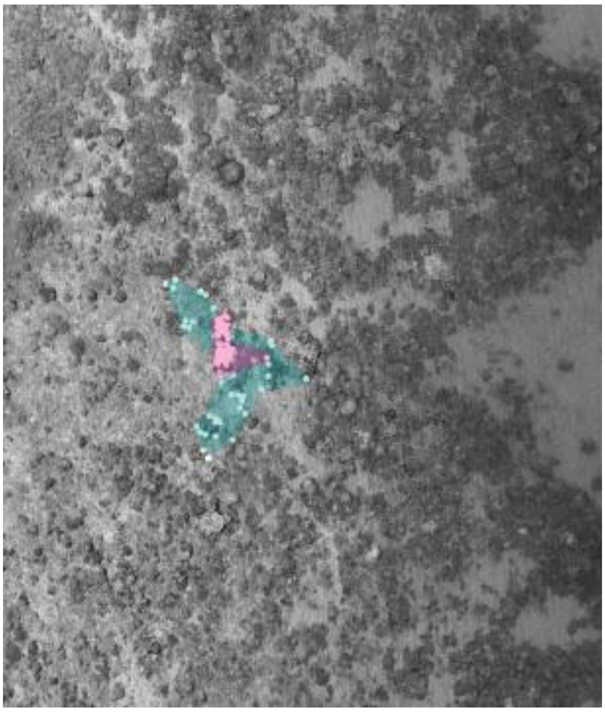
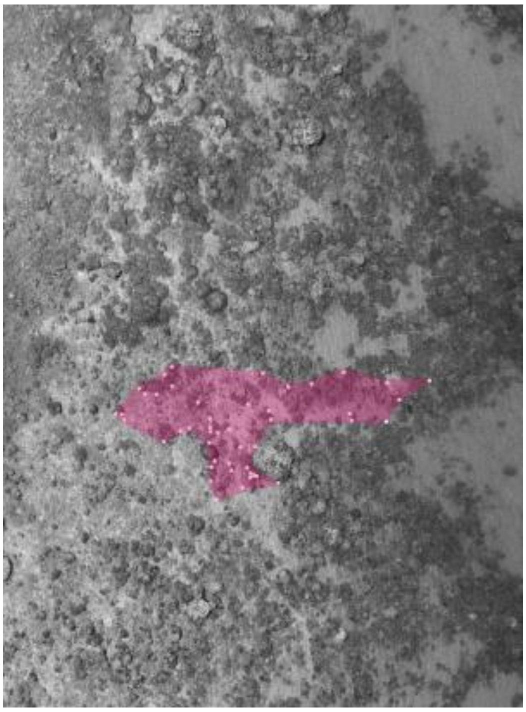


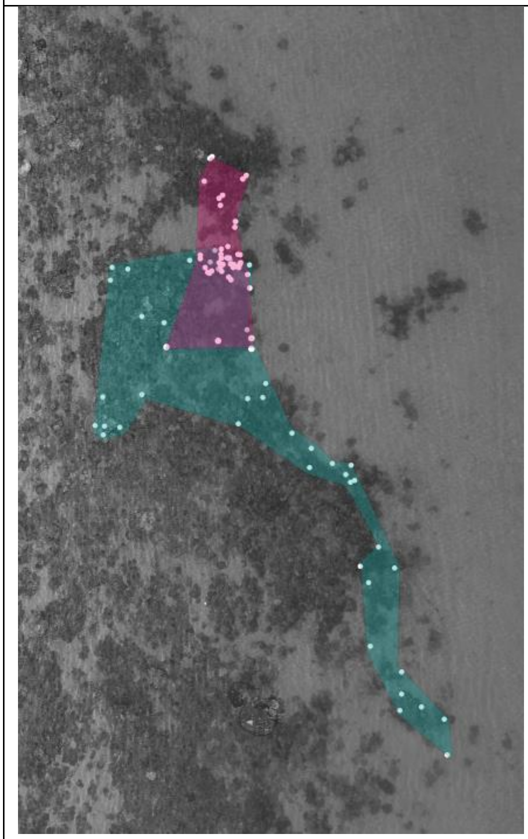
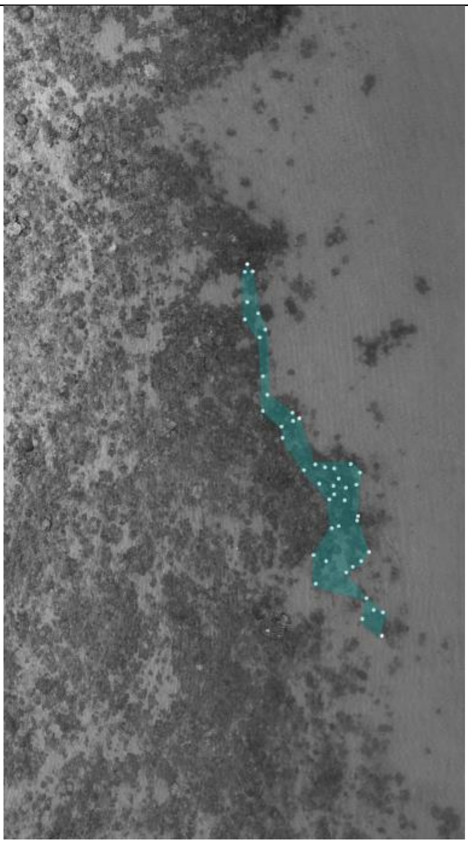
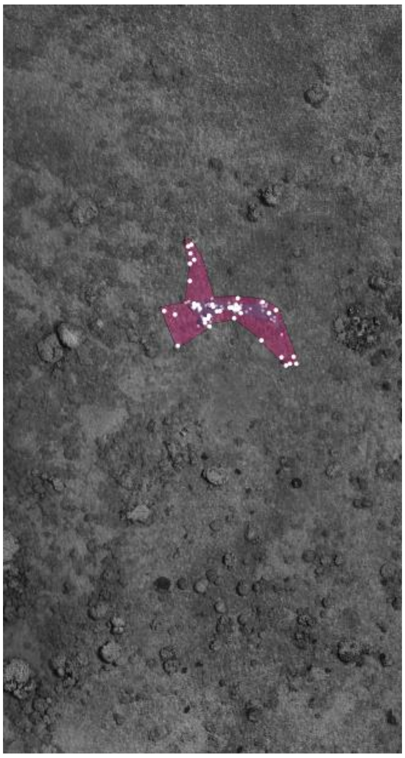
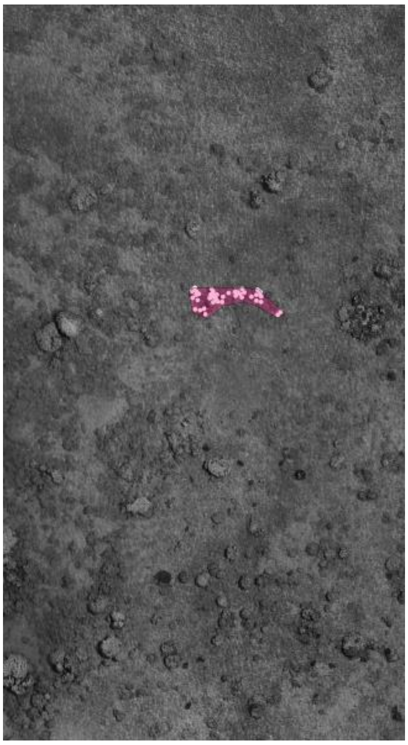


S15.2j: LUWhitie

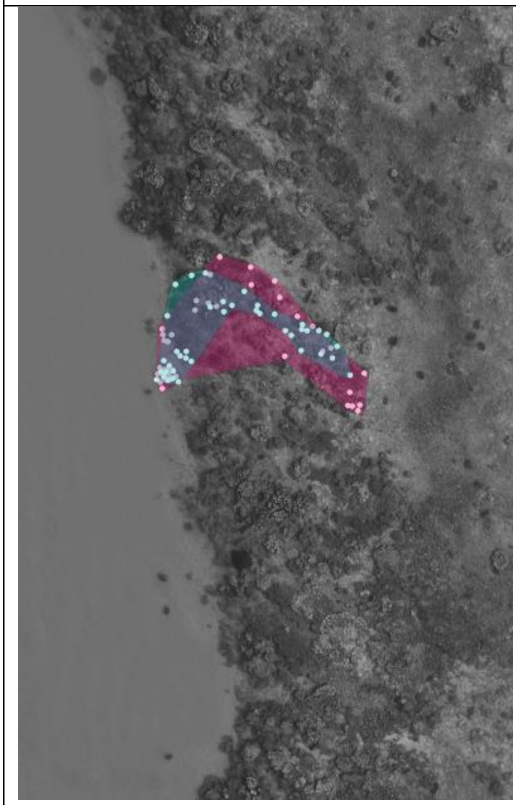


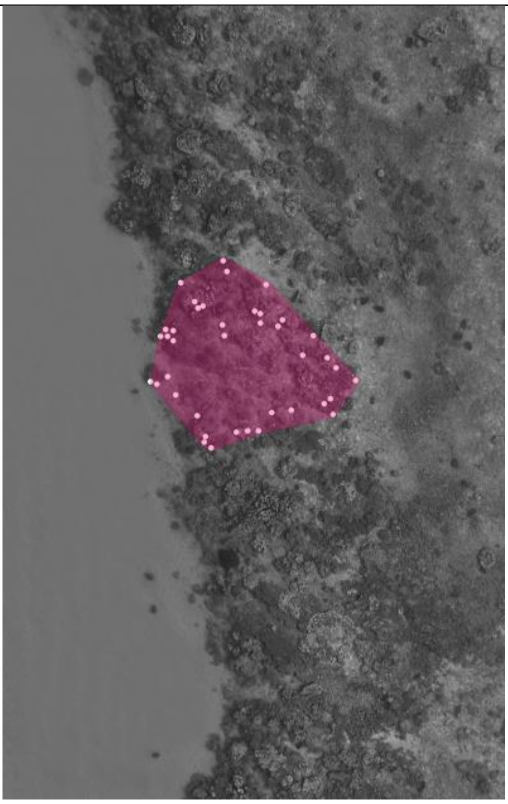


S15.2s : ORFPP	
	
S15.2r : ORFGGMP	
	

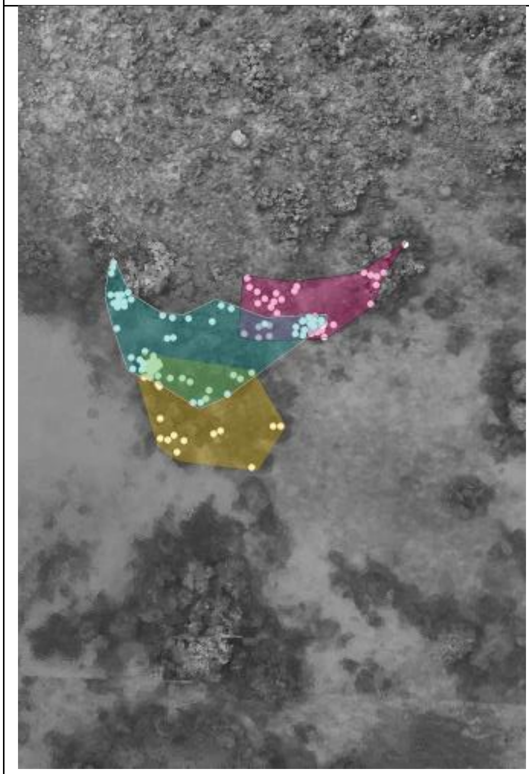
S15.2q : OLMPY	
	
S15.2n : MLApprentist	
	

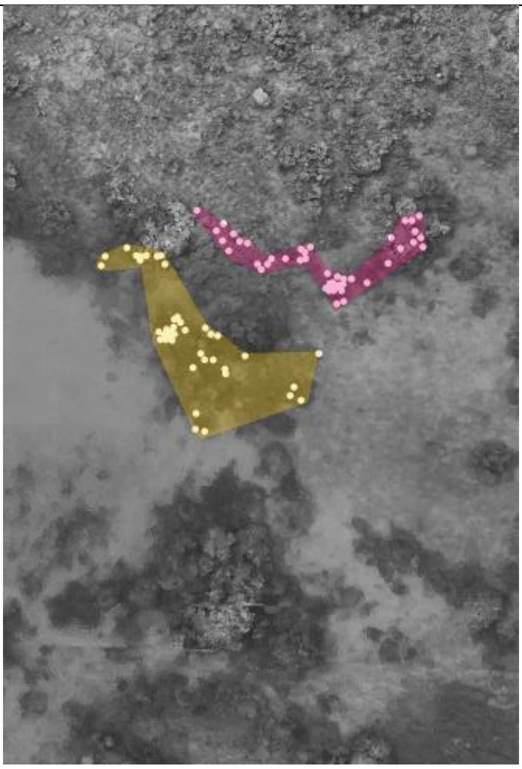
S15.2u : WLFPY



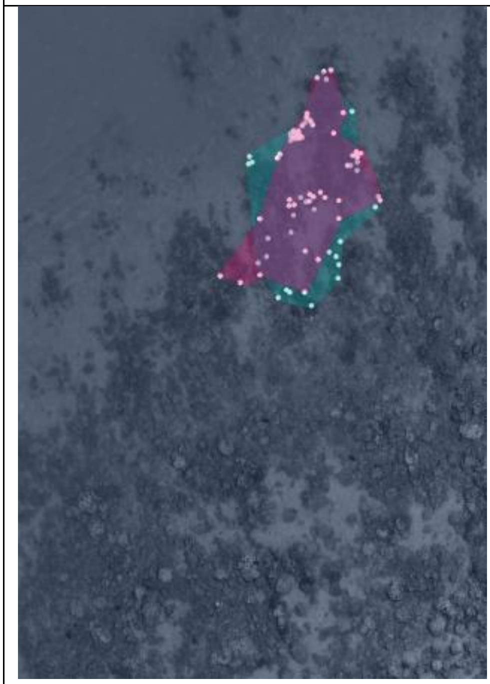


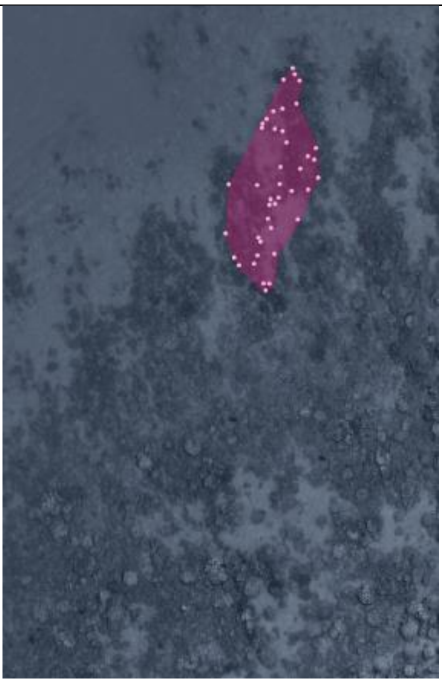
S15.2l : MBWierdo, MBIslGirl



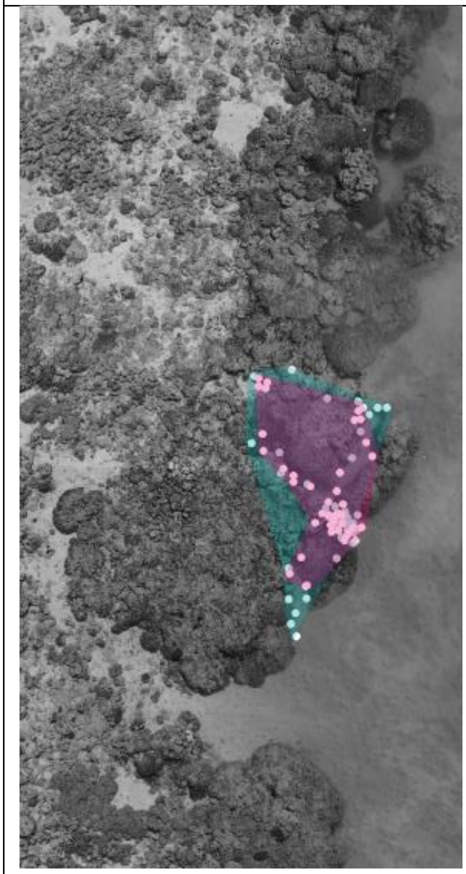


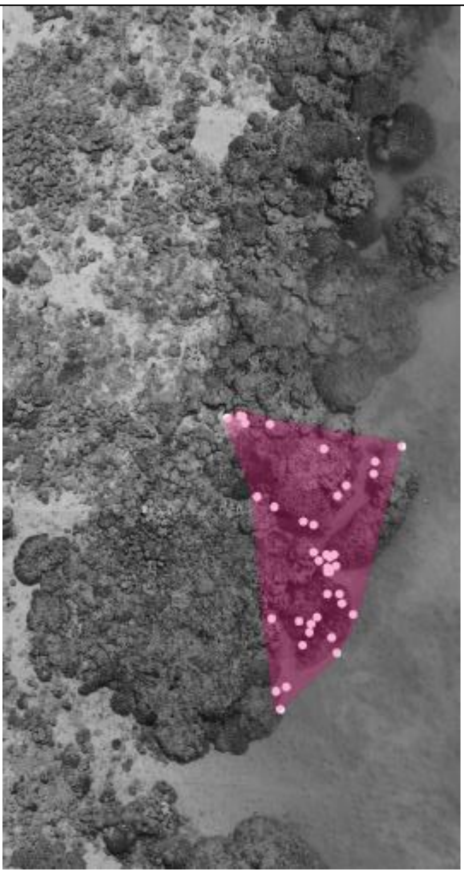
S15.2a : CGLFGG



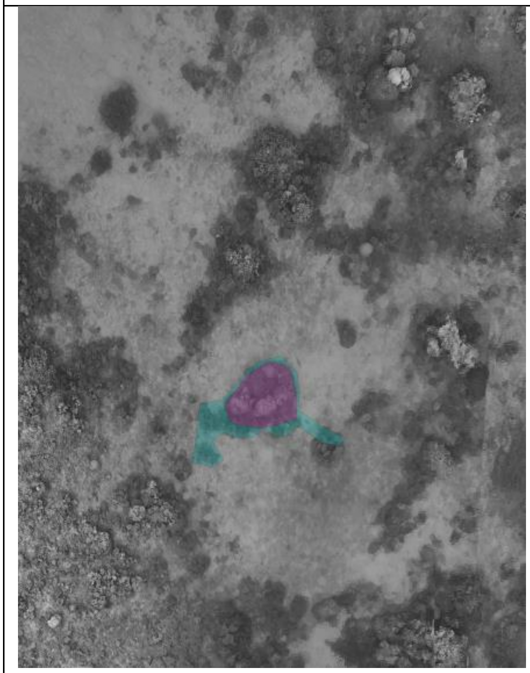


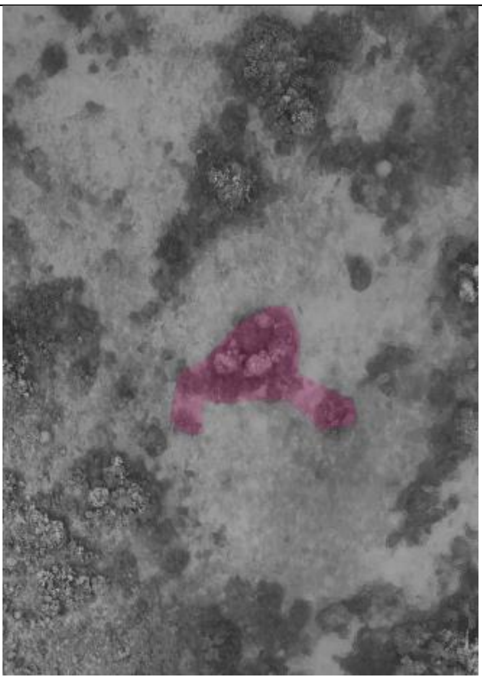
S15.2i : LUBlackSpot2



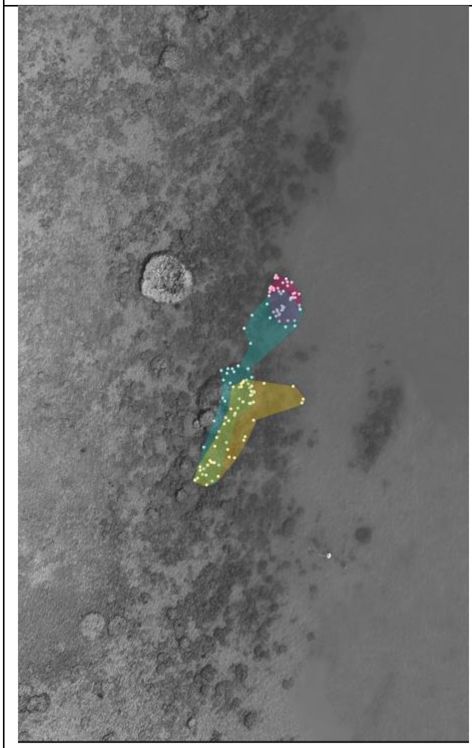


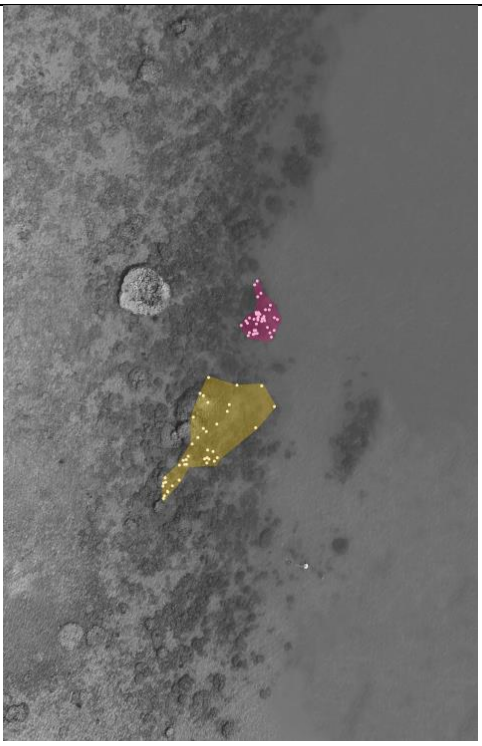
S15.2k : MBB2Alpha





S15.2o : MRAlphaRR, MRNewLFWW





Supplement 16: Migrant supplementary information

Table S16: Migrants information. The table details the number of juveniles and adult females (TL >= 50mm) gained by migrants after sex change.

Migrant	Sex Change Size	Nb Juveniles	Nb Adults	Social System
CGLFGG	75.5	1	1	Linear
CGNewLFPP	77.9	1	4	Linear
HLMRR	59.7	1	0	Linear
HRMYY	71	0	2	Linear
LUAnnFriend	80.9	1	1	Linear
LUBS2	89	0	5	Linear
MLApprentist	69.1	1	3	Linear
MLApprentist2	75	0	1	Linear
MLLFYR	65.5	2	0	Linear
MLNewRFWW	77	4	5	Branching
MRLMWW	77.7	2	2	Branching
MRNewLFWW	77.6	2	3	Branching
ONewBBFemale	73.9	3	3	Branching
ORFPY	68.9	3	0	Branching
WLFPY	72	1	1	Linear
LUAnninuccia	93.7	1	1	Linear

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Seager J. 2006. EventMeasure.

Chapter 3: Social control, not service quality, explains fast growth in the cleaner wrasse *Labroides dimidiatus*

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Manuscript information

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Author contributions

All authors contributed to the project design. LP conducted the fieldwork, performed data and statistical analyses, and led manuscript writing. RB supervised the project and contributed to conceptual development and revision of the manuscript.

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Abstract

Interactions between cleaner fish *Labroides dimidiatus* and client fish, from which cleaners remove ectoparasites and mucus, represent a textbook example of mutualism involving sophisticated strategic decision-making. However, cleaners must also face intraspecific social challenges within a size-based hierarchy, where the largest females may eventually change sex and become males with higher reproductive rates. Following 540 individuals over 11 months, we found that, contrary to expectations, slow-growing females spent more time cleaning and cheated more frequently, without causing more negative client responses than fast-growing females did. Instead, variation in growth was best explained by social factors: fast-growing individuals experienced reduced social control, while slow growers spent more time in proximity to dominant individuals. As there was no evidence that spawning activity affected growth patterns, it appears that fast growth as a viable strategy for becoming a male largely depends on the lack of control by dominants.

Keywords

Life-history, tradeoffs, *Labroides dimidiatus,* fast growth, cleaning mutualism, sex change.

Introduction

Sequential hermaphroditism (sex change) may evolve when reproductive success differs between the sexes across body size or age, such that one sex achieves higher fitness when small or young and the other when large or old (Ghiselin 1969; Warner 1975; Warner 1988b; Warner 1988a; Munday et al. 2006). Under these conditions, individuals can maximize lifetime reproductive success by functioning first as the sex with higher reproductive output at smaller sizes and later transitioning to the sex that achieves greater reproductive success at larger sizes (Munday et al. 2006). Because the terminal sex typically has the highest reproductive output (Munday et al. 2006; Benvenuto et al. 2017), individuals of the initial sex may compete over access to the opportunity to change sex, raising the question of which features may enhance the likelihood of changing sex.

Protogyny, in which individuals begin life as females and later change into males (Ghiselin 1969; Sadovy and Shapiro 1987; Ross 1990: 199; Munday et al. 2006), provides a useful framework for investigating how individuals navigate such competition. Protogyny is particularly common in haremic fishes, where a dominant male monopolizes reproduction within a group of females (Warner and Robertson 1978). In these systems, sex change allows a former female to take over a breeding territory, resulting in a substantial reproductive advantage (Munday et al. 2006). Because dominance hierarchies are typically size-based, the largest female, usually the highest-ranking individual, has the highest probability of changing sex and assuming the male role (Warner and Robertson 1978; Warner and Robertson 1978; Shapiro 1979; Sadovy and Shapiro 1987; Moyer 1990; Ross 1990; Warner and Swearer 1991; Devlin and Nagahama 2002; Avise and Mank 2009; The Tree of Sex Consortium. 2014; Nelson et al. 2016; Kuwamura et al. 2020). This may create pressure on females to adopt strategies that increase their likelihood of reaching the terminal male stage.

Cleaner wrasse *Labroides dimidiatus* are a classic example of a monoandric protogynous hermaphrodite that lives in haremic social groups structured by size-based dominance hierarchies (Robertson 1972; Robertson 1974a; Robertson 1974b; Kuwamura 1984; Nakashima et al. 2000a). All individuals are born female, and some large females may eventually change sex and become a harem male when the opportunity arises (Pessina and Bshary 2026a). This species is particularly interesting because males not only achieve higher reproductive output but also appear to have higher survival (Pessina and Bshary 2026b), making sex change a key life history objective for females in this system. Recent work has further shown that these size-based hierarchies are unusually unstable compared with other well-studied systems, such as anemonefish (*Amphiprion spp.*) (Buston 2003b; Buston 2004; Buston and Cant 2006), coral gobies (*Paragobidon xanthosoma)* (Wong et al. 2007), or cooperative breeders like *Neolamprologus pulcher* (Taborsky 1984; Heg et al. 2004), where the threat of eviction enforces strict social control and maintains highly stable rank structures. Apparently, the lack of cohesive group living, due to each female occupying her own core area, reduces the dominants' control over subordinates and leads to common cases of rank reversal, in which smaller individuals outgrow initially larger harem members (Pessina and Bshary 2026a). These observations suggest that adopting a fast-growing life history could improve an individual's future competitive position and its prospects of reaching the terminal male stage (Pessina and Bshary 2026a).

Currently, the mechanisms underlying variation in growth rate remain poorly understood. Here, we focus on a few key components linked to individual life-history decision-making, without investigating the underlying physiological mechanisms. Such key components are food intake, social control, mortality risk, and reproductive effort. Fast growers could be characterized by efficient/extended foraging, and/or increased mortality, and/or low investment in current reproduction, and/or reduced social control. In cleaner wrasses, foraging is a very interesting component of their lives. This is because nearly all food is obtained through cleaning interactions with client fishes (Grutter 1999), which visit cleaning stations to have ectoparasites removed (Randall 1958; Potts 1973; Grutter 1996; Grutter 1999; Grutter 2001). The interactions between the cleaners and clients represent a textbook example of mutualism involving sophisticated strategic decision-making. Although clients overall benefit from parasite removal (Bshary et al. 2007; Ros et al. 2011; Waldie et al. 2011; Ros et al. 2020), interactions are characterized by a conflict of interest: cleaners prefer to feed on client mucus rather than parasites (Bshary 2001; Grutter and Bshary 2003), a behavior that constitutes cheating and negatively affects client health (Ebran et al. 1999; Reverter et al. 2018). Clients often respond to cleaner mucus feeding with a conspicuous body jolt, revealing the expressed conflict within this mutualism (Bshary and Grutter 2002a). In response, clients have evolved several behaviors that reduce a cheating cleaner's gains and hence act as partner-control mechanisms, including punishment by resident species with access to the local cleaner only, partner switching by visiting clients with access to several cleaning stations within their home ranges, and image scoring (Bshary 2002; Bshary and Grutter 2002a; Bshary and Grutter 2002b; Bshary and Schäffer 2002; Bshary and Grutter 2005; Bshary and Grutter 2006; Johnstone and Bshary 2007; Pinto et al. 2011). In turn, cleaners show high levels of strategic sophistication by adjusting the service quality to a variety of parameters, including client features such as size, parasite load, mucus quality, and maneuverability (Grutter and Bshary 2004; Roche et al. 2021) as well as client strategic options (Bshary 2001; Pinto et al. 2011; Triki et al. 2019 Jun 29). Individuals showing locally adaptive behavior harbor relatively larger forebrains than individuals failing to do so (Triki et al. 2020). Because cleaning interactions provide the primary source of food for cleaners (Grutter 1997), differences in time spent cleaning or in service quality could influence energy intake and, in turn, growth trajectories. Such factors might also be influenced by cleaner and client densities, which are known to differ between neighboring reefs within the same population and across years (Wismer et al. 2014; Triki et al. 2018).

Variation in growth rates could also arise from individuals managing standard life history trade-offs (Stearns 1988) differently. Fast growth may cause increased mortality because of lowered somatic development (Carrier and Leon 1990; Arendt and Wilson 2000), reduced immune function (Lochmiller and Deerenberg 2000; Van der Most et al. 2011), as well as lowered resistance to physiological stressors (Bradshaw 1971; Mangel and Stamps 2001). Non-mutually exclusive, investment in growth must be traded off against current reproduction (Folkvord et al. 2014).

A final factor that may influence growth rates concerns social interactions within the harem. In size-structured hierarchies, dominant individuals may suppress the growth of subordinates through aggression, thereby maintaining their competitive advantage (Hattori 1991; Hofmann et al. 1999; Kokko and Johnstone 1999; Buston 2003b; Heg et al. 2004; Russell et al. 2004; Buston and Cant 2006; Dengler-Crish and Catania 2007; Wong et al. 2007; Young and Bennett 2010; Dubuc and Clutton-Brock 2019). While dominant cleaner fish cannot threaten to evict smaller group members because each individual uses its unique core area (Pessina and Bshary 2026a), aggression and/or mere presence may still affect subordinate growth.

Here, we investigate factors that may contribute to fast growth as a correlate of achieving sex change in female cleaner wrasse. Specifically, we examine four main aspects: (i) time spent cleaning and service quality in their interactions with client fish, which may more globally be affected by cleaner and client densities, (ii) how service quality may relate to mortality risk, (iii) reproductive behavior, and (iv) social interactions with conspecifics. We expected that social competence expressed during cleaning interactions would be a main predictor of fast growth, meaning that we should identify an optimal level of cheating and providing tactile stimulation, which may depend on cleaner and client densities. More time spent cleaning should also translate into faster growth. Furthermore, we expected females showing less frequent evidence of reproductive activity to grow faster. Finally, individuals who are rarely targeted by larger, more dominant females should also grow fast, as low aggression and/or less time spent with dominants indicate a lack of social control. By linking growth trajectories with behavioral and ecological variables, we aim to identify how cleaning strategies, reproductive strategies, and dominance interactions interact to allow some females to increase their probability of reaching the terminal male stage.

Methods

Study site and population

Fieldwork was conducted at Lizard Island between July 2022 and June 2023 across eight reef sites (Supplementary Figure S1) differing in cleaner wrasse and client fish densities, as part of a long-term monitoring program. Full methodological details can be found in Pessina et al. (2026a,b) (Pessina and Bshary 2026b; Pessina and Bshary 2026a), as well as Supplementary Material S1. Individuals were captured via SCUBA using hand nets (10 x 15 cm) and barrier nets (4.7 x 1.8m or 1 x 1.2m), tagged in situ with visual implant elastomers (VIE), and released within two minutes to minimize disturbance. Adult fish received two-color tag combinations across multiple body positions (Supplementary Figure S2), while juveniles were marked with single high-contrast tags. Some individuals exhibited idiosyncratic features that enabled identification using natural markings (Supplementary Figure S3). In total, 540 individuals were tracked throughout the year (see Supplementary Table S1). Only the female phase of focal individuals was included in this study. Sex identification followed the methodology of Pessina et al. (2026a,b) (Pessina and Bshary 2026b; Pessina and Bshary 2026a), as detailed in Supplementary Material S1. Observations were conducted year-round (~1,750 hours across ~1,000 dives), allowing consistent individual recognition and monitoring. Tag retention and visibility remained high throughout the study, with no observed loss and confirmed durability through opportunistic recaptures. As sites were spatially isolated and cleaner wrasse exhibit strong site fidelity, inter-site movement was negligible, allowing independent site-based sampling.

Transects to characterize cleaner and client densities

To quantify reef-scale ecological variables, including cleaner and client fish densities, we conducted standardized underwater visual census using belt transects. Fish counts included all reef fish, except for nocturnal and cryptic species. Surveys were conducted once during the Australian summer of 2023 and were stratified by the reef habitats where our focal cleaner resided: the reef crest and the reef base. The reef crest is defined as the outer edge of the reef flat (Green 1994), and the reef base as the lower reef slope where it meets the sandy substrate (Green 1994).

Within each habitat and site, five 30-meter transects, spaced 2 meters apart, were surveyed running parallel to the reef contour. Fish counts were completed running three consecutive swims per transect, each targeting a different size or taxonomic group: (i) large-bodied fishes swimming above the reef were counted within a 5 m wide belt; (ii) medium-sized fishes occupying the reef matrix were recorded within a 3 m belt; and (iii) damselfishes (Pomacentridae) were surveyed within a 2 m belt. The intermediate belt width was selected based on prior work demonstrating its suitability for accurately surveying wrasse species (Green 1994).

To minimize disturbance effects, each transect swim was preceded by a 2-minute pause. Transects were surveyed at a constant pace and completed in approximately 10 minutes. Only individuals measuring ≥4 cm total length were included in the analyses. Fish were identified to species level whenever possible, following WORMS taxonomic standards. Across all surveys, 343 species representing 51 families were recorded.

These counts were then used to calculate cleaner and client densities (standardized to 150 m2), which then allowed us to estimate cleaner-to-client ratios at our sites.

Characterizing fast, slow, and average growers

Growth measurements were collected using an underwater stereo camera system following the approach of Pessina et al. (2026a,b). A detailed methodological description is provided in Supplementary Materials S2. From these data, we reconstructed two types of growth curves: deme-specific growth trajectories and a population-level curve for Lizard Island.

The deme-specific curves were used to classify individuals into distinct growth strategies (fast, average, or slow) within each site. Classification was based on each fish's final observed size relative to its deme-specific growth curve. Individuals exceeding half of the upper standard-deviation threshold were classified as fast growers, whereas those falling below half of the lower standard-deviation threshold were classified as slow growers; the remaining individuals were considered average growers. The use of half-standard-deviation thresholds was chosen to limit inflation of the average category while maintaining balanced group sizes.

These growth classifications were then used to examine differences in cleaning behavior, spawning frequency, and intraspecific interactions among growth strategies. In parallel, the population-level growth curve was used to assess how local cleaner and client densities influenced the distribution of growth strategies, allowing density effects to be evaluated independently of local growth dynamics.

Collecting cleaning observations

Cleaning observations were collected for 34, 93, and 67 fast-, slow-, and average-growing adult focal females, respectively, totaling 914 videos (120 fast, 471 slow, 323 average). Behavioral observations consisted of 20-minute video recordings obtained using a GoPro Hero 9, with a scuba diver positioned approximately 2–3 m from the focal individual.

Each video was subsequently analyzed to characterize cleaning interactions. A cleaning interaction was defined as beginning with the first physical contact between the cleaner and a client and ending when the two individuals were separated for more than 5 seconds. For each interaction, we recorded: (i) client taxonomic identity (species when identifiable, otherwise genus); (ii) interaction duration; (iii) number of jolts; (iv) client responses to jolts, either through punishment of the cleaner or premature termination of the interaction; and (v) the occurrence of tactile stimulation.

Clients were assigned to one of two residency categories, namely resident or visitor. Because size information was unavailable for individual clients, classification was made at the family level (Supplementary Materials S3). Although most families can be classified as being mostly resident or visitor, we acknowledge the existence of exceptions (e. g., Pomacentridae is mostly resident, but the genus *Abudefduf* includes visitor-like species). Nevertheless, family-level classification remains a reasonable proxy for residency status. Moreover, given the greater complexity of the reef habitat compared to that studied by Bshary (2001), applying a finer-scale methodology was not feasible.

From these observations, we constructed two datasets. The first dataset was used to address questions related to cleaning service quality. For each focal video, data were initially aggregated by client species cleaned during that recording. For each species, we calculated the total number of interactions, the total duration of cleaning, the total number of jolts, the percentage of jolts that elicited a negative response (punishment or termination of the interaction), and the percentage of interactions involving tactile stimulation. Jolt rate was calculated by dividing the total number of jolts by the total cleaning time. These metrics were then summarized at the video level by client type (resident or visitor), by summing the number of interactions and total cleaning time, and by averaging jolt rates, client responses to jolts, and tactile stimulation. Finally, data were aggregated to the cleaner ID level within each client type by averaging across all videos.

To examine client responsiveness to jolts, we constructed a second dataset following the same general workflow, with one key difference. To account for zero inflation in client responses, we did not perform an initial species-level aggregation. Instead, data were aggregated directly at the video and client-type levels**.**

Collecting intraspecific observations

A total of 746 of those videos were also analyzed for intraspecific patterns (fast = 102, slow = 382, average = 262) for 177 focal cleaners (fast = 33, slow = 83, average = 61). Intraspecific analyses involved recording information of the interacting partner regarding their sex, relative size, and rank in relation to the focal individual, and identity when possible. The nature of cleaner-cleaner interaction varied from neutral to negative. Interactions involving either aggression towards or aggression received (through different degrees of chasing) from another cleaner were classified as negative interactions. When no negative interactions occurred in videos in which the focal cleaner encountered conspecifics, these instances were recorded as 0 and included in the analyses conducted in RStudio (RStudio Team 2020). Social rank for both focal and partner individuals was assigned using a monthly-updated social hierarchy dataset. To define social rank, individuals within each group were ordered strictly by body size (TL). *Labroides dimidiatus* is known to form a simple, stable, size-based dominance hierarchy governed by a “size principle,” in which aggression flows almost exclusively down the size gradient (Robertson 1972; Robertson 1974a; Robertson 1974b; Kuwamura 1984; Nakashima et al. 2000b). We empirically validated this in our study population in Pessina et al. (2026a) where body size reliably indicated intra-group aggressive interactions, making the use of additional ranking algorithms based on behavioral matrices unnecessary. Using these data, we constructed a dataset to assess potential differences in the proportion of negative intraspecific interactions between growth strategies. For each Cleaner ID, we calculated the proportion of time during which the focal cleaner was either aggressing subordinates or being aggressed by dominants by dividing total interaction time invested in being attacked or attack by the sum of all videos' durations. These proportions gave one value per fish. A similar methodology was used to build a dataset on the proportion of time each fish would spend in the presence of larger dominant individuals, without restricting to negative interactions.

From the same video analyses, a spawning dataset was also compiled. For each fish, three binary measures of reproductive behavior were recorded: (i) presence or absence of a distended belly, a proxy for egg development and the least precise but most abundant measure; (ii) female engagement in the Body-Sigmoid display, a behavior directly implying the presence of eggs (Robertson 1974a); and (iii) actual spawning events, which necessarily imply the occurrence of the previous two behaviors. Because spawning activity in the cleaner wrasse is known to be influenced by lunar phase and tides (Robertson 1974a; Kuwamura 1981; Kuwamura 1984; Sakai and Kohda 2001), these variables were also included in the dataset. For each video, the lunar phase was classified as waxing, waning, full, or new. In addition, for tidal conditions, the temporal distance (in hours) between the video recording time and the nearest high tide was calculated. Only high tides occurring between sunrise and sunset were considered, as fish are largely inactive outside daylight hours. Videos that did not properly record the time of day in which they were taken were not considered, leading to a total of 373 videos (fast = 87, slow = 286, average = 286) for 177 cleaner fish focal individuals (fast = 32, slow = 83, average = 62).

Statistical methods

Data analyses were conducted in R version 4.3.1 (R Core Team 2023) using RStudio (RStudio Team 2020). Depending on the question, we used Generalized Linear Mixed-Effects Models (GLMM), Linear Mixed-Effects Models (LMM), Linear Models (LM), General Linear Models (GLM), and Pearson's product–moment correlation tests. Models were fitted using lme4 (Bates et al. 2015), glmmTMB (Mollie et al. 2017), and stats (R Core Team 2023) packages. Model assumptions were verified through residual analyses and visual inspections of model fit. When appropriate, post hoc comparisons were performed with the emmeans package (Lenth 2023). Models were simplified based on non-significance and AIC values.

Analyses related to cleaning behavior

To test for differences in cleaning patterns between growth strategies, we fitted three LMMs and two GLMMs. All models include growth strategy, client type, site, and their interaction as fixed factors, and account for non-independence of observations by including a random intercept for cleaner ID.

First, we examined whether fast, slow, and average growers differed in the average time spent cleaning during a 20-minute video (Model 1). The response variable was log-transformed average cleaning duration (ln(duration + 3.05)), and the model was fitted with an LMM. The model accounted for heterogeneity in variability across growth strategies by modeling the dispersion parameter as a function of strategy, client type, and site.

Second, we tested for differences in the average number of cleaning interactions per video between growth strategies (Model 2). The response variable was the log-transformed average number of interactions (ln(number + 2.9)), and the model was fitted using an LMM.

The third and fourth models focused on investigating the quality of the cleaning service. The LMM model investigating potential differences in average jolt rate (Model 3) used the log-transformed (ln(response + 1.61)) as the response variable. The model investigating differences in average percentage of tactile stimulation was a GLMM that accounted for heterogeneity in variability across growth strategies by modeling the dispersion parameter of the beta distribution as a function of strategy, client type, and site (Model 4). Here, the average percentage of interactions with tactile stimulation was used as the response variable.

Using the second cleaning dataset, we then examined potential differences in client responsiveness to jolts between growth strategies (Model 5). This analysis was performed using a GLMM with a Tweedie distribution, with the response variable being the average proportion of jolts that were either punished or led to termination of the interaction.

In addition to these analyses, we investigated a potential link between service quality, growth strategy, and survival. To do so, we first performed a principal component analysis (PCA) using *dudi.PCA* function (Dray and Dufour 2007) on our centered and standardized cleaning variables. For this analysis, data were aggregated per cleaner ID by averaging per 20 minute video the total number of interactions (Tot int.), the total duration (Duration), the percentage of interaction with jolt (jolt), the percentage of interaction with tactile stimulation (TS), and the percentage of interactions with jolts that were negatively responded to (Resp.). Here, behavioral variables were aggregated across client types (i.e., resident and visitor clients were not analyzed separately) to avoid instability and dispersion issues in the model. We retained the first two principal components (PC1 and PC2), which together explained 63% of total behavioral variance (PC1 = 41%, PC2 = 22%). Individual PC scores were used in subsequent analyses.

To test whether survival probability was associated with cleaning behavior and growth strategy, we fitted a GLMER with a binomial distribution and a logit link function (Model 6). Here, the binary response variable was survival, PC1, PC2, growth strategy, and its interactions with the principal components were used as fixed factors, and site was included as a random intercept to account for spatial clustering and shared environmental conditions.

Analyses related to cleaner and client densities

To examine associations between behavioral variables and environmental context, Pearson's product–moment correlation tests were conducted between the proportion of time spent interacting with larger individuals, the proportion of time spent being aggressed by larger individuals, and cleaner reef fish density. Correlations were computed using complete-case observations (Models 7.1-7.2).

A GLM model with a binomial distribution was used to investigate whether the proportion of growth strategies is determined by the cleaner-to-client ratio (Model 8.1). The model included growth strategy, cleaner-to-client ratio, and their interaction as predictors. The model was fitted using the total number of fast and slow growers at each reef as weights. Pairwise correlations between cleaner density, client density, and cleaner-to-client ratio were computed using Pearson's product-moment correlation tests as well (Model 8.2-8.4).

Analyses related to spawning behavior

We computed three separate GLMMs models with a binomial response using the reproductive measures Belly (Model 9), Body-Sigmoid display (Model 10), and actual Spawning (Model 11) to investigate our question. Fixed effects included growth strategy and the distance to the nearest high tide, modeled with both linear and quadratic terms to capture non-linear patterns in spawning activity. The quadratic term was included to represent biologically realistic peaks in spawning probability at intermediate tidal distances, allowing estimation of the optimal distance for peak spawning using the formula $x_{\text{peak}} = -\beta_{\text{linear}} / (2\beta_{\text{quadratic}})$, where β_{linear} and $\beta_{\text{quadratic}}$ are the coefficients of the linear and quadratic tidal terms, respectively. Random intercepts were included for individual fish to account for repeated observations, and for moon phase to account for phase-specific variation in spawning activity. Model fit and assumptions were assessed using residual diagnostics, and marginal and conditional R^2 values were calculated to quantify the proportion of variance explained by fixed effects alone and by both fixed and random effects.

Analyses related to intraspecific interactions

We analyzed variation in intraspecific aggression using an LMM (Model 12). Specifically, we modelled the proportion of time cleaners spent engaged in negative interactions (i.e., attacking subordinates or being attacked by dominants) as a function of growth strategy, aggression type (attack vs. attacked), and their interaction. The response variable was log-transformed (ln(prop)) to improve normality and model fit, and models were fitted with a Gaussian error structure. To account for repeated observations, a cleaner identity nested within the site was included as a random intercept. Observations were weighted by the number of videos contributing to each estimate. Sample sizes were: fast (n = 66), average (n = 122), and slow (n = 166).

We then examined differences in the overall proportion of time spent interacting with larger individuals (irrespective of interaction type) using an additional LMM (Model 13). The log-transformed proportion of time (ln(prop)) was used as the response variable, with growth strategy as a fixed effect. Site was included as a random intercept to account for spatial clustering, and observations were weighted by the number of videos. Sample sizes were: fast (n = 33), average (n = 61), and slow (n = 83).

Cleaner reef fish density was not included in the main models because growth strategies were defined at the deme level using site-specific growth curves. Including density would have required using the categories at a population level, thereby losing the within-site resolution necessary to assess interaction patterns.

Results

Cleaning patterns differ between growth strategies

Growth strategy and client type both strongly shaped cleaning behavior (Figure 1A). Cleaners differed in the average time spent cleaning depending on their growth strategy (Model 1; Analysis of Deviance: Chisq = 15.16, df = 2, $p < 0.001$) and the type of client serviced (Model 1; Analysis of Deviance: Chisq = 214.55, df = 1, $p < 0.0001$), with no significant interaction between the two predictors (Model 1; Analysis of Deviance: Chisq = 1.12, df = 2, p = 0.57). Site had an overall effect on cleaning duration (Model 1; Analysis of Deviance: Chisq = 21.41, df = 7, p = 0.003), but it did not interact with the effect of growth strategy (Model 1; Analysis of Deviance: Chisq = 16.48, df = 14, p = 0.29). Site did, however, interact with the effect of client type (Model 1; Analysis of Deviance: Chisq = 27.8, df=7, $p < 0.0001$; Supplementary Figure S5). Simplification of the model by removing non-significant interactions did not alter the significance of the main effects, and post hoc comparisons revealed that slow growers spent more time cleaning than fast growers (p = 0.0013; 57.5% and 52.6% more with resident and visitor respectively) but no difference was found for neither fast (p = 0.13) nor slow growers (p-value = 0.18) with average growers. Additionally, visitor clients received longer cleaning interaction than resident clients in all but two sites (p: 6 sites < 0.001; p: 2 sites > 0.05; Supplementary Figure S5).

Patterns in the number of interactions mirrored those observed for cleaning duration (Figure 1B). Both growth strategy (Model 2; Analysis of deviance: Chisq = 8.59, df = 2, p = 0.01) and client type (Model 2; Analysis of deviance: Chisq = 18.87, df = 1, $p <0.0001$) significantly affected the number of cleaning interactions, with no evidence for an interaction between predictors (Model 2; Analysis of deviance: Chisq = 2.29, df = 2, p = 0.32). Site was a significant predictor (Model 2; Analysis of deviance: Chisq = 14.87, df = 7, p = 0.04), but it did not significantly interact with the effect of growth strategy (Model 2; Analysis of deviance: Chisq = 13.06, df = 14, p = 0.52). However, Site did interact with client type (Model 2; Analysis of deviance: Chisq = 67.05, df = 7, $p < 0.0001$; Supplementary Figure S6). After model simplification, significance remained, and post hoc analyses showed that slow growers interacted more than fast growers (p = 0.02; 39.9% and 38% more with resident and visitor, respectively), but no difference was found for either fast (p = 0.35) or slow growers (p-value = 0.19) with average growers. Only at two of the study sites were visitor clients involved in significantly more interactions than residents (p: 6 sites > 0.05; 2 sites < 0.001, Supplementary Figure S6).

Cheating rates differed significantly between growth strategies (Model 3; Analysis of deviance: Chisq = 13.17, df = 2, p = 0.001, Figure 1C) and client types (Model 3; Analysis of deviance: Chisq = 9.64, df = 1, p = 0.002), while the interaction between growth strategy and client type was not statistically significant (Model 3; Analysis of deviance: Chisq = 2.38, df = 2, p = 0.30). Site had no significant effect on jolt rate (Model 3; Analysis of deviance: Chisq = 5.14, df = 7, p = 0.64) and it not interact with growth strategy (Model 3; Analysis of deviance: Chisq = 18.7, df = 14, p = 0.18), nor with client type (Model 3; Analysis of deviance: Chisq = 10.79, df = 7, p = 0.15). After model simplification, significances remained and post hoc analyses revealed that slow growers cheated more than both fast (p = 0.01; 65.6% and 45.3% more with resident and visitor respectively) and average growers (p = 0.02; 42.5% and 70.7% more with resident and visitor respectively), while no difference was found between fast and average growers (p = 0.67). Resident clients were cheated on more than visitor clients (p = 0.002).

Tactile stimulation showed a different pattern (Figure 1D). The proportion of interactions involving tactile stimulation depended strongly on client type (Model 4; Analysis of Deviance: Chisq = 223.02, df = 1, p < 0.0001), and marginally on site (Model 4; Analysis of Deviance: Chisq = 14.14, df = 7, p = 0.05) but was unaffected by growth strategy (Model 4; Analysis of Deviance: Chisq = 3.98, df = 2, p = 0.14). The interaction between growth strategy and client type was not significant (Model 4; Analysis of Deviance: Chisq =1.27, df = 2, p = 0.53). Similarly, site did not interact either with growth strategy (Model 4; Analysis of Deviance: Chisq = 16.48, df = 14, p = 0.28) or client type (Model 4; Analysis of Deviance: Chisq = 6.02, df = 7, p = 0.53). After model simplification, significances remained, and post hoc comparisons confirmed that cleaners provided more tactile stimulation to visitor clients than to resident clients (p < 0.0001).

Client responses to cheating were likewise primarily driven by client type (Figure 1E). Responsiveness to jolts differed significantly between resident and visitor clients (Model 5; Analysis of Deviance: Chisq = 15.2, df = 1, p < 0.0001), while growth strategy (Model 5; Analysis of Deviance: Chisq = 5.65, df = 2, p = 0.06), and site (Model 5; Analysis of Deviance: Chisq = 9.34, df = 7, p = 0.23) had no overall effect. None of the interactions resulted in a significant effect (p > 0.1). After model simplification, significances remained, and post hoc analyses indicated that, despite the interaction between growth strategy and client type not being significant, visitor clients were more responsive than resident clients when interacting with slow- (p = 0.004) and average-growing cleaners (p = 0.03), whereas no such difference was observed for fast growers (p = 0.16).

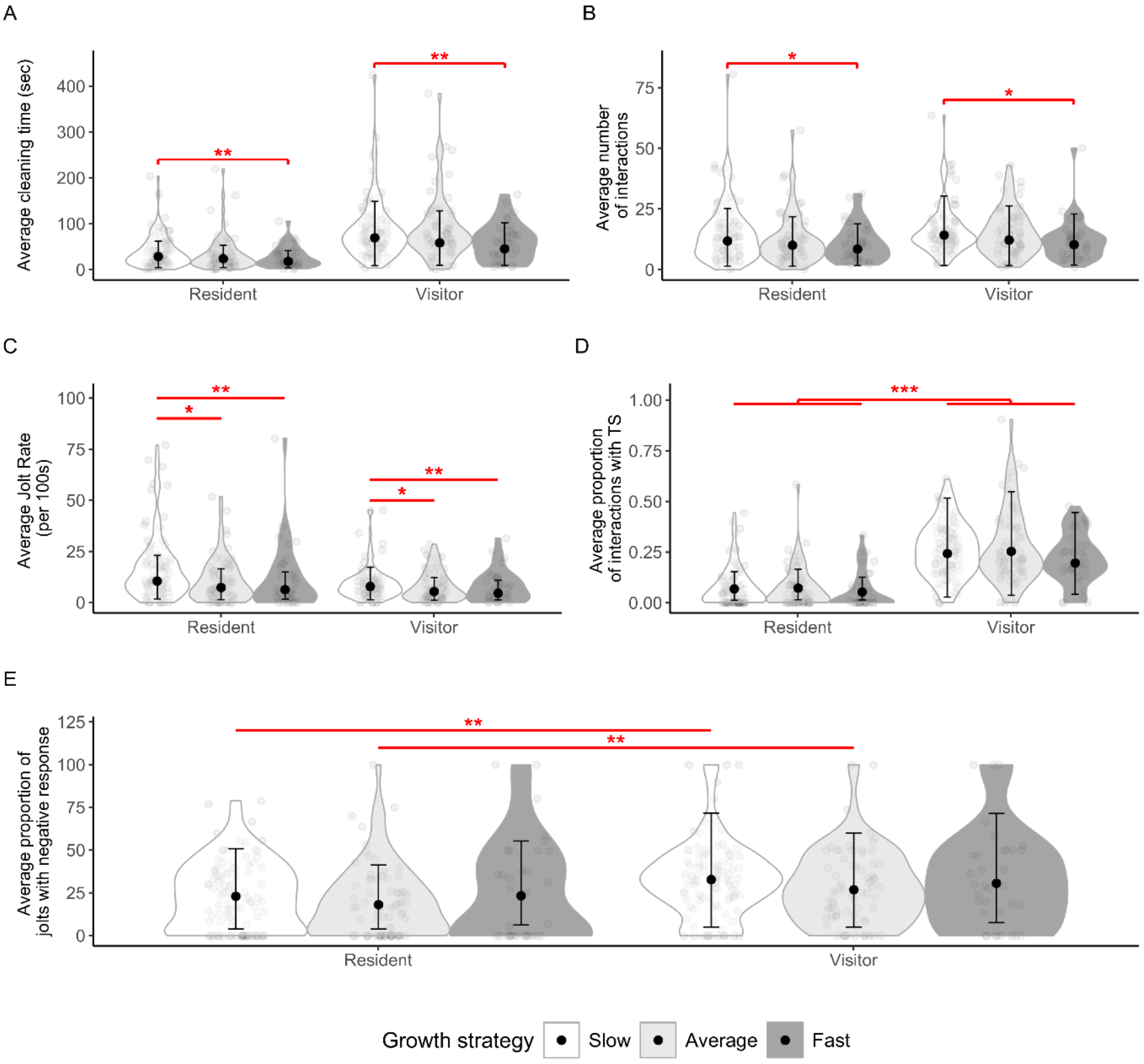

Figure 1: Cleaning patterns of fast, slow, and average growers. For each level of client type (resident and visitor) and growth strategy (fast, slow, and average), these graphs show: A. Distribution of average cleaning duration (Model 1; Gaussian LMM); B. Distribution of average number of cleaning interactions (Model 2; Gaussian LMM); C. Distribution of average jolt rate (Model 3; Gaussian LMM); D. Distribution of the average proportion of interactions with tactile stimulation (Model 4: Beta GLMM); and, E. Distribution of the average proportion of jolts with negative response (Model 5; Tweedie GLMM). All graphs show distribution as violin plots with jittered points representing raw individual-level data. The overlaid points and error bars indicate model-estimated means ± standard errors (SE). The line connecting the violins with an asterisk indicates a significant difference between the two groups involved (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$). Cleaning data includes 914 videos (fast = 120, slow = 471, average = 323) for 194 cleaner ID (fast = 34, slow = 93, average = 67).

For the PCA (Figure 2A), PC1 described a gradient primarily associated with overall interaction investment (average number of interaction durations and tactile stimulation). Individuals with lower PC1 scores engaged in more frequent and longer interactions and provided more tactile stimulation. PC2 was mainly associated with cheating-related dynamics, contrasting cleaners that elicited more client jolts and responses with those that did not. Fast-, slow-, and average-growing individuals showed substantial overlap in multivariate behavioral space.

Survival probability showed an association with PC1 (Model 6; Analysis of Deviance: Chisq = 5.32, df = 1, p = 0.02, Figure 2B), but not with PC2 (Model 6; Analysis of Deviance: Chisq = 0.02, df = 1, p = 0.88), suggesting that interaction investment rather than cheating patterns predict survival probability. The lower the PC1 score, which translates into greater cleaning investment, the higher the survival (Figure 2B). Growth strategy did not significantly influence survival (Model 6; Analysis of Deviance: Chisq = 0.9, df = 2, p = 0.64), and there was no evidence that the relationship between cleaning behavior and survival differed between growth strategies as neither the interaction with PC1 (Model 6; Analysis of Deviance: Chisq = 0.20, df = 2, p = 0.90) nor PC2 (Model 6; Analysis of Deviance: Chisq = 1.76, df = 2, p = 0.42) were significant. For this analysis, behavioral variables were aggregated across client types (i.e., resident and visitor clients were not analyzed separately) to avoid model instability and dispersion issues.

Cleaner densities have an important role

The proportion of time spent being aggressed by conspecifics was not correlated with cleaner density (Pearson's correlation: Corr = 0.02, t = 0.43, df = 746, p = 0.67). In contrast, the proportion of time spent interacting with larger individuals was weakly but significantly positively correlated with cleaner density (Pearson's correlation: Corr = 0.12, t = 3.24, df = 746, p = 0.001), indicating a small increase in interaction time with increasing cleaner density.

Proportions of fast, slow, and average growers in the reef were significantly different (Model 8.1; Analysis of Deviance: Chisq = 16.7600, df = 2, p = 0.0002), and this difference was significantly dependent on cleaner-to-client ratio (Model 8.1; Analysis of Deviance: Chisq = 13.709, df = 2, p = 0.0001). Fast- and average- growing strategies have a tendency to be more abundant at high cleaner-to-client ratios, while the slow-growing strategy follows the opposite trend (Figure 3). Post hoc analyses revealed that this trend was significant for the slow growth category (0.03) but not for the fast (0.37) and the average one (0.75). Cleaner fish reef density was moderately but significantly positively correlated with client density (Model 8.2; Pearson's correlation: Corr = 0.49, t = 2.62, df = 22, p = 0.02). However, the cleaner-to-client ratio was only strongly correlated with cleaner reef density (Model 8.3; Pearson's correlation: Corr = 0.78, t = 5.78, df = 22, p < 0.0001), and showed no correlation with client Density (Model 8.4; Pearson's correlation: Corr = -0.16, t = -0.75, df = 22, p = 0.46).

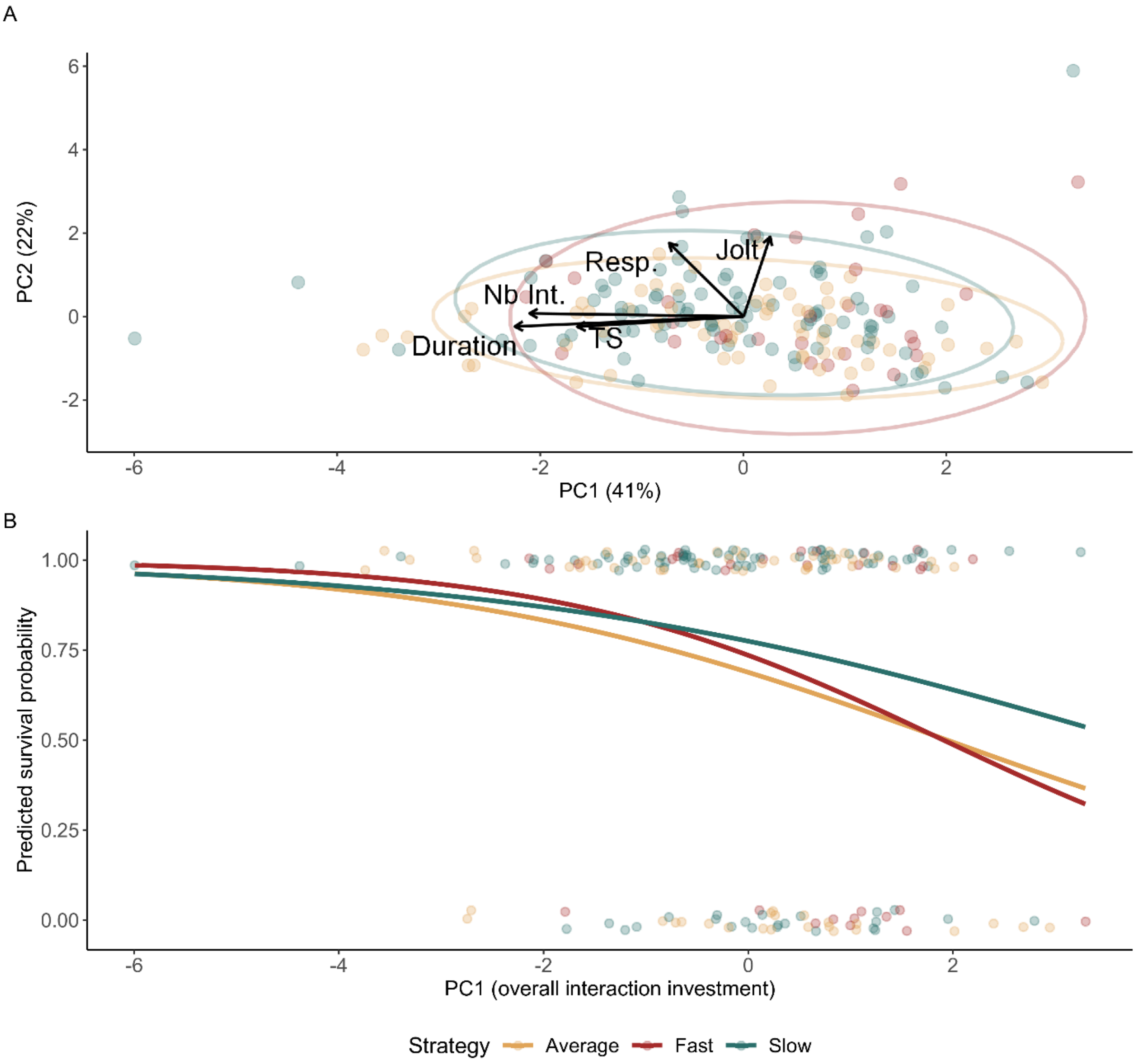

Figure 2: Cleaning behavior and its association with survival probability. A. Principal Component Analysis (PCA) of cleaning service characteristics. The PCA summarizes variation in five behavioral variables: average number of interactions (Nb Int.), average interaction duration (Duration), average proportion of interactions with tactile stimulation (TS), average jolt rate (Jolt), and average proportion of jolts that elicited a client's negative response (Resp.). Points represent individual cleaner wrasse, colored by growth strategy. Arrows indicate variable loadings, and ellipses represent 95% confidence intervals for each growth strategy. PC1 and PC2 explain 41% and 22% of the total variance, respectively. B. Predicted survival probability of the three growth strategies based on levels of PC1. Raw individual observations are shown as jitter, and the overlaid lines represent model predictions (Model 6; Binomial GLMM). Survival data include 190 cleaner ID (fast = 30, slow = 91, average = 69).

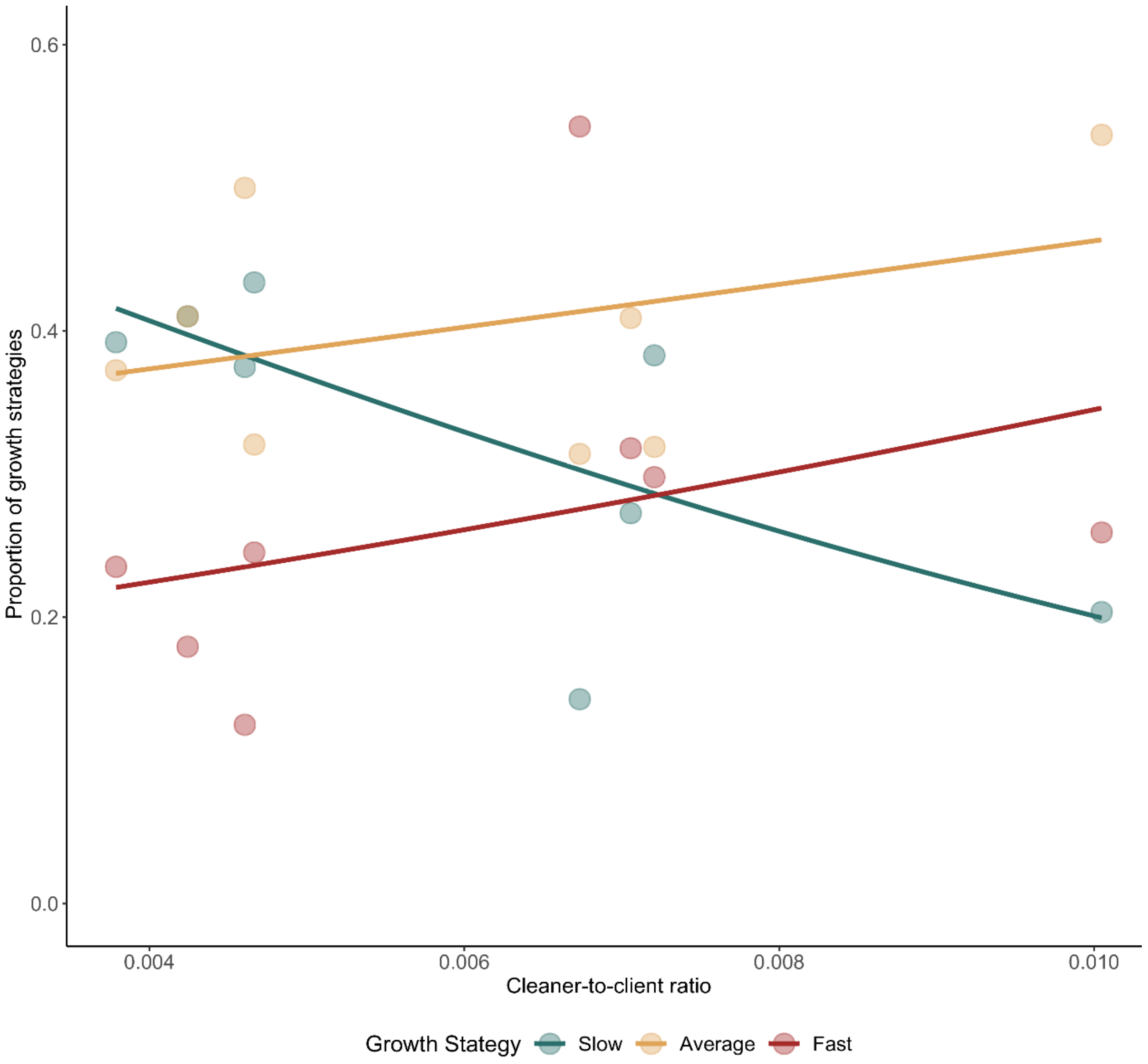

Figure 3: Scatter plot of the relationship between the cleaner-to-client ratio and the proportion of fast, slow, and average growth strategies. The jitter represents raw site-level data (n = 8, strategies = 3), while overlaid lines represent model-estimated means ± standard errors (SE) from Model 8.1. For these two analyses, the general growth curve was used to define the growth strategy, allowing for site differences in cleaner density.

Lack of evidence for a reproductive trade-off

We tested whether fast-, slow-, and average-growing fish differ in reproductive investment using three measures of reproductive activity: presence of a distended belly, Body-Sigmoid display, and actual spawning.

For the belly measure, there was no effect of growth strategy on the probability of a female showing a distended belly (Model 9; Analysis of Deviance Table: Chisq = 2.25, df = 2, p = 0.3248). Belly was also neither linked to distance to the tide (Model 9; Analysis of Deviance Table: Chisq = 1.03, df = 1, p = 0.3094), nor its quadratic effect (Model 9; Analysis of Deviance Table: Chisq = 1.5127, df = 1, p =

0.2187). Marginal R^2 for the model was low (0.017), whereas conditional R^2 was higher (0.292), suggesting that individual variation and lunar phase explained most of the variation in belly occurrence.

For the Body-Sigmoid display, growth strategy again had no effect (Model 10; Analysis of Deviance Table: Chisq = 0.2067, df = 2, p = 0.90182), whereas the quadratic effect of distance to high tide resulted significant (Model 10; Analysis of Deviance Table: Chisq = 6.1194, df = 1, p = 0.01337), with peak display probability occurring roughly 2 hours after high tide. The marginal R^2 of this model was slightly higher than for belly alone (0.085), as well as the conditional R^2 (0.416).

For the spawning, growth strategy had no effect (Model 11; Analysis of Deviance Table: Chisq = 1.1813, df = 2, p = 0.55397), whereas the quadratic effect of distance to high tide resulted significant (Model 11; Analysis of Deviance Table: Chisq = 15.4901, df = 1, $p < 0.0001$), with peak display probability occurring roughly 30 minutes after high tide. The marginal R^2 (0.922) and the conditional R^2 (0.922) of this model were higher than those of the previous models.

Social control plays an important role

The proportion of time spent in negative interactions with conspecifics does not seem to be affected by growth strategy (Model 12; Analysis of Deviance: Chisq = 5.0034, df = 2, p = 0.08194; Figure 4A), but by type of aggression alone (Model 12; Analysis of Deviance: Chisq = 25.4417, df = 1, $p < 0.0001$). However, there was a significant interaction between the effect of growth strategy and aggression type (directed to subordinates or received by dominants) on the proportion of time spent in negative interaction (Model 12; Analysis of Deviance: Chisq = 34.69, df = 2, $p < 0.0001$). Post hoc analyses showed that slow growers received 79% and 55% more aggression than average and fast growers, respectively. However, only the comparison between slow and average growers was significant (p-value = 0.002).

The proportion of general time spent with larger individuals was, however, strongly dependent on growth strategy (Model 13; Analysis of deviance: Chisq = 11.45, df = 2, p = 0.003; Figure 4B). Post hoc analyses revealed that fast growers spent significantly less time with larger individuals than both slow (p = 0.003; 49.3% less) and average growers (p = 0.02; 40% less).

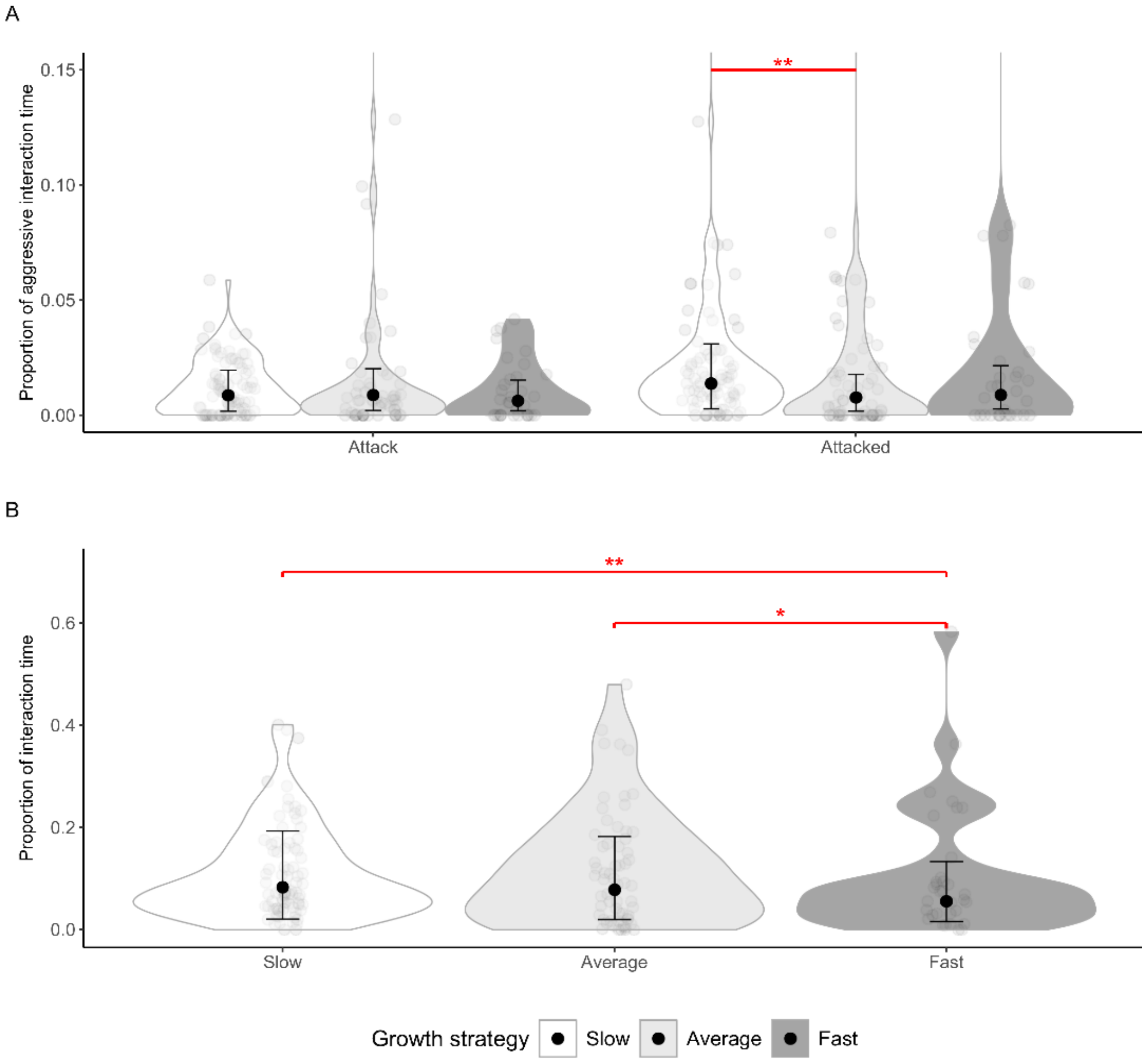

Figure 4: Intraspecific patterns and growth strategy. For each level of growth strategy, these graphs show: A. Proportion of time spent in negative interactions by aggression type (attacked by dominants or attack subordinates; Model 12; Gaussian LMM); B. Proportion of time spent with larger individuals irrespective of the nature of interaction (Model 13; Gaussian LMM). In both graphs, distribution is shown as violins, the jitter represents raw individual-level data, and overlaid points and error bars represent model-estimated means ± standard errors (SE). Here, local population growth curves were used to define the growth strategy. The line connecting the violins with an asterisk indicates a significant difference between the two groups involved (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$). Intraspecific data include 746 videos (fast = 102, slow = 382, average = 262) for 177 cleaner ID (fast = 33, slow = 83, average = 61).

Discussion

We had asked how foraging strategies, reproductive investment, and hierarchical interactions combine to explain fast and slow growth in cleaner fish *Labroides dimidiatus*, a species well known for the strategic sophistication shown in cleaning interactions with clients. Contrary to our predictions, variation in parameters measuring cleaning behavior did not explain variation in growth patterns, nor did indicators of reproductive activity. According to evidence provided in the study, the degree of social control by dominant harem members emerged as the only factor affecting growth patterns. Notably, slower-growing individuals spent more time in the presence of dominants, despite experiencing similar levels of aggression. This indicates that the mere presence of dominant individuals, rather than active aggression, may be sufficient to regulate subordinate growth. None of our measured parameters interacted with growth patterns to predict mortality risks. Below, we discuss each aspect in more detail.

Cleaning patterns and densities

Despite our predictions, fast-growing individuals did not appear to obtain more energy because of superior cleaning performance. Instead, two results suggest the opposite, i.e. that slow-growing individuals may obtain more food from cleaning interactions. In this context, the observation that individuals of intermediate growth show largely intermediate results strengthens the view that results are not due to one growth category doing something distinctively different. First, slow growers spent overall more time in cleaning interactions. Time spent cleaning is at least in part affected by clients' decisions about choosing a cleaner, how long to stay, and how to respond to cleaners' cheating (Bshary 2002; Bshary and Grutter 2002b; Bshary and Grutter 2002a; Bshary and Schäffer 2002; Bshary and Grutter 2005; Bshary and Grutter 2006; Pinto et al. 2011). Second, the observation that, across study demes, individuals at sites with lower competition among cleaners for access to clients (i.e., a lower cleaner-to-client ratio) tended to grow more slowly is consistent with the general conclusion that food intake does not predict growth patterns, thereby contradicting previous hypotheses (Pessina and Bshary 2026a). However, as shown in previous research (Triki et al. 2019 Jun 29), cleaner and client densities are positively correlated. This correlation could support the working hypothesis that high fish densities provide a greater abundance of ectoparasites (Grutter 1995; Grutter 1996), thereby rendering foraging during cleaning interactions more efficient. Consequently, although fast-growing individuals do not appear to gain more energy through longer or more frequent interactions, they may potentially be more efficient cleaners and thus achieve similar overall energy intake. However, because our data do not allow us to quantify feeding rates in terms of bite rate or foraging efficiency, this remains an open question.

Lack of reproductive and survival trade-offs

As we did not find evidence that fast growth is due to higher food intake, an alternative explanation could be that fast and slow-growing individuals manage trade-offs differently. However, our data do not provide evidence for this. Our three measures of spawning activity did not yield any evidence that slow growers invest more into current reproduction. It is possible that our proxies merely reflect reproductive readiness rather than actual reproductive investment (Villegas-Ríos et al. 2014). We currently cannot exclude that females following different growth strategies differ in the quantity of eggs produced or in gonadal allocation while maintaining similar levels of spawning behavior. Moreover, reproductive behavior may sometimes serve social functions independent of immediate reproductive investment. In sequential hermaphrodites, the behavioral expression of reproductive roles can precede or occur independently of physiological changes in gonadal function (Warner and Swearer 1991; Nakashima et al. 2000a). For example, in some protogynous reef fishes, including the cleaner wrasse, the largest female rapidly adopts male-typical spawning behavior following the disappearance of the dominant male, even while still undergoing gonadal transition (Warner and Swearer 1991; Nakashima et al. 2000a). Such decoupling suggests that reproductive behavior may partly function to maintain social position rather than directly reflect reproductive investment (Warner and Swearer 1991; Nakashima et al. 2000a). In our system, females may similarly maintain spawning behavior toward the dominant male regardless of their current reproductive investment, either to avoid social conflict or to maintain their position within the reproductive hierarchy. We therefore acknowledge that, ideally, we would have obtained egg count data from spawning events as well (as previously measured by Kuwamura (1981) (Kuwamura 1981). However, the presence of a large belly as an indicator of egg mass did not yield evidence of systematic differences either.

Also, it does not appear that fast growth causes major health risks that would lead to increased mortality, adding to the trade-offs we lack evidence for. As we do not have any physiological measures in a long-term field observation project, it remains an open question whether more subtle physiological costs of fast growth would be identifiable.

The role of intraspecific interactions

The main emerging explanation for variation in growth rates is that slow growers are constrained by stronger intraspecific control. Interestingly, the mere presence of a dominant individual, rather than active aggression, seems sufficient to regulate subordinate growth. This result aligns with previous findings on sex change in this species at Lizard Island, for which the combined effect of reduced interaction with the harem male and the next largest female would lead to the early sex change of a subordinate (Pessina and Bshary 2026a).

This pattern is consistent with predictions from size-based hierarchy theory, in which individuals selectively control those directly below them in rank to maintain a competitive size advantage and reproductive position. In such systems, subordinates are expected to strategically adjust their growth trajectories in response to social pressure (Hofmann et al. 1999; Kokko and Johnstone 1999; Buston 2003a; Heg et al. 2004; Russell et al. 2004; Buston and Cant 2006; Dengler-Crish and Catania 2007; Wong et al. 2007; Young and Bennett 2010; Dubuc and Clutton-Brock 2019), thereby reducing the risk of escalated conflict or eviction (Taborsky 1985; Reeve 1992; Reeve and Nonacs 1997; Reeve et al. 1998: 198; Buston 2003a; Buston and Cant 2006; Wong et al. 2007). Consistent with this interpretation, fast-growing individuals in our study appeared to experience reduced social control, allowing them to maintain higher growth rates despite comparable ecological conditions.

Failure to control fast-growing individuals may result from multiple mechanisms. At Lizard Island, the cleaner wrasse exhibits two types of social structures: branching and linear. Branching systems are characterized by a larger number of females compared to linear systems (Pessina and Bshary 2026a), distributed across several groups (branches) that occupy non-overlapping territories. This spatial separation allows for the coexistence of codominant females, individuals of similar size that avoid interacting with one another. In contrast, linear systems consist of a single group of females of different sizes occupying overlapping territories (Kuwamura 1984).

In branching systems, a codominant female may experience rapid growth due to reduced female-female control and decreased attention from the male, who must divide his time among multiple branches and individuals (Pessina and Bshary 2026a). Alternatively, within a branch or in linear systems, a fast-growing individual may occupy a core area located farther from dominant individuals, making it more difficult for them to monitor and regulate her growth. A further possibility is that rapid growth is tolerated when there is a large size gap between the fast-growing individual and the next largest competitor. Finally, some dominant individuals may simply fail to exert effective control. Regardless of the mechanism, such failures in social regulation support the idea that social control plays a key role in shaping growth strategies.

Despite the lack of significance with fast growers, slow growers were still the growth strategy most likely to be pursued more aggressively by higher-rankers (79% and 55% more than average and fast growers, respectively). This tendency, together with the documented increase in social control associated with the presence of dominant individuals, could lead to higher levels of stress. Under chronic stress, fish divert resources from growth toward maintenance and survival (Gilmour et al. 2005; Goodrich and Clark 2023), and stress-related neuroendocrine mechanisms can directly suppress somatic growth (Jonsson 2025). This association makes it unlikely that the cleaner fish system operates as cooperatively breeding fish do. In the latter, an experiment in which both dominant and subordinate individuals were fed ad libitum, subordinates did not increase in length but instead accumulated energy reserves and became heavier (Taborsky 1984; Heg et al. 2004). We do not expect slow-growing cleaners to be heavier than fast growers, because the mechanism of stress induction could prevent this.

Regarding between-group intraspecific interactions, because the cleaner-to-client ratio was strongly correlated with cleaner density, our data suggest that sex change is not only a driver of fast growth within a deme but also between demes. Individuals from neighboring harems could indeed represent competitors for access to sex change opportunities (Robertson 1972; Pessina and Bshary 2026a).

Limitation of the study

Like many life history projects, our methodology relied entirely on non-invasive techniques to preserve the study populations and their natural social dynamics. Consequently, we were unable to use otolith extraction to collect true chronological age data for our focal fish. Instead, we relied on model-based estimates of individual ages and deme-specific growth curves constructed from regular size measurements. Furthermore, we can only provide correlational measures of life-history components: cleaning duration and client jolts as indicators of energy gains, and presence/aggression by dominants as measures of exerted social control. With respect to reproductive investment, we had to rely on visual indicators, such as the presence of a large belly, to estimate egg mass and behavioural proxies of spawning activity. In an ideal world, we would have measured caloric intake, body condition, fat reserves, stress hormones, immune parameters, and the number of eggs produced for each spawning event.

Conclusion

Together, our results point to two main conclusions. First, the potential for rapid growth in slow-growing individuals appears to be socially constrained by intraspecific interactions. Second, fast-growing individuals do not seem to acquire the energy required for accelerated growth through increased cleaning effort or higher service quality. Instead, differences in growth are more likely to arise from variation in how energy is allocated, including potential trade-offs between growth, storage, maintenance, and reproduction. Future work directly measuring body condition, fat reserves, and gonadal energy content would help determine whether differences in physiological allocation underlie the divergence in growth strategies observed here. Integrating these physiological measures with behavioral and social data could provide a more complete understanding of how energy intake, social environment, and strategic allocation interact to shape life history trajectories in sequentially hermaphroditic reef fishes. Beyond physiological research, our results raise a major challenge for cognitive research on cleaner fish: given the documented variation in forebrain size and cell numbers and associated strategic sophistication of cleaners, what are the exact benefits of being smart in a cleaner’s daily life?

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Supplementary Materials for Chapter 3

Supplement S1: Study sites and populations

Study sites

Fieldwork was conducted at Lizard Island (Great Barrier Reef, Australia) as part of an ongoing long-term monitoring program initiated in July 2022. The present study focuses exclusively on a continuous 11-month period spanning July 2022 to June 2023, during which data were collected year-round.

Eight reef sites were selected based on different densities of cleaner wrasse and client fishes (Fig. S1). Sampling effort was distributed across all months within the study period, capturing both austral winter and summer conditions. To simplify, we defined winter as June to November and summer as December to May. At each of our sites, we created a population of individually identifiable cleaner wrasses by catching and tagging them with visual implant elastomers (VIEs).

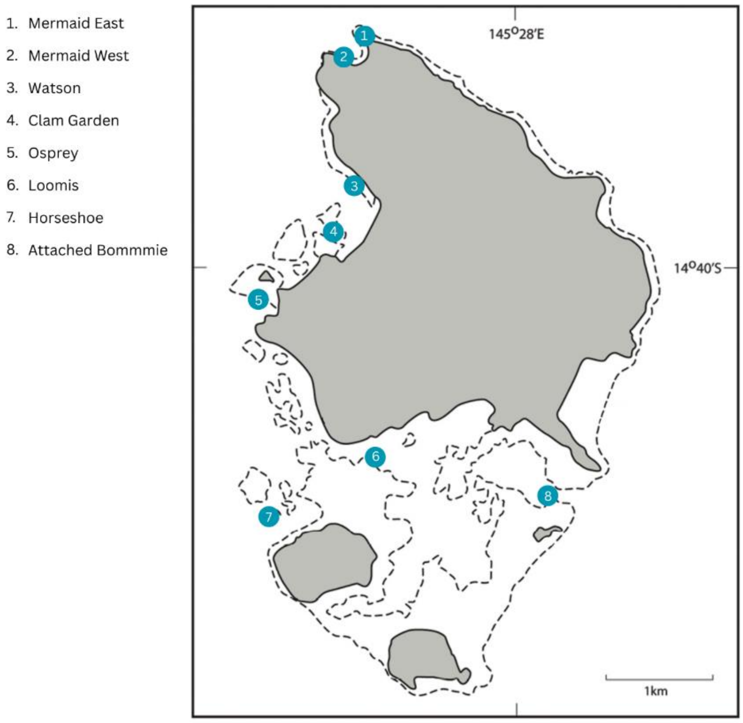

Figure S1: Field observation sites on the coral reefs surrounding Lizard Island, Australia.

Individual identification and tagging protocol.

Cleaner wrasse were captured while SCUBA diving using hand nets (10 x 15 cm) and barrier nets (4.7 y 1.8m or 1 x 1.2m). Handling time was minimized: from capture to release, individuals were restrained in a hand net for less than two minutes. All fish resumed normal behavior immediately after release, and no non-target individuals were captured

Individual identification primarily relied on VIE tags, a widely used technique for small reef fishes (Jungwirth et al. 2019). Tagging was conducted underwater to avoid removal from the reef environment. Adult focal individuals received two elastomer injections placed in clear tissue (light band above the black lateral stripe), with injection sites distributed across four possible body locations (anterior/posterior and left/right; Figure S2). Six colors (red, pink, yellow, green, blue, white) were used, yielding up to 1,296 unique tag combinations, with additional differentiation possible when tag order was considered.

Juvenile individuals were marked with a single injection using high-contrast colors (red, pink, or yellow), allowing 108 unique codes. In cases where individuals could be reliably distinguished based on natural markings, such as pigmentation asymmetries or irregularities in the lateral band, tagging was deemed unnecessary (Figure S3).

A total of 280 adults were tagged, and an additional 95 adults were identified based on markings (Table S1). From November 2022, monitoring was expanded to include approximately 505 juveniles. Of these, 165 reached a total length of 40 mm, at which point they were tagged and incorporated into the present dataset. In total, 540 individuals were tracked throughout the study period, with sample sizes ranging from 47 (Loomis) to 88 (Mermaid East).

The primary researcher participated to all fieldwork, totaling ~1,000 dives and ~1,750 hours of underwater observation. This continuous monitoring and field presence enabled consistent recognition of both tagged and untagged individuals. Continuous monitoring enabled the reliable identification of both tagged and untagged individuals.

Tag composition and retention

VIE tags consist of a pigmented elastomer that may be combined with a hardening agent to improve structural stability during growth (Northwest Marine Technology, Inc. 2017). In this study, the hardener was not used as it sets rapidly at high water temperatures, causing the whole syringe to solidify and go to waste. Despite this, no tag loss was observed over the study period. Some tag expansion occurred as individuals grew, but visibility remained high.

Tag retention was further verified through opportunistic recaptures of previously marked individuals 12–20 months after initial tagging. All recaptured fish retained clearly visible marks. These observations served exclusively to confirm tag durability and are not included in subsequent analyses. Overall, tag persistence exceeded values previously reported for this species (Jungwirth et al. 2019).

With the exception of two adjacent sites (Mermaid East and Mermaid West), all study locations consisted of isolated reef patches separated by sand or open water. As cleaner wrasse are strongly site-attached and do not traverse open water, movement among sites was not possible. Tag combinations were therefore reused across sites, except between the two Mermaid locations, where unique combinations were maintained.

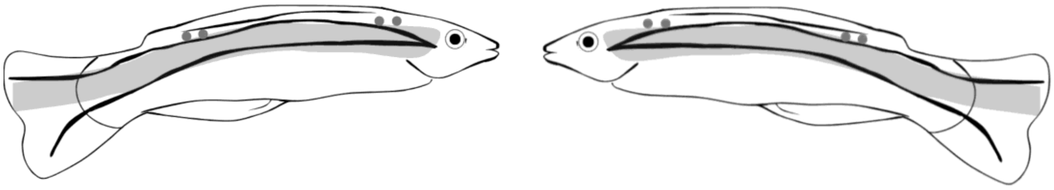

Figure S2: Illustration of the four locations for VIE.

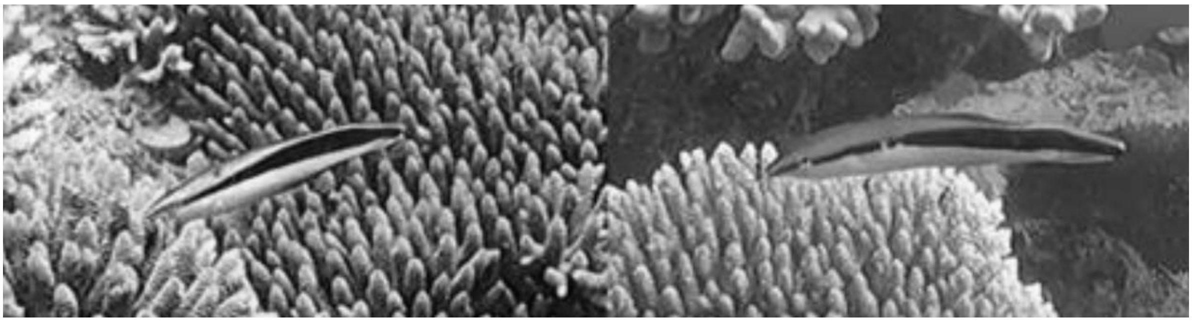

Figure S3: Examples of two individuals that can be recognized without VIE.

Sex identification

Males and females were identified based on behavioral observations in the field, a widely used method in fish behavioral ecology. In this species, males and females exhibit clearly differentiated behaviors, such as territoriality and specific courtship actions, which have been consistently reported in earlier studies and confirmed through physiological measures, including examination of the gonads (Robertson 1974). Accordingly, the determination of sex in the present study relied on these validated criteria, which included: (i) Flutter-Run, a rapid display in which males swim past females while fluttering their tails and spreading their fins, presenting a lateral profile (Robertson 1974); (ii) Sexual signaling, where females respond to male courtship with behaviors such as the Body-Sigmoid, a static S-shaped body curve with the belly oriented toward the male, typically indicating readiness to spawn (Robertson 1974); (iii) Coloration patterns, with females exhibiting distinct sexual colors during courtship that are absent in males (Robertson 1974); and (iv) Spawning posture, where males assume a dominant position during the later stages of courtship, including straddling the female in an upward spiral and leading the ascent (Robertson 1974). Beyond these qualitative traits, quantifiable behavioral differences were also noted. Males tolerated the presence of females in close proximity more than females did, especially near feeding areas, and showed higher levels of movement within their territories, frequently visiting females and patrolling territorial boundaries (Robertson 1974). These behaviors were only used to determine the sex of the focal individuals and were not included as variables in the behavioral analysis described below.

Sex identification was also supported by observations of spawning behavior. Individuals identified as males consistently spawned with smaller partners, whereas females spawned with larger partners. Each spawning event involved only two individuals, ruling out the participation of sneaker males.

Table S1: Total number of focal cleaner wrasses at the 8 sites. This table summarizes he total number of tagged (VIE) and non-tagged (No VIE) for the 8 sites: Mermaid East (ME), Mermaid West (MW), Watson (W), Clam Garden (CG), Osprey (O), Horseshoe (H), Loomis (LU), and Attached Bommie (AB).

Site	Adult Males		Adult Females		Juveniles	Total	Sex changers
	VIE	No VIE	VIE	No VIE	VIE		
ME	3	1	45	5	34	88	6
MW	6	0	29	10	28	73	7
W	3	3	31	8	19	64	4
CG	5	1	31	9	12	58	5
O	2	3	33	10	19	67	7
H	6	0	38	17	18	79	4
LU	3	1	18	9	16	47	5
AB	5	5	22	13	19	64	4
	33	14	247	81	165	540	42
Total	47		328		165	540	42

Supplement S2: Stereo camera sizing error

Following the approach described in Pessina and Bshary (2026a), fish body size was quantified on a monthly basis using a stereo-photogrammetric camera system composed of two GoPro Hero 8 cameras (Seager 2006). The paired cameras were mounted on a rigid frame and operated by the primary diver while swimming along the reef, allowing three-dimensional length measurements to be extracted from video recordings. Video footage was processed using EventMeasure software (Seager 2006), after camera calibration in CAL (Seager 2006).

Stereo photogrammetry is known to provide substantially greater accuracy than underwater visual estimates (Michael et al. 2011), with previously reported measurement errors on the order of 1–2 mm (Euan et al. 2010). Calibration trials conducted for this study confirmed an overall mean error of ± 1.13mm when measuring a reference bar of known length. Because measuring a moving object is more challenging, the software's accuracy was then investigated by comparing the stereo camera measurements of fish longer than 70cm with manual size measurements taken less than 30 days prior. This method yielded an average error of ±1.81 mm (Figure S4, Table S2). Attempts were made to obtain size measurements using the stereo system within 1 week of the fish's manual post-capture measurement. However, this proved challenging, as the fish required more time to re-acclimate to human presence and often swam too quickly or attempted to escape, making accurate measurements difficult within this short time frame. Nevertheless, the errors associated with our fish measurements did not show a significant increase in variance (variance = 2.324) compared to those observed with the calibration toolbar (variance = 2.264). This suggests that the software's measurement error remains consistent when applied to real fish. The positive shift in the median error for the fish measurements (median = 1.48 mm) reflects the fish's natural growth over the 30 days between the two measurements. This consistency in error variance across both methods indicates that the software performs reliably for measuring wild fish. In cases where sequential measurements indicated an apparent decrease in length, the earlier measurement was retained to conservatively account for measurement uncertainty.

Individuals were typically revisited approximately once per month (median interval = 28 days, mean = 35 days). Changes in body size between consecutive measurements were generally small (median = 1 mm; mean = 2.5 mm). Because the software of the photogrammetric sizing camera records body size as continuous values rather than fixed size classes, measurements did not occur at uniform size intervals among individuals. We therefore used linear interpolation between consecutive measurements to estimate the time required for each fish to reach successive millimeter increments. This procedure reconstructed continuous, evenly spaced size trajectories for each individual, enabling direct comparisons among fish and facilitating the construction of deme-level size–age growth curves

To derive deme-specific growth rates, we calculated the mean time required for individuals at each site to grow by 1 mm at a given body size. These estimates were then used to infer expected size-age relationships, providing approximate age estimates in the absence of direct age data. Growth trajectories for each deme were subsequently modelled using the von Bertalanffy Growth Function (VBGF), fitted via non-linear least-squares regression with the nlsLM() function from the *minpack.lm* package (Elzhov et al. 2023).

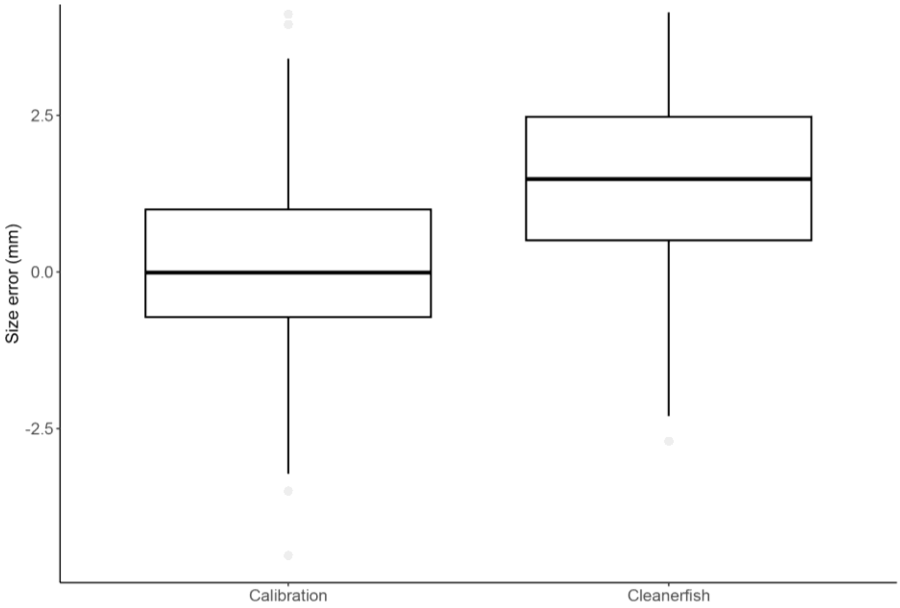

Figure S4: Sizing error using the calibration tool and the focal cleaners. The following figure shows the size error of the software obtained using sizing focal cleaners ("Cleanerfish") measured 30 days from their manual sizing, and using the objects of known size ("Calibration").

Table S2: System's errors obtained with the different methods.

Method	Mean Error (mm)
Small	± 0.981
Medium	± 1.08
Large	± 1.37
General Tool	± 1.13
Fish	± 1.81

Supplement S3: Resident and Visitor families

Table S3: Residency classification of families.

Family (spp. nb)	**Type**
Acanthuridae (n = 25)	Visitor
Apogonidae (n = 17)	Resident
Balistidae (n = 7)	Visitor
Belonidae (n = 1)	Visitor
Blenniidae (n = 12)	Resident
Caesionidae (n = 10)	Visitor
Caragidae (n =2)	Visitor
Carcharhinidae (n = 1)	Visitor
Chaetodontidae (n = 24)	Visitor
Dasyatidae (n = 1)	Visitor
Diodontidae (n = 1)	Visitor
Ephippidae (n = 3)	Visitor
Gobiidae (n = 7)	Resident
Haemulidae (n = 13)	Visitor
Hemiraphidae (n = 1)	Visitor
Holocentridae (n = 12)	Resident
Kyphosidae (n = 2)	Visitor
Labridae (n = 50)	Visitor
Lethrinidae (n = 9)	Visitor
Lutjanidae (n = 12)	Visitor
Microdesmidae (n = 2)	Resident
Monacanthidae (n = 2)	Resident
Mullidae (n = 9)	Visitor
Muraenidae (n = 1)	Visitor
Nemipteridae (n = 6)	Visitor
Ostraciidae (n = 2)	Visitor
Pempheridae (n = 1)	Resident
Pinguipedidae (n = 4)	Resident
Plesiopidae (n = 1)	Resident
Pomacanthidae (n = 7)	Visitor
Pomacentridae (n = 62)	Resident
Priacanthidae (n = 2)	Resident
Pseudochromidae (n = 2)	Resident
Scaridae (n = 26)	Visitor
Scombridae (n = 1)	Visitor
Serranidae (n = 25)	Visitor
Siganidae (n = 8)	Visitor
Sphyraenidae (n = 3)	Visitor
Synodontidae (n = 3)	Resident
Tetraodontidae (n = 9)	Visitor
Zanclidae (n = 1)	Visitor

Supplement S4: Model Details and Assumption Checks

Table S4: Glossary for tables S5 and S6.

Term	**Definition**
Aggression Type	Attacked by dominants, attacking subordinates.
Belly	Presence of a distended belly (indication of eggs).
Body Sygmoid	A behaviour directly implying the presence of eggs.
Chose_Diff	Distance in time to the nearest high tide (in hours).
Client D.	Client fish reef density within a deme (per $150m^2$).
Cleaner D.	Adult cleaner fish reef density within a deme (per $150m^2$).
Duration	Individual average time spent cleaning during a 20-minute video.
General	Average proportion of time individuals spend in presence of dominant individuals during a 20 minute video.
ID	Cleaner ID used as a random factor to control for repeated measures.
Jolt	Individual average jolt rate.
Moon	Moon phase.
Number	Individual average number of cleaning interactions.
Response	Individual average proportion of jolts that were wither punished or led to termination of the interaction.
Site	Study deme from which the fish is from.
Strategy	Growth strategy (fast, slow, or average grower) deriving form deme-specific growth curves.
Strategy g.	Growth strategy (fast, slow, or average grower) deriving form population-wide growth curve.
Survival	Binary : alive (1) or dead (o) at the end of the study period.
Type	Resident or Visitor client.
TS	Individual average percentage of interactions with tactile stimulation.

Table S5: Model Description.

Model	Description
1	Investigates differences in average cleaning duration between growth strategies.
2	Investigates differences in average number of cleaning interactions between growth strategies.
3	Investigates differences in average jolt rate duration between growth strategies.
4	Investigates differences in average percentage of cleaning interactions with tactile stimulation duration between growth strategies.
5	Investigates differences in average client responsiveness between growth strategies.
6	Investigates survival of fast, slow, and average growers in relation to two principal components formed by our cleaning service variables.
7.1	Investigates a correlation between cleaner density and the proportion of time spent with dominant individuals.
7.2	Investigates a correlation between cleaner density and the proportion of aggression received.
8.1	Investigates if proportion of growth strategies is affected by client reef density and cleaner to client ratio.
8.2	Investigates a correlations between cleaner density and client density.
8.3	Investigates a correlation between cleaner density and cleaner-to-client ratio.
8.4	Investigates a correlation between client density and cleaner-to-client ratio.
9	Investigates frequency of distended belly (proxy of spawning activity) in fast, slow, and average growers.
10	Investigates frequency of Body sigmoid (proxy of spawning activity) in fast, slow, and average growers.
11	Investigates frequency of spawning in fast, slow, and average growers.
12	Investigates differences in the average proportion of time spent with larger individuals between growth strategies.
13	Investigates if the average proportion of aggression directed and received is affected by cleaner fish reef density for both growth strategies.

Table S6: Model Summary.

Model	Type	Formula	Nb of Video (nb of ID)
1	LMM (Gaussian)	log(Duration+3.05)~Strategy+Type+Site+Strategy:Type+ Strategy:Site+Type:Strategy+(1|ID), dispformula = ~Site	Fast =120(34), Average = 323(67), Slow = 471(93)
Simplified to:		log(Duration+3.05)~Strategy+Type+Site +Type:Strategy+(+|ID), dispformula = ~Site*Type+Strategy	
2	LMM	log(Number+2.9)~Strategy+Type+Site+Strategy:Type+Strategy:Site +Type:Site+(1|ID)	Fast =120(34), Average = 323(67), Slow = 471(93)
Simplified to:		log(Number+2.9)~Strategy+Type+Site+Type:Site+(1|ID)	
3	LMM	log(Jolt+1.61)~Strategy+Type+Site+Strategy:Type+Strategy:Site+ Type:Site+(1|ID)	Fast =120(34), Average = 323(67), Slow = 471(93)
Simplified to:		log(Jolt+1.61)~Strategy+Type+Site+(1|ID)	
4	GLMM (Beta, logit)	TS~Strategy+Type+ Site+ Strategy:Site+Strategy:Type+ Type:Site+(1|ID), dispformula =~Strategy+Type+Site	Fast =120(34), Average = 323(67), Slow = 471(93)
Simplified to:		TS~Strategy+Type+ Site+ Type:Site+(1|ID), dispformula =~Strategy+Type+Site	
5	GLMM (Tweedie, log)	Response ~ Strategy +Type + Site+ Strategy:Type + Strategy:Site + Type:Site + (1 | ID)	Fast =120(34), Average = 323(67), Slow = 471(93)
Simplified to:		Response ~ Strategy *Type + Site + (1 | ID)	
6	GLMM (Binomial, logit)	Survival ~(PC1 + PC2)*Strategy + (1|Site)	Average = 69, Slow =91, Fast = 30
7.1	Cor.test	cor.test(General, Cleaner d.)	n=748 id=177
7.2	Cor.test	cor.test(Attacked, Cleaner d.)	n=748 id=177
8.1	GLMM (Binomial, logit)	Prop~Strategy*Ratio, weights = Tot	Sites = 8
8.2	Cor.test	Cor.test(Cleaner d., Client d.)	Sites =8
8.3	Cor.test	Cor.test(Ratio, Cleaner d.,)	Sites =8
8.4	Cor.test	Cor.test(ratio, Client d.,)	Sites =8
9	GLMM (Binomial, logit)	Belly ~ Strategy +Chose_Diff + I(Chose_Diff^2) +(1|Site) +(1 | ID)+(Chose_Diff | Moon)	Fast=87(32), Avg = 188(62), Slow= 286(83)
10	GLMM (Binomial, logit)	Body Sygmoid ~ Strategy +Chose_Diff + I(Chose_Diff^2) +(1|Site)+(1 | ID)+(Chose_Diff | Moon)	Fast=87(32), Avg = 188(62), Slow= 286(83)
11	GLMM (Binomial, logit)	Spawn ~ Strategy +Chose_Diff + I(Chose_Diff^2) +(1|Site)+(1|Moon)	Fast=87(32), Avg = 188(62), Slow= 286(83)
12	LMM	Log(Attacked) ~Strategy * Aggression Type+(1|Site/ID), weights = number videos.	Fast=102(33), Slow = 382(83), Avg = 262(61)
13	LMM	Log(General)~Strategy+(1|Site), weights = number of video	Fast=102(33), Slow = 382(83), Avg = 262(61)

Supplement S5: Details for Model 1

Table S7: Analysis of deviance: Type II Wald Chi-square Tests, for Model 1.

Term	Chisq	Df	Pr (> Chisq)
Strategy	15.1590	2	0.0005108**
Type	214.5500	1	<2.2e-16***
Site	21.4119	7	0.0032060**
Strategy:Site	16.4789	14	0.2850118
Strategy:Type	1.1243	2	0.5699758
Type:Site	27.8120	7	0.0002378***

Table S8: First Emmeans Contrast for Model 1.

Contrast Resident-Visitor					
Contrast	**Estimate**	**SE**	**Df**	**T ratio**	**p-value**
CG	-1.080	0.105	347	-10.3	<.0001***
H	-0.321	0.181	347	-1.772	0.0772
LU	-0.350	0.296	347	-1.182	0.2379
AB	-1.141	0.238	347	-4.786	<.0001***
ME	-1.376	0.189	347	-7.268	<.0001***
MW	-1.139	0.218	347	-5.234	<.0001***
O	-0.712	0.179	347	-3.977	0.0001***
W	-0.483	0.206	347	-2.339	0.0199*
Contrasts are still on the log(mu + 3.5) scale.					

Table S9: Second Emmeans Contrast for Model 1.

Contrast Resident-Visitor					
Contrast	**Estimate**	**SE**	**Df**	**T ratio**	**p-value**
Slow-Average	0.161	0.0912	347	1.771	0.1810
Slow-Fast	0.401	0.1130	347	3.538	0.0013**
Average-Fast	0.239	0.1240	347	1.933	0.1310
Results are averaged over the levels of: Type, Site					
Note: contrasts are still on the log(mu + 3.05555555555556) scale.					

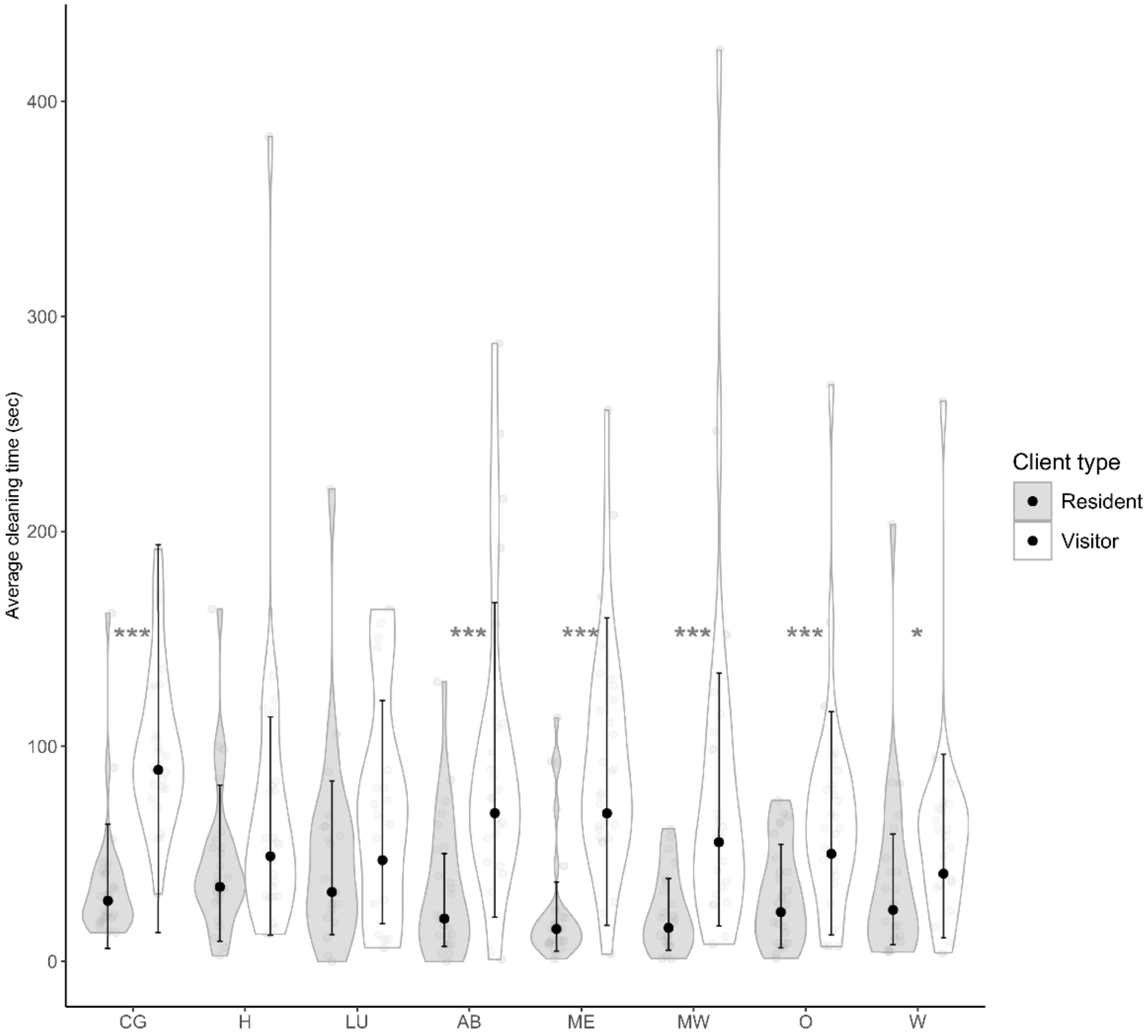

Figure S5: Effect of site on average cleaning time. For each level of client type (Resident or Visitor) and growth strategies, this graph shows the distribution of average cleaning duration for each site and each client type as violin plots. Jittered points represent raw individual-level data. The overlaid points and error bars indicate model-estimated means ± standard errors (SE; Model 1; Gaussian LMM). The asterisk indicates a significant difference between the two groups involved (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$). Cleaning data includes 914 videos (fast = 120, slow = 471, average = 323) for 194 cleaner ID (fast = 34, slow = 93, average = 67).

Supplement S6: Details for Model 2

Table S10: Analysis of deviance - Type II Wald Chi-square Tests for Model 2.

Term	Chisq	Df	Pr (> Chisq)
Strategy	8.5892	2	0.01364 *
Type	18.8748	1	1.396e-05***
Site	14.8732	7	0.03776*
Strategy:Type	2.2924	2	0.31784
Strategy:Site	13.0641	14	0.52184
Type:Site	67.0498	7	5.818e-12 ***

Table S11: First Emmeans Contrast for Model 2.

Contrast Resident-Visitor					
Site	**Estimate**	**SE**	**Df**	**T ratio**	**p-value**
CG	-0.330	0.111	182	-2.978	0.0033**
H	0.222	0.111	182	2.006	0.0463*
LU	0.159	0.130	186	1.224	0.2224
AB	-0.113	0.113	185	-1.002	0.3178
ME	-0.685	0.106	185	-6.456	<.0001***
MW	-0.559	0.116	182	-4.840	<.0001***
O	-0.111	0.106	185	-1.048	0.2958
W	0.193	0.121	182	1.599	0.1116
Contrasts are still on the log(mu + 2.9) scale.					

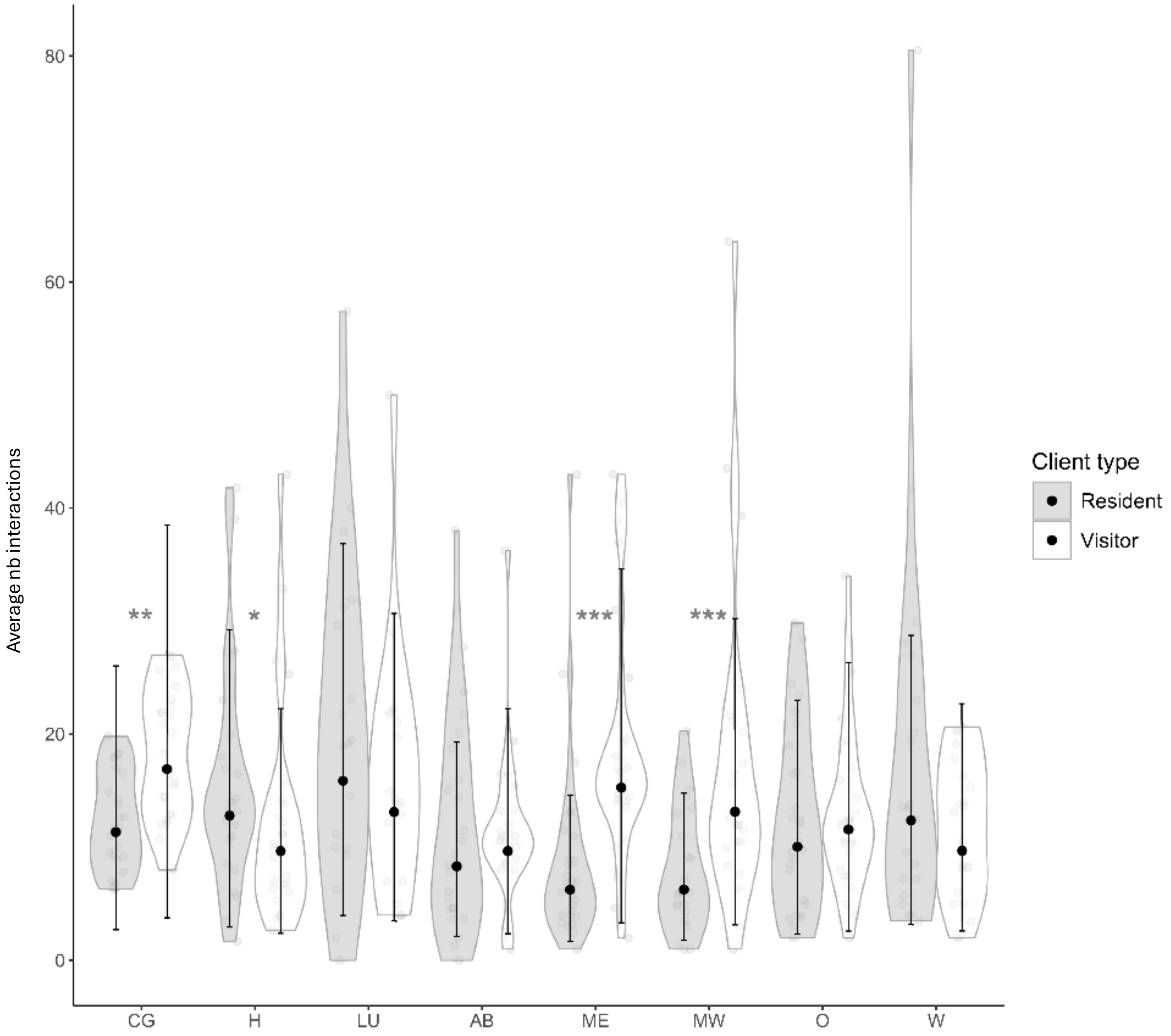

Figure S6: Effect of site on average number of interactions cleaning time. For each level of client type (Resident or Visitor) and growth strategies, this graph shows the distribution of average number of cleaning interactions for each site and each client type as violin plots. Jittered points represent raw individual-level data. The overlaid points and error bars indicate model-estimated means ± standard errors (Model 2: Gaussian LMM). The asterisk indicates a significant difference between the two groups involved (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$). Cleaning data includes 914 videos (fast = 120, slow = 471, average = 323) for 194 cleaner ID (fast = 34, slow = 93, average = 67).

Table S12: Second Emmeans Contrast for Model 2.

Contrast	Estimate	SE	Df	T ratio	P value
Average-Fast	0.133	0.0972	185	1.374	0.3567
Average-Slow	-0.127	0.0733	183	-1.732	0.1961
Fast-Slow	-0.261	0.0925	185	-2.816	0.0149*
contrasts are still on the log(mu + 2.9) scale.					

Supplement S7: Details for Model 3

Table S13: Analysis of deviance - Type II Wald Chi-square Tests for Model 3.

Term	Chisq	Df	Pr (> Chisq)
Strategy	13.1738	2	0.001378**
Type	9.6372	1	0.001907**
Site	5.1440	7	0.642395
Strategy:Type	2.3844	2	0.303552
Strategy:Site	18.6959	14	0.176897
Type:Site	10.7936	7	0.147878

Table S14: First Emmeans Contrast for Model 3.

Contrast	Estimate	SE	Df	T ratio	p-value
Slow-Average	0.299	0.108	182	2.764	0.0172*
Slow-Fast	0.421	0.137	185	3.076	0.0068*
Average_fast	0.122	0.144	185	0.846	0.6746
Contrasts are still on the log(mu + 1.61) scale.					

Table S15: Second Emmeans Contrast for Model 3.

Contrast	Estimate	SE	Df	T ratio	P value
Resident-Visitor	0.249	0.0806	192	3.083	0.0024**
Contrasts are still on the log(mu + 1.61) scale.					

Supplement S8: Details for Model 4

Table S16: Analysis of deviance - Type II Wald Chi-square Tests for Model 4.

Term	Chisq	Df	Pr (> Chisq)
Strategy	3.9821	2	0.13655
Type	223.0188	1	<2e-16***
Site	14.1353	7	0.04883*
Strategy:Site	16.4819	14	0.28484
Strategy:Type	1.2688	2	0.53025
Type:Site	6.0246	7	0.53688

Table S17: First Emmeans Contrast for Model 4.

Contrast	Estimate	SE	Df	Z ratio	p-value
Slow-Average	-0.058	0.131	Inf	-0.442	0.8980
Slow-Fast	0.271	0.172	Inf	1.575	0.2566
Average_fast	0.329	0.183	Inf	1.794	0.1714
Results are averaged over the levels of : Strategy, Site. Results are given on the log odds ratio (not the response) scale.					

Table S18: Second Emmeans Contrast for Model 4.

Contrast	Estimate	SE	Df	Z ratio	p-value
Resident-Visitor	-1.47	0.101	Inf	-14.578	<.0001***
Results are averaged over the levels of : Strategy, Site. Results are given on the log odds ratio (not the response) scale.					

Supplement S9: Details for Model 5

Table S19: Analysis of deviance - Type II Wald Chi-square Tests for Model 5.

Term	Chisq	Df	Pr (> Chisq)
Strategy	5.6484	2	0.05936 .
Type	15.2009	1	9.666e-05***
Site	9.3391	7	0.22922
Strategy:Site	13.1226	14	0.51690
Strategy:Type	0.2381	2	0.88775
Type:Site	9.1693	7	0.24073

Table S20: First Emmeans Contrast for Model 5.

Resident/Visitor	Estimate	SE	Df	Z ratio	p-value
Type = Resident					
Average/Fast	0.803	0.159	Inf	-1.109	0.5086
Average/Slow	0.785	0.121	Inf	-1.573	0.2574
Fast/Slow	0.978	0.180	Inf	-0.122	0.9919
Type = Visitor					
Average/Fast	0.848	0.150	Inf	-0.932	0.6200
Average/Slow	0.776	0.105	Inf	-1.885	0.1430
Fast/Slow	0.914	0.150	Inf	-0.544	0.8495

Results are averaged over the levels of: Site
Tests are performed on the log scale

Table S21: First Emmeans Contrast for Model 5.

Resident/Visitor	Estimate	SE	Df	Z ratio	p-value
Strategy = Fast	0.757	0.1490	Inf	-1.409	0.1588
Strategy = Average	0.717	0.1090	Inf	-2.191	0.0285*
Strategy = Slow	0.708	0.0837	Inf	-2.920	0.0035**

Results are averaged over the levels of: Site
Tests are performed on the log scale

Supplement S10: Details for Model 6

Table S22: Analysis of deviance - Type II Wald Chi-square Tests for Model 6.

Term	Chisq	Df	Pr (> Chisq)
PC1	5.3176	1	0.02111*
PC2	0.0225	1	0.88077
Strategy	0.8998	2	0.63769
PC1:Strategy	0.2070	2	0.90170
PC2:Strategy	1.7580	2	0.41520

Supplement S11: Details for Model 7

Table S23: Pearson's product-moment correlations for Model 7.1 and 7.2.

Contrast	Correlation	T-value	Df	p-value
7.1: General/Cleaner D.	0.1176949	3.2371	746	0.001261**
7.2: Attacked/Cleaner D.	0.01581289	0.43195	746	0.6659

Supplement S12: Details for Model 8

Table S24: Analysis of deviance - Type II Wald Chi-square Tests for Model 8.1.

Term	LR Chisq	Df	Pr (> Chisq)
Strategy general	16.7600	2	0.000022294***
Ratio	0.0.000	1	0.9999997
Strategy general :Ratio	13.709	2	0.00010545***

Table S25: Pearson's product-moment correlations for Model 8.2, 8.3, and 8.4.

Contrast	Correlation	T value	Df	p-value
Cleaner D./Ratio	0.7766087	5.7821	22	8.121e-06***
Client C./Ratio	-0.156875	-0.74503	22	0.4641
Cleaner D./Client D.	0.4881177	2.6232	22	0.01553*

Supplement S13: Details for Model 9

Table S26: Analysis of deviance - Type II Wald Chi-square Tests for Model 9.

Term	Chisq	Df	Pr (> Chisq)
Strategy	2.2389	2	0.3248
Chose_Diff	1.0332	1	0.3094
I(Chose_Diff^2)	1.5127	1	0.2187

Supplement S14: Details for Model 10

Table S27: Analysis of deviance - Type II Wald Chi-square Tests for Model 10.

Term	Chisq	Df	Pr (> Chisq)
Strategy	0.2065	2	0.90189
Chose_Diff	1.6477	1	0.19927
I(Chose_Diff^2)	6.1207	1	0.01336*

Supplement S15: Details for Model 11

Table S28: Analysis of deviance - Type II Wald Chi-square Tests for Model 11.

Term	Chisq	Df	Pr (> Chisq)
Strategy	1.1813	2	0.55397
Chose_Diff	2.8034	1	0.09406.
I(Chose_Diff^2)	15.4901	1	8.294e-05***

Supplement S16: Details for Model 12

Table S29: Analysis of deviance - Type II Wald Chi-square Tests for Model 12.

Term	Chisq	Df	Pr (> Chisq)
Strategy	11.484	2	0.003208**

Table S30: First Emmeans Contrast for Model 12.

Contrast	Estimate	SE	Df	T ratio	p-value
Average-Fast	0.339	0.124	172	2.741	0.0185*
Slow-Average	0.062	0.084	172	-0.737	0.7417
Slow-Fast	0.401	0.119	172	-3.379	0.0026
Results are given on the log (not the response) scale. P value adjustment: tukey method for comparing a family of 3 estimates					

Supplement S17: Details for Model 13

Table S31: Analysis of deviance - Type II Wald Chi-square Tests for Model 13.

Term	Chisq	Df	Pr (> Chisq)
Strategy	5.0034	2	0.08194.
Aggression Type	25.4417	1	4.560e-07***
Strategy : Aggression Type	34.6935	2	2.927e-08***

Table S32: First Emmeans Contrast for Model 13.

Contrast	Estimate	SE	Df	T ratio	p-value
Type = Attack					
Slow-Average	-0.0143	0.171	345	-0.084	0.9961
Slow-Fast	0.3323	0.217	345	0.2760	0.2760
Average-Fast	0.3466	0.227	345	0.2800	0.2800
Type = Attacked					
Slow-Average	0.5835	0.171	345	3.419	0.0020
Slow-Fast	0.4444	0.217	345	2.053	0.1014
Average-Fast	-0.1391	0.227	345	-0.612	0.8134
Results are given on the log (not the response) scale.					
P value adjustment: tukey method for comparing a family of 3 estimate					

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General Discussion

A brief summary of the main results

In this thesis, I aimed to address two main gaps in the study of protogyny through a long-term observational study of the cleaner wrasse (*Labroides dimidiatus),* at Lizard Island on the Great Barrier Reef, Australia. First, I investigated sex-specific life-history traits, particularly survival and growth, in a sequentially hermaphroditic polygynous system. I tested the prediction that sex-changing life histories can deviate from the typical pattern of higher male mortality observed in gonochoristic species. Second, I set out to deepen our understanding of sex change in protogynous species with size-based hierarchies that lack the threat of eviction and have limited social control. Specifically, I asked whether such systems conform to the classical expectation that only the largest female changes sex upon the male's disappearance. Finally, building on the results of the first two chapters, I highlighted, specifically for the cleaner wrasse, which life-history trade-offs underlie the strategy of fast growth to increase a female's chance of sex change.

Our first chapter shows that terminal-phase males consistently have higher survival rates than initial-phase females under both normal and extreme conditions. It illustrates that sequential hermaphroditism can significantly impact sex-specific life history trajectories as well as demographic responses to climate extremes in polygynous systems. The second chapter demonstrates that, despite existing in a size-based hierarchy, social control in the cleaner wrasse is incomplete. I observe frequent rank reversals and find that nearly half of all sex changes occur while the dominant male remains present, especially in spatially dispersed, branching social systems where male attention is divided. Moreover, females employ strategies such as rapid growth and opportunistic harem migration to increase their chances of becoming males. The third chapter shows that reduced social suppression by the dominant individual is the main suppressor of rapid female growth, a strategy that increases the likelihood of sex change.

The analyses presented in the chapters of this thesis focus on specific subsets of the overall dataset collected during this project. In this general discussion, I occasionally draw on additional observations and exploratory analyses that were not included in the main chapters but provide complementary context and help generate hypotheses for future work. These results should be considered preliminary and will be developed further in follow-up studies. Hereafter, they are referred to as “preliminary analyses”.

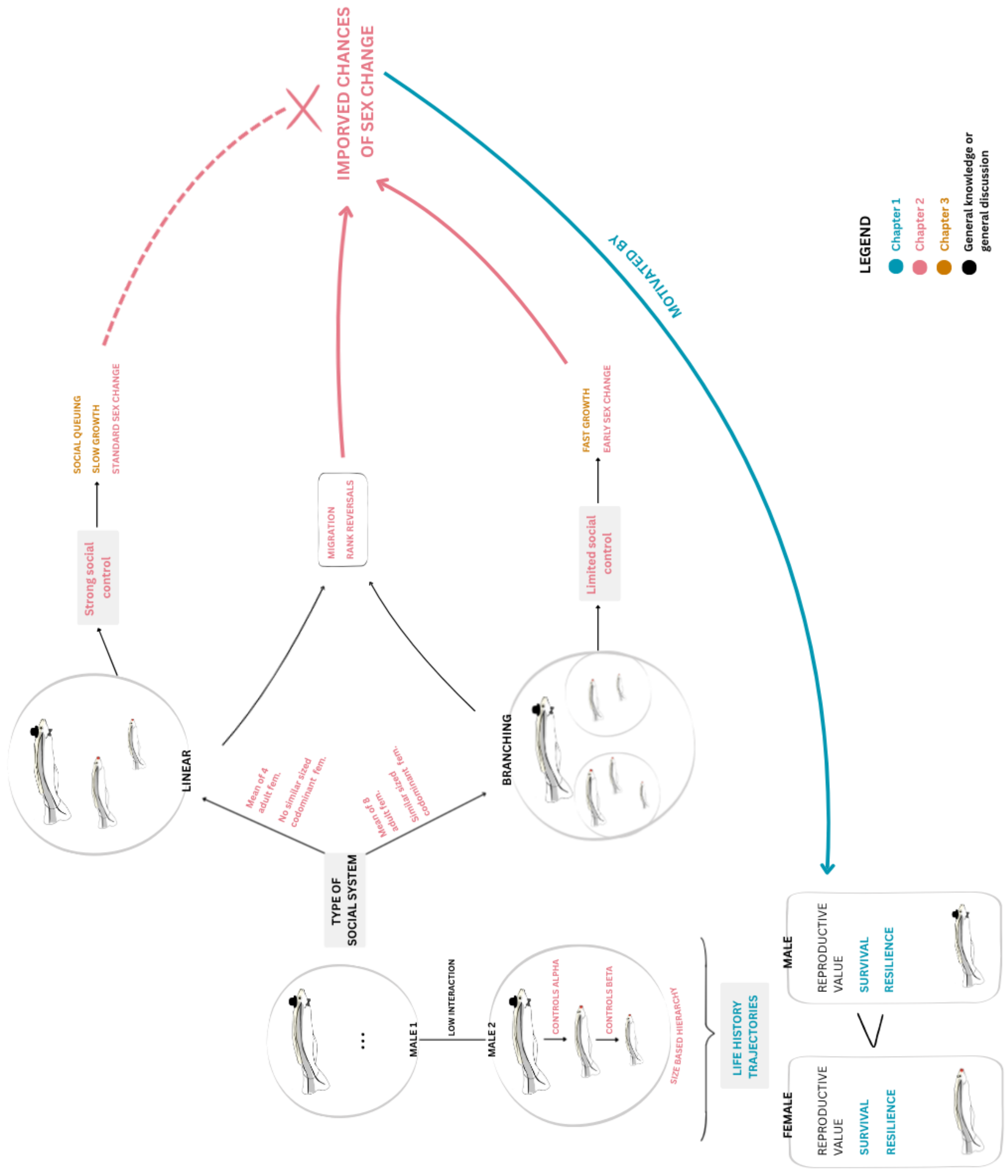

Figure 1: Summary of the main findings of the three chapters of this thesis. Colors highlight from which chapter the result comes from (Blue = Chapter 1, Pink = Chapter 2, Orange = Chapter 3, Black = general knowledge or general discussion).

About the survival of the cleaner wrasse at Lizard Island

General picture

Earlier studies on the life history of the cleaner wrasse have attempted to estimate its survivorship. At One Tree Reef on the southern Great Barrier Reef in Australia, Eckert (1987) extrapolated a 50% probability of surviving up to 5.1 years and a 10% probability of living 8.7 years. Before that, Robertson (1974) estimated a maximum life expectancy of 3-4 years for the cleaner wrasses inhabiting Heron Island in Australia. Finally, Kuwamura (1981) estimated a maximum life expectancy of 6 years on the northern limits of the cleaner wrasse's distribution in Shiramana, Japan. None of these studies differentiated between male and female survival.

Preliminary analyses of our demographic data from Lizard Island revealed that only terminal-phase males appear to benefit from longer survivorship, whereas non-sex-changed females rarely survived beyond 2 years. Using the population-level age-size predictions and average size at sex change (78.35 mm, TL) from **Chapter 2**, we can extrapolate an average age at sex change of 1.9 years. The average size at death of males that died during my PhD was 87.65 mm (TL), suggesting a minimal male life expectancy of 3.3 years. During the last trip in January 2026, 14 of these 95 initial males were still alive. Given an estimated minimal male age of 1.9 years and a 3.5-year study period, the potential maximum life expectancy is 5.3 years. Because the fish have not been observed since, it could be even longer.

This result, together with the consistently higher female mortality observed in **Chapter 1**, indicates that males in this species exhibit a clear survival advantage. Moreover, males appear less vulnerable to extreme environmental conditions, reinforcing the robustness of this pattern. Taken together, these findings suggest that the evolutionary benefits of attaining male status in the cleaner wrasse extend beyond increased reproductive rate and include enhanced survival.

Higher male survival

The leading hypotheses proposed in **Chapter 1** to explain sex differences in survival adopt a female-centered perspective. Specifically, females may be more vulnerable due to the higher energetic costs of egg production, or males may represent a subset of high-quality individuals who have successfully survived the challenges associated with the female phase before undergoing sex change. However, insights from subsequent chapters shift this perspective toward a male-centered view. Instead of questioning why females tend to have higher mortality rates, we should ask why males seem to have a survival advantage over females.

This male survival advantage is, in fact, unexpected for several reasons. First, males are older individuals, and as such, they could be expected to have higher mortality rates than younger individuals due to senescence. Second, in polygynous systems, males generally experience higher mortality rates and lower longevity (Williams 1957; Trivers 1972; Leutenegger and Kelly 1997; Clutton-Brock and Isvaran 2007).

The latter general pattern arises from fundamental differences in reproductive investment between the sexes. Because egg production is more costly than sperm production, females are often the limiting sex, leading to strong intersexual selection and female choosiness, with preference given to males that possess higher social status or greater access to resources (Kruger 2021). When males can monopolize multiple females, as in harem-based polygynous systems, male reproductive success becomes highly skewed, intensifying male-male competition (Kruger 2021). This, in turn, favors traits such as large body size, risk-prone behavior, and weaponry (Bell 1980; Plavcan and van Schaik 1997), which typically carry substantial energetic and survival costs (Kruger 2021) and are associated with reduced longevity (Williams 1957; Hämäläinen et al. 2018) and increased mortality (Trivers 1972; Leutenegger and Kelly 1997).

Male guarding, the formation of harems, and intrasexual competition are direct consequences of population structure. In gonochoristic polygynous species, the sex ratio at birth is typically 1:1 (Trivers 1972; Bell 1980), but higher male mortality subsequently biases the adult population ratio toward females (Trivers 1972; Bell 1980; Smith et al. 1982). Despite this, male-male encounters remain frequent, maintaining high levels of intrasexual competition. Moreover, the operational sex ratio, the number of fertilizable females per sexually active males (Emlen and Oring 1977; Mitani et al. 1996), is typically male-biased because males are continuously sexually active, whereas females are receptive only during brief, asynchronous periods (Emlen and Oring 1977).

However, this framework does not fully apply to protogynous systems such as the cleaner wrasses. Although terminal-phase males are larger and defend a harem of females, they are not subject to the same competitive dynamics as males in gonochoristic polygynists. In protogynous species, the adult sex ratio is biased towards the first sex (Allsop and West 2004). Under the size-advantage model, individuals maximize fitness by reproducing first as females and changing sex only once they are large enough to monopolize reproductive opportunities (Ghiselin 1969). This process limits the number of males in the population and reduces direct male-male competition, leading to a relatively stable adult sex ratio (approximately 1:4 at Lizard Island). Additionally, the cleaner wrasse is a free spawner, and large females are known to spawn daily with their harem male (Robertson 1974). Even though the spawning frequency of smaller reproductive females is less stable (Robertson 1974), the operational sex ratio of the cleaner wrasse remains at least 1:1.

Male reproductive tactics, such as sneakers and satellites, are absent in this species, reducing further sources of intrasexual competition (Taborsky 1998; Alonzo et al. 2000; Sato et al. 2004; Oliveira et al. 2008). Empirical observations from **Chapter 2,** support this reduced competitive environment. Early sex change was consistently linked to rapid and successful reproduction within the new harem, either originating from a fission of the previous male's harem or acquired from females outside the initial harem. This type of early sex change is called “harem fission” (Shapiro 1979; Shapiro and Lubbock 1980; Hoffman et al. 1985; Aldenhoven 1986) and differs from the type called “bachelor male” for which early sex changers go through prolonged periods of reproductive inactivity (Clavijo 1982; Moyer and Zaiser 1984; Hoffman et al. 1985; Aldenhoven 1986; Ross 1990) and represent a potential source of conflicts for the male harem.

Consistent with this, direct male-male aggression appears to be extremely rare. Over four years of observations at Lizard Island, only two clear male-male conflicts were recorded, both involving limited and localized changes in harem structure. The first involved two harem males and resulted in one losing part of his harem. The second case involved an early sex changer that disappeared after its original male regained control of the branch. Shortly thereafter, in the same branch, a new early sex changer appeared, and the male lost the branch again.

Rather than engaging in direct competition with other males, dominant males primarily maintain their status by controlling the sex change tendencies of females within their harem. As shown in **Chapter 2,** this control is facilitated by the size-based hierarchy characteristic of this species. Because competitive interactions are strongest between individuals of similar size (Enquist et al. 1987; Jennions and Backwell 1996; Cant and Johnstone 2000; Nathan et al. 2001; Bender et al. 2005), females effectively regulate each other, reducing the need for active male enforcement. Therefore, from a game-theoretical perspective, the reduced effort required for males to acquire and maintain reproductive dominance could explain the lack of survival cost typically associated with the male sex, in addition to reduced need for further growth and the classic cheaper gametes.

Table 1: Summary of the key differences between classical polygynous systems and the protogynous haremic system of the cleaner wrasse that could explain observed differences in sex-specific survival rates.

	Classical polygynous systems	**Protogynous haremic system (cleaner wrasse)**	**Consequences for cleaner wrasse males**
Adult sex ratio	Sex ratio at birth is typically 1:1	Strongly female-biased due to sex change (1:4)	Fewer male-male competitive encounters
Gametes cost	Male gametes are less costly	Male gametes are less costly	Similar energetic cost
Operational sex ratio	Male-biased (many sexually active males, few receptive females)	Rather balanced females spawn frequently)	Reduced competition for access to mates
Male-male competition	Intense, frequent	Extremely rare	Lower injury, stress, and risk-taking
Male reproductive role	Actively compete, fight, and guard access to females against other males	Maintain the harem and suppress sex change. However, females perform part of his duties (size-based hierarchy.	Lower energetic and behavioural costs
Path to dominance	Direct competition with other males	Mostly queuing in a size hierarchy among females	Dominance requires waiting rather than fighting
Growth strategy	Growing faster than females is favoured for competition	Growth slows after sex change	Reduced energetic expenditure
Source of males	Born male (no filtering)	Derived from surviving females (quality filter)	Males could be high-quality individuals
Cost of being a male	High	Low	Explains survival

Factors related to changes in survival

In **Chapter 1**, the increased female survival in winter 2024 is speculated to be linked to either greater access to cleaning opportunities or reduced intraspecific competition. Both possibilities stem from a reduction in both cleaner density and the cleaner-to-client ratio in 2024 compared to 2023.

The hypothesis of reduced intraspecific competition concerns levels of aggression and control among individuals within the same and/or adjacent harems. However, this hypothesis is not supported by the results of subsequent chapters. First, even though cleaners spend less time with dominants at lower densities (**Chapter 3**), the incidence of aggression from conspecifics remains unchanged at these lower densities (**Chapter 3**). This indicates that direct competitive interactions do not diminish as population density decreases. Second, Harem size was not correlated with cleaner density (**Chapter 2**), indicating that individuals experience a similar number of competitors within harems regardless of overall population density. Together, these findings do not support the idea that reduced aggression underlies the observed survival patterns.

Instead, the results support the second hypothesis presented in **Chapter 1**. The positive correlation between overall time spent with dominant individuals and cleaner densities (**Chapter 3)**, suggests that at lower densities, cleaners may compete less with same-harem individuals for access to cleaning opportunities, even though the number of cleaners per harem remains the same (**Chapter 2**). Additionally, in **Chapter 3**, I show a direct positive correlation between overall investment in cleaning interactions and survival.

Therefore, given the lower cleaner-to-client ratio in winter 2024, these results suggest that variation in survival is not mediated by reduced intraspecific competition per se, but rather by differences in access to cleaning opportunities. This interpretation is further supported by patterns observed in 2023, a year unaffected by El Niño. In that year, female mortality showed a consistent seasonal trend with client density: during winter, when client density was lower, female mortality was higher than in summer.

About growth patterns of the cleaner wrasse at Lizard Island

General picture

Growth strategies and strategic growth in the cleaner wrasse have not been previously explored. Earlier studies focused primarily on describing general growth patterns, such as population growth curves and sizes at key life-history transitions (Robertson 1974; Kuwamura 1981).

Like many fish, cleaner wrasse exhibit indeterminate growth, continuing to increase in length and weight throughout life, although growth rates decline with age (Robertson 1974). Juveniles settle onto the reefs at approximately 10 mm in total length, following a pelagic larval phase (Robertson 1974; Kuwamura 1981). Early growth rates vary geographically: for example, initial growth at Shiramana (Japan) is nearly three times faster than that at Heron Island on the Great Barrier Reef, although growth there halts during winter due to low temperatures at the northernmost limit of the species' range (Robertson 1974; Kuwamura 1981). Based on these studies, females were estimated to reach sexual maturity at around 60 mm and to require growth to approximately 95 mm before attaining a size sufficient to take over and sex change (Robertson 1974; Kuwamura 1981).

At Lizard Island, growth patterns are more similar to those of Heron Island (Robertson 1974). This is especially true for the initial growth rate, as model predictions indicate that it would take roughly 7 months to reach 50mm in size from settlement. However, in contrast to previous findings, growth does not slow during winter under normal conditions, but it increases.

More importantly, two key differences emerge. First, from preliminary analyses, sexual maturity appears to occur at smaller sizes: females were observed spawning from 50 mm onwards, with occasional observations of individuals as small as 40-45 mm displaying reproductive behavior such as body-sigmoid displays or spawning. Second, the average size at sex change reported in **Chapter 2** is approximately 18% smaller at Lizard Island (78.3 mm, TL). These differences may partly reflect methodological improvements, with more accurate size estimation in the present study. Alternatively, they may indicate that early sex change occurs more frequently than previously reported, thereby shifting both the timing of maturation and the size at sex change. Interpreting this pattern as a true absence of early sex change in populations such as Shiramana or Heron Island, however, seems unlikely. A more parsimonious explanation is that its prevalence has been underestimated due to methodological biases: earlier studies often induced sex change experimentally by removing males, which likely skewed observations toward socially regulated, "classical" pathways and limited detection of naturally occurring early sex change.

Growth patterns, social control, and cleaning

The same two hypotheses proposed in **Chapter 1** to explain reduced female mortality in winter 2024, namely intraspecific competition and access to cleaning opportunities, were also considered as potential drivers of the observed increase in growth rates for both females and males. However, results from subsequent chapters point to a different conclusion for growth than for survival.

Although increased access to cleaning opportunities, driven by both reduced time spent with dominant individuals (**Chapter 3**) and a lower cleaner-to-client ratio (**Chapter 1**), clearly enhanced survival (**Chapter 3**), it does not predict variation in growth strategies. Instead, growth patterns are better explained by differences in social control, with reduced constraints from dominant individuals allowing faster growth (**Chapter 3**). While the physiological trade-offs underlying this accelerated growth remain unclear, this pattern is consistent with game-theoretical predictions for species structured by size-based hierarchies and aligns with the findings of **Chapter 2**.

Here, I show that the cleaner wrasse is structured by a size-based hierarchy in which individuals exert control over those directly below them in rank. As a result, individuals socially queue and strategically regulate their growth to avoid approaching too closely in size to their nearest competitor (Hofmann et al. 1999; Kokko and Johnstone 1999; Buston 2003; Heg et al. 2004; Russell et al. 2004; Buston and Cant 2006; Dengler-Crish and Catania 2007; Wong et al. 2007; Young and Bennett 2010; Dubuc and Clutton-Brock 2019). This interpretation is further supported by the patterns of strategic growth observed when females upgrade in rank.

Moreover, rapid growth appears to be a potential strategy that increases a female's likelihood of undergoing sex change. Because other aspects of early sex change are associated with reduced social control from both dominant males and higher-ranking females, this finding completes the picture: the adoption of a fast-growth strategy is itself shaped by variation in social control.

In both **Chapter 2** and **Chapter 3**, the proportion of fast growers increases with cleaner wrasse density. This pattern likely reflects increased competition from neighboring individuals. At higher densities, the number of potential external competitors is greater, reducing a female's likelihood of inheriting a harem following male disappearance. Under these conditions, the whole female population could be incentivized to grow faster, allowing social control within a harem to remain stable because the size gaps between females do not reduce.

Importantly, the expression of this strategy is only possible because harem size remains constant across densities (**Chapter 2**). Since the number of females within a harem does not increase with density, within-harem rank structure is preserved and does not become more compressed. This stability allows individuals to adjust growth strategically in response to external competitive pressure, rather than being constrained by changes in internal group composition. However, the same question remains about where females get the energy to actually grow faster.

The role of temperature

While rapid growth appears to be primarily driven by variation in social control, patterns observed in 2023 indicate that additional environmental factors also contribute. In that year, female growth rates were lower in winter than in summer, despite no corresponding seasonal differences in cleaner wrasse density (**Chapter 1**). If social pressures within and between harems were the sole determinant of growth, no seasonal differences would be expected.

Instead, these results suggest that temperature also plays an important role in shaping growth dynamics. This interpretation is further supported by the 2024 El Niño period, during which unusually warm summer conditions were associated with reduced growth rates. Together, these patterns suggest that, in addition to social factors, seasonal temperature variation may influence growth even under non-El Niño conditions.

The reduction in growth rates during both the normal and the unusually warm summer can be explained by how temperature affects energy and performance in organisms. An increase in temperature increases the standard metabolic rate, the baseline energy required for bodily maintenance (Gillooly et al. 2001). The fish must offset these heightened maintenance costs through higher foraging activity, which in turn drives up metabolic costs. Whether the cleaner wrasse actually increases cleaning activity during summer and El Niño remains an open question. Nevertheless, this data was collected during my PhD and will be included in upcoming analyses.

Once temperatures exceed the species' thermal optimum, these metabolic demands outpace the fish's ability to acquire and process energy (Neubauer and Andersen 2019). At these high-temperature extremes, the fish may also hit a physiological ceiling where its cardiovascular system can no longer supply enough oxygen to tissues (a limitation of its aerobic scope), resulting in a sharp decline in the energy available for somatic growth (Gillooly et al. 2001; Neubauer and Andersen 2019). Thermal performance in a fish follows a dome-shaped curve (Neubauer and Andersen 2019), reconciling our findings with the ones of Kuwamura (1981), who observed reduced growth rates at extremely cold temperatures. At temperatures below the optimum, the enzymatic processes that drive digestion, energy assimilation, and metabolism are reduced, preventing the fish from generating the surplus energy needed for growth (Neubauer and Andersen 2019). Ultimately, growth is constrained at both ends of the temperature spectrum, forming a continuous curve in which any significant deviation above or below the optimal temperature range negatively impacts development.

The impact of temperature on survival is less direct. In a year unaffected by thermal anomalies, neither male nor female mortality rates showed a seasonal pattern. The only seasonal difference was a stark decrease in the female mortality rate during the 2024 winter compared with the warm ENSO summer. Although survival could, in principle, be influenced by the same physiological processes described above, these results suggest that temperature does not play a strong direct role in shaping mortality in this system.

About the role of cleaning in life-history patterns

I predicted that efficient/extended foraging and service quality could be associated with fast growth for two reasons. The first hypothesis is that efficient or extended foraging correlates with increased energy intake, potentially increasing the energy budget available for somatic growth. This prediction is plausible because cleaning interactions constitute the main source of energy intake in the cleaner wrasse (Grutter 1999).

The second hypothesis extends to the social competence of the cleaner wrasse, defined as the ability of an animal to optimize the expression of its social behavior as a function of the available social information (Taborsky and Oliveira 2012). As a matter of fact, because fast growth enhances a female's chance of sex change (**Chapter 2**), this could be interpreted as a socially competent strategy in a species where sex change comes with such great fitness advantages (**Chapter 1**). Because cleaning interactions have been used to demonstrate social competence in this species, it is reasonable to expect that socially competent fish, which maximize their cleaning opportunities through optimal behavior, grow faster.

Cleaners are exposed to a range of complex social “games”, including punishment (Bshary and Grutter 2002b; Bshary and Grutter 2005), partner switching (Bshary and Grutter 2002b; Bshary and Grutter 2002a; Bshary and Grutter 2005), and image scoring (Bshary 2002; Bshary and Schäffer 2002; Bshary and Grutter 2006; Johnstone and Bshary 2007; Pinto, Oates, A. Grutter, et al. 2011). As a result, they are able to fine-tune their behavior according to available social information, adjusting their actions to the type of client, the risk of retaliation, and the broader social context (Bshary 2001; Bshary 2002; Bshary and Grutter 2002b; Bshary and Grutter 2002a; Bshary and Schäffer 2002; Bshary and Grutter 2005; Bshary and Grutter 2006; Cant and Johnstone 2006; Pinto, Oates, A.S. Grutter, et al. 2011). Furthermore, socially competent individuals demonstrate the ability to engage in behaviors that are appropriate and effective in the current social/ecological context (Taborsky and Oliveira 2012; Bshary and Oliveira 2015). Overall, socially competent fish should optimize their opportunities for cleaning.

Our results, however, point to the opposite pattern: slow growers, rather than fast growers, seem to engage in more and longer interactions, suggesting that this strategy is the socially competent one. Instead, as highlighted by the results in **Chapters 2 and 3**, much like early sex change, this strategy could be an opportunistic outcome of reduced social control.

Alternatively, it could be argued that the number and duration of interactions are not the best proxy of optimal performance. Slow growers could be inefficient cleaners that require longer / more frequent interactions to acquire as much energy as efficient fast growers. Their cleaning patterns do, however, represent an increase of almost 40% and 50% in effort duration and number of interactions, respectively. This suggests a very high inefficiency that may not be explained by a lower feeding rate alone. Slow growers do, however, have an almost double cheating rate than fast growers. Although the probability that a cheating event elicits a negative response is the same across growth strategies, clients respond negatively to slow growers twice as often on a daily basis. Because negative responses also involve punishments in the form of chases, which carry energetic and stress-related costs, this, along with a potentially lower biting rate, could better explain the inefficiency in cleaning performance. Also, cheating could come at the cost of actual foraging, leading to the need for longer and more frequent interactions to allow the fish to feed. Finally, high-quality clients (i.e., larger, more parasites) could potentially learn to avoid these cheating cleaners. Having access only to lower-quality clients could contribute to inefficient cleaning.

A potential explanation for why a slow-growing female could, in fact, be a socially competent cleaner is that she chose not to play the sex-changing game and instead maximized her time as a female. Dominant females of some protogynous species sometimes refrain from sex-changing at the disappearance of the male in cases where their reproductive value would not largely improve (Munday et al. 2006). In the cleaner wrasse, because higher cleaning effort increases survival, females could choose to invest in maximizing their lifespan rather than competing for the dominant male position.

Nevertheless, there would have to be physiological and immunological reasons why the females could not participate in the game. Additionally, because there were no clear differences in survival between growth strategies, no differences in reproductive investments between strategies, and no evidence that they were living the game (same levels of aggression, though the time spent with subordinates remains to be explored), this represents a less probable explanation.

Defining whether fast growth is, in fact, the socially competent strategy would have an interesting implication for studies investigating the effects of sex change on brain size. Amman et al (in prep.) show that male cleaner wrasses have larger forebrain sizes than females. The size of this brain part was previously shown to correlate with social competence (Triki et al. 2020): socially competent fish present a larger forebrain size than non-socially competent ones. Therefore, if fast growth was the socially competent strategy because it enhances the chances of sex change, it could suggest that males have larger forebrains because they were females with larger forebrains. Alternatively, if slow growing was the socially competent strategy, it would suggest that sex changers allocate energy to brain development after the transition.

The role of cleaner density

To investigate how local demographics influence the life history and social dynamics of the cleaner wrasse, this thesis uses a multi-site design by collecting data at eight sites that naturally varied in cleaner wrasse density. Previous research has established that the behavioural flexibility, strategic sophistication, and neurological development of the cleaner wrasse are heavily influenced by the environmental complexity in which they develop (Wismer et al. 2014; Triki et al. 2018; Triki et al. 2019). Specifically, variations in the cleaner fish market affect an individual's level of strategic sophistication. This thesis confirms the previously established correlation between cleaner and client densities while further demonstrating that, across our study sites, only cleaner density is positively correlated with the cleaner-to-client ratio.

From a site-level perspective, cleaner fish density affected certain aspects of the cleaner wrasse's growth patterns. Specifically, at higher cleaner densities, we observed a larger proportion of fast-growing individuals and a larger average size at sex change. However, while individuals spend more overall time with dominants at higher densities, local cleaner density does not correlate with conspecific aggression levels. Moreover, it does not predict the fundamental social structure of the harem; the number of adult females and the branching-versus-linear system remain invariant across different population densities.

Ultimately, the primary gain of the design was our ability to interpret the unusual temporal demographic patterns observed during the 2024 winter. By leveraging our findings on the effects of cleaner density at the site level, we could deduce that the temporal reduction in cleaner density in winter 2024 favoured higher female survival by increasing access to cleaning opportunities, while simultaneously facilitating faster somatic growth through reduced dominant social control.

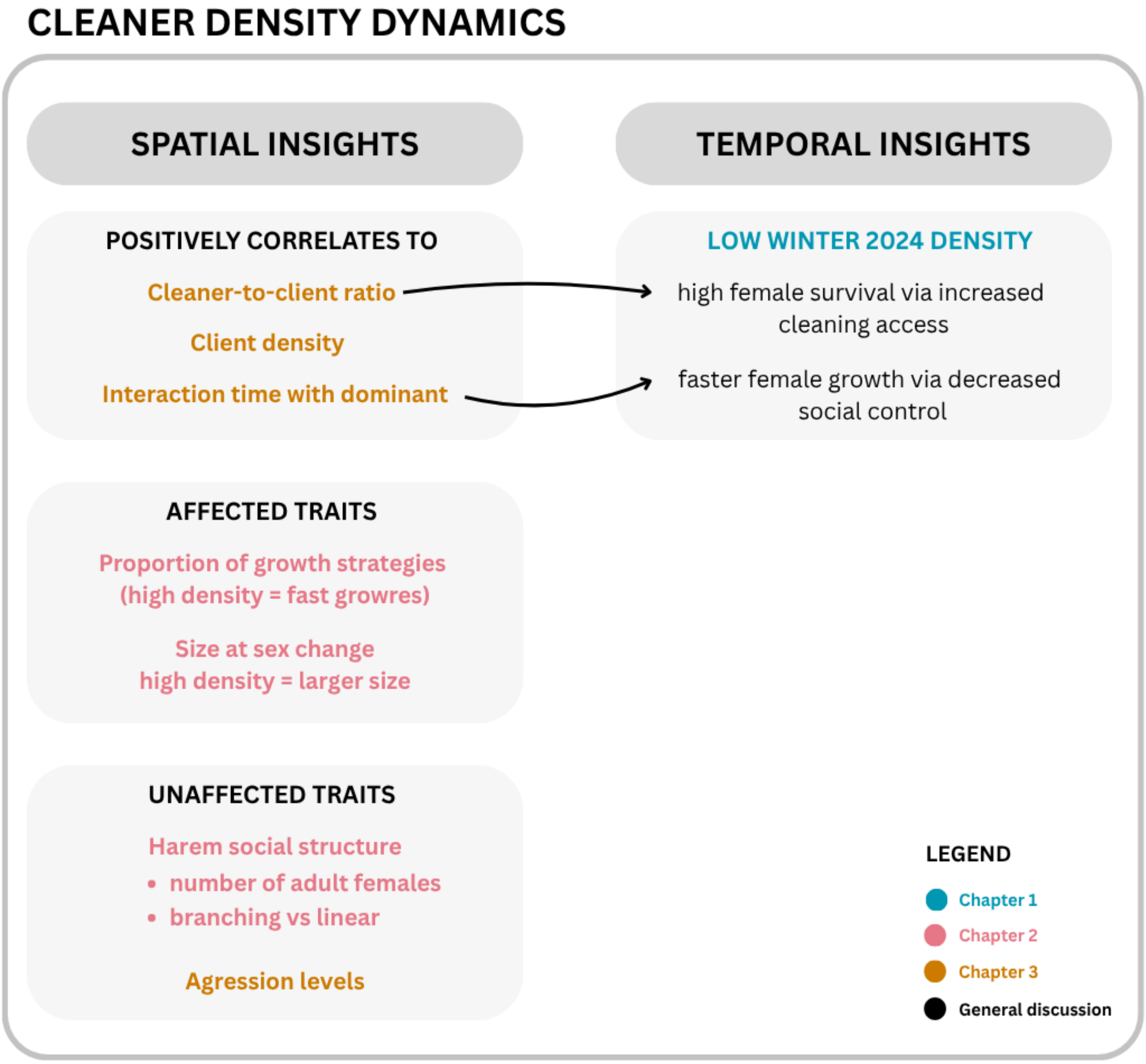

Figure 2: Summary of the main findings on the effects of cleaner density. Colors highlight from which chapter the result comes from (Blue = Chapter 1, Pink = Chapter 2, Orange = Chapter 3, Black = general discussion).

Generalizing the results

This thesis investigates sex-specific life-history patterns and sex-change dynamics in a protogynous hermaphrodite species that plays a key role in the coral reefs (Bshary 2003; Grutter et al. 2003; Ros et al. 2011; Waldie et al. 2011; Triki et al. 2016). However, the cleaner wrasse is not the only protogynous fish of relevance. Many other protogynous species are either essential to coral reef functioning (Bonaldo et al. 2014; Kuwamura et al. 2020) or support valuable commercial and recreational fisheries (Easter et al. 2020).

Protogynous species are known to be disproportionately affected by fishing pressure (Easter et al. 2020). Conservation efforts aimed at restoring natural population dynamics are often implemented through marine protected areas (MPAs) (Klein et al. 2015). However, the effectiveness of MPAs is typically assessed using short-term changes in population abundance and compared to models that rely on simplified assumptions, such as fixed sexes and equal proportions, ignoring the complex effects of size-selective harvest on sex-specific survival, sex ratios, and fertilization success (Easter et al. 2020). Because fisheries disproportionately target larger individuals (Coleman et al. 1996; McGovern et al. 1998; Hawkins and Roberts 2004; Hamilton et al. 2007), and these are predominantly males in protogynous species, harvesting can skew the operational sex ratio toward females. This imbalance may limit reproductive opportunities and influence population recovery within an MPA (Easter et al. 2020).

Although the results of this thesis require validation across other protogynous species, they can already inform fisheries management in several ways. First, they suggest that the recovery of male abundance and sex ratio could be more rapid than for non-sex-changing species. In haremic systems, models show in fact that species operate under a “low importance male system,” meaning that high fertilization can be achieved with few males (Easter et al. 2020). Additionally, my data show that male vacancies due to harvest would be rapidly filled by sex changing females **(Chapter 2)**. However, this could be different in species that do not have flexible, socially cued sex change (Easter and White 2016).

Second, our data suggest that the effectiveness of MPAs for protogynous species should be evaluated over the long term rather than through short-term monitoring, which currently remains the most prevalent strategy (Easter et al. 2020). Population recovery is, in fact, measured through both abundance and reproductive output. Although the sex ratio may recover quickly, sex change can result in the loss of the largest, most reproductive females. Additionally, our results indicate that a new alpha female is unlikely to rapidly achieve a large body size. Following a sex change, males exhibit reduced growth **(Chapter 2)**, and in a size-based hierarchy, females adjust their growth accordingly **(Chapter 2)** (Hofmann et al. 1999; Kokko and Johnstone 1999; Buston 2003; Heg et al. 2004; Russell et al. 2004; Buston and Cant 2006; Dengler-Crish and Catania 2007; Wong et al. 2007; Young and Bennett 2010; Dubuc and Clutton-Brock 2019). Moreover, under low-density conditions, the proportion of slow growers increases at the population level **(Chapter 2)**.

Finally, the lower male mortality rates and vulnerability to extreme events **(Chapter 1)**, introduces two additional considerations. First, this suggests that climate-related disturbances may not compound fishing pressure on males. Second, it highlights additional benefits of MPAs: by stopping or reducing fishing pressure, they protect larger size classes, which include the most climate-resilient individuals in the population. This may help ensure that the most tolerant individuals persist in ecosystems facing increasingly frequent extreme events.

Limitations

The long-term nature of the study

My PhD chapters are based on a long-term observational study that began in July 2022 and continued until January 2026. While some aspects of our chapter would have benefited from more direct sampling and/or experimental manipulations, such approaches would have disrupted observations of the natural dynamics of the cleaner wrasse at Lizard Island, limiting the scope of our life-history data collection. For example, excluding individuals to collect precise physiological, histological, sexual, and age-related data would have introduced bias into survival information and disrupted the natural sex-changing trajectories of our populations. Therefore, I decided to rely entirely on non-invasive techniques to preserve the study populations and their natural social dynamics.

Consequently, I was unable to collect true chronological age data for our focal fish, as direct age determination (e.g., via otolith extraction) would have required sacrificing the subjects. Instead, we relied on model-based estimates of individual ages and deme-specific growth curves constructed from regular size measurements. While this indirect method has inherent limitations, it represents the most robust compromise to answer our research questions without compromising the long-term integrity of the study.

This same requirement for non-invasive monitoring constrained our assessment of potential trade-offs between growth and reproduction. To evaluate reproductive effort, I relied on visual indicators, such as the presence of a large belly to estimate egg mass, and behavioral proxies of spawning activity. However, these behavioral proxies may reflect reproductive readiness or social signaling rather than actual reproductive investment. Because I could not obtain direct egg-count data from spawning events, I cannot rule out the possibility that fast- and slow-growing females differ in the actual quantity of eggs produced or in their gonadal allocation.

Similarly, avoiding disruptions to the social system meant we could not obtain direct physiological measures of the focal individuals to definitively track how energy is partitioned internally. As a result, it remains an open question whether there are more subtle physiological costs or health risks associated with fast growth that our survival data might not capture.

Study design

The study's design required distributing efforts across eight distinct sites. Each site was characterized by unique challenges: some were shallow and accessible only during high tides (Watson and Loomis); one was close to a sandy shore and consistently exhibited poor visibility (Osprey); some were exposed to strong winds and sea conditions (Mermaid and Attached Bommie), allowing access only during favorable weather conditions. Furthermore, sightings of dangerous wildlife (such as crocodiles and jellyfish), storms, spring tides, and cyclones frequently made certain sites inaccessible for extended periods. In addition to natural factors, health-related issues frequently contributed, including ear infections, colds, covid, among others, thereby pausing our work.

Despite spending a total of 2 years on the island and planning our dive routine to the best of my ability, these factors still led to compromises in the quality and/or quantity of our data. First, it was not always possible to visit all individuals and have a balanced number of video observations. It was also sometimes difficult to successfully size fish at a site, and measurements had to be taken on more favorable days, which sometimes affected the time intervals between sizing. The most relevant qualitative compromise concerns the difficulty of collecting reproductive data. Consistent access to all populations at every tide and moon phase proved unfeasible. As spawning typically occurs shortly after high tide and is correlated with the moon phase, establishing a precise dataset on spawning frequency across all individuals was challenging. Additionally, collecting sufficient, detailed data to elucidate the dependence of spawning on tides and the moon at Lizard Island was similarly problematic.

Sizing camera

The stereo camera system and associated software used in this study represent a clear methodological improvement over the visual estimation of fish size. The system and its measurement accuracy are described in detail in the supplementary material. However, one important practical limitation related to camera overheating remains to be discussed.

The system, acquired in 2022, was originally designed to 2020 specifications for the GoPro Hero 8, the latest model at the time. During this PhD, however, obtaining compatible batteries became increasingly difficult, and the system was not readily adaptable to newer camera models. As a result, overheating became a recurring issue that could not be easily resolved.

Even under relatively cool winter conditions, cameras would stop functioning after approximately 40-50 minutes, requiring rapid sampling and limiting the number of individuals that could be measured per dive. In summer, overheating occurred even more quickly, necessitating additional diving days to complete size measurements. These constraints contributed to irregular sampling intervals and made it difficult to maintain consistent time gaps between measurements. They also explain why some individuals were consistently not measured, as fish located at the periphery of study sites were often reached only after the cameras had stopped functioning.

Future and current directions

Several questions emerge from this thesis, some of which may contribute to addressing certain speculations discussed in this general discussion.

Current cleaner directions

Several studies are currently underway to address some of these questions. Although cleaning behavior was used in **Chapter 3** to explore potential life-history trade-offs, more detailed analyses are still in progress.

In particular, three ongoing projects focus on cleaning patterns in the cleaner wrasse population at Lizard Island. The first examines variation in cleaning behavior across life-history stages and sites. These analyses will help determine whether sites with a higher proportion of fast-growing individuals are associated with increased cleaning activity, potentially compensating for higher energetic demands. In addition, comparing cleaning effort between males and females may, for the first time, provide evidence that males invest less time in cleaning than females. Such a pattern could help explain the reduction in growth rate observed after sex change (**Chapter 2**). Alternatively, if males are found to clean as much as, or more than, females, this would suggest a different energetic trade-off. In this case, the reduced somatic growth of males could reflect increased allocation to brain development, consistent with the larger forebrain size reported by Aman M. (in prep.).

The second study examines temporal variation in cleaning behavior across periods before, during, and after the 2024 ENSO event. Its results will help assess whether the relationship between survival and cleaning effort identified in this thesis is robust. In particular, it will test whether cleaning effort increased during winter 2024, thereby providing a potential explanation for the observed patterns in survival.

Beyond confirming these patterns, this study also addresses a key unresolved question in the literature. Previous work has reported a reduction in strategic sophistication following environmental perturbations similar to the 2024 ENSO event, which caused a simplification of the social environment (e.g., lower cleaner densities or cleaner-to-client ratios) (Wismer et al. 2014; Triki et al. 2018; Triki et al. 2019). However, it remains unclear whether this reduction arises from developmental effects, juveniles growing up in simpler social environments, or from behavioral plasticity in adults adjusting to new market conditions. This study aims to disentangle these alternatives by testing whether changes in behavior are restricted to individuals that developed under simplified conditions or are also expressed by adults that experienced more complex environments earlier in life.

Finally, a third study is investigating the quality of cleaning stations of alpha, beta, and gamma females. Over the years, I have observed an intriguing pattern in the spatial use of the cleaner wrasse: the male primarily spends his time at the alpha female's cleaning station, and once the alpha disappears, another female quickly takes her place. This study aims to test whether the quality of the cleaning station improves with rank and whether the disappearance of an individual prompts low-ranking females to move to the next-best cleaning station. In this case, moving to the next best cleaning station once freed would represent a behavioral pattern amongst cleaners that could potentially fit the definition of tradition. Based on (i) the accelerated growth observed after rank upgrade (**Chapter 2**) and (ii) the absence of a relation between growth strategy and cleaning effort (**Chapter 3**), I predict that higher-ranking females occupy higher-quality cleaning stations, particularly in terms of client composition (e.g., a higher proportion of visitor species), without a corresponding increase in overall cleaning effort.

Additionally, some of the ecological and behavioral data collected during my PhD are currently being analyzed alongside data on the cognitive performance and brain size by the PhD student Marine Amann. Some of her chapters will therefore present a more integrative picture of how the ecological background can explain variation in cognitive performance and brain morphology in the cleaner wrasse at Lizard Island.

Current ecological directions

While the chapters of this thesis use our transect data only to obtain a general picture of cleaner and client densities, this data could also be employed to address ecological questions in greater detail. Transect data are, in fact, collected at the species level, and they include detailed pictures of precise sections of the reef at our sites that Prof. Gal Eyal is currently using to build 3D models of the substrate. Once analyzed, I will be able to better describe the consequences of ENSO 2024 on the reefs at Lizard Island. I will also create a detailed picture of the species most commonly available at each site and see whether cleaners' cleaning habits match it (locally and temporally), or whether they show specific preferences for certain fish species. Specific differences between life stages will also be investigated.

Future cleaner directions

There are several questions that could still be answered with the data from my PhD. First, one could investigate if the frequency of early sex change remains the same in 2024. The latter could be expected based on the findings that even though lower density means less inter-harem competition, the number of females in a harem is invariant to cleaner density (**Chapter 2**). This would suggest that despite the decrease in cleaner density in 2024, social control still faces the same challenges in 2024 that it did in

2023. Second, it would be interesting to reanalyze our videos to describe the cleaning efficiency of fast- and slow-growing females and address our speculations about cleaning efficiency versus effort. Finally, it would also be interesting to use our videos to build a detailed ethogram of the cleaner wrasse's behaviors. Such an ethogram could then be used to investigate the cleaner wrasse's social competence from an intraspecific perspective. Social competence can, in fact, be proven in an intraspecific context only if I can find evidence that the specific behaviors of a dominant individual have direct consequences for the expression of specific behaviors of a subordinate.

A few future directions will instead require novel data and methodologies. Investigating the physiology and immunology of sex-changing and non-sex-changing females could help address some of the speculations about the survival gap between males and females. Similarly, studying sex-specific life histories of protogynous, sex-changing species in which satellites, sneakers, and bachelor males are present could clarify whether such levels of male-male competition suffice to re-establish the costs of being a male in a polygynous system. A potential candidate species could be *Thalassoma bifasciatum* (Warner and Hoffman 1980; Munday et al. 2006).

Future work directly measuring body condition, fat reserves, and gonadal energy content would help clarify if more subtle differences in physiological allocation could indeed underlie the divergence in growth strategies observed in **Chapter 3**. Integrating these physiological measures with behavioral and social data could provide a more complete understanding of how energy intake, social environment, and strategic allocation interact to shape life history trajectories in sequentially hermaphroditic reef fishes.

Additionally, future studies should investigate early sex change in populations of cleaner wrasses inhabiting fragmented and patchy reefs, such as those studied early on by Prof. Redouan Bshary in Egypt. This thesis shows that habitat structure plays a central role in shaping social and reproductive dynamics. In continuous reef habitats, like those studied here and in early studies (Robertson 1972; Robertson 1974; Kuwamura 1984), individuals can move between neighboring harems without crossing risky open sand, harems can form branches and spread over larger areas, and female territories can be spatially dispersed. In contrast, in highly fragmented reef systems, stronger spatial constraints may reinforce social control and limit opportunities for early sex change.

Finally, an informative experimental test would be to compare the survival of sex-changing individuals under optimal versus suboptimal conditions. Sex change could be induced in large alpha females (via male removal) and in smaller beta or gamma females (by removing all higher-ranking individuals). In the latter case, increased male pressure from neighboring harems may compound the challenges of social control, potentially leading to higher mortality. Such results would provide support for the assumptions underlying the observed sex-specific mortality patterns.

Conclusion

Through the integration of behavioral ecology, mutualism, and climate impacts, this thesis demonstrates that sequential hermaphroditism can fundamentally alter the demographic trajectories traditionally expected in polygynous species. By using the cleaner wrasse as a model, our findings challenge the classic assumption that, in polygynous mating systems, intense competition inevitably makes males the most vulnerable and least long-lived sex. Instead, the shifting fitness target of protogynous hermaphroditism ensures that individuals can strategically maximize their survival and reproductive output, ultimately attaining a terminal male phase that is highly resilient to both social and environmental extremes.

Furthermore, this research reveals that size-based hierarchies in sequential hermaphrodites do not universally function as rigidly controlled, stable queues. Classic models rely on the assumption that dominant individuals maintain strict control through repeated interactions and the threat of eviction in cohesive groups. However, I demonstrate that when social structures are spatially dispersed or non-cohesive, social control is inherently incomplete. Rather than passively waiting for social rank upgrades, subordinate females actively leverage these spatial structures and social loopholes to escape dominant suppression and optimize their growth, a strategy that is independent of their mutualistic service quality.

Ultimately, this thesis reframes sex change not merely as an automatic response to male disappearance, but as a dynamic interaction of female strategies and the circumvention of intraspecific constraints. Future theoretical frameworks concerning life-history, sequential hermaphroditism, and size-based hierarchies must explicitly move beyond models of strict queuing to incorporate the profound impacts of spatial dispersion, incomplete social control, and flexible individual strategies.

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