

# Rank Change and Growth Within Social Hierarchies of the Orange Clownfish, *Amphiprion Percula*

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## Research Article

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# Abstract

Social hierarchies within groups define the distribution of resources and provide benefits that support the collective group or favor dominant members. The progression of individuals through social hierarchies is a valuable characteristic for quantifying population dynamics. On coral reefs, a number of small site-attached fish maintain size-based hierarchical communities where individuals queue through social ranks. The cost of waiting in a lower-ranked position is outweighed by the reduced risk of eviction and mortality. Clownfish exist in stable social groups with subordinate individuals queuing to be part of the dominant breeding pair. Site attachment to their host anemone, complex social interactions, and relatively low predation rates make them ideal model organisms to assess changes in group dynamics through time in their natural environment. Here, we investigate the rank changes, and isometric growth rates of individual orange clownfish, *Amphiprion percula*, from 247 naturally occurring social groups in Kimbe Island, Papua New Guinea (5°12'13.54" S, 150°22'32.69" E). We use DNA profiling to assign and track individuals over an eight-year time period in 2011 and 2019. Over half of the individuals survived alongside two or three members of their original social group, with twelve breeding pairs persisting over the study period. Half of the surviving individuals increased in rank and experienced double the growth rate of those that maintained their rank. Examining rank change over a long-term period in a wild fish population gives new insights and highlights the complexity and importance of rank and social hierarchy in communal site-attached reef fish.

**Subject Area:** behavior, ecology, evolution

## 1. Introduction

The establishment of social hierarchies helps animals living in social groups to distribute resources, including food, shelter, and mating privileges (Koski et al. 2015). Individuals are ranked by their position in the hierarchy, which is driven by physical and competitive fitness (e.g., size, strength, coloration), and how they contribute to the functioning of the social group (Koski et al. 2015). Hierarchies are typically structured according to the individuals' size, age, or sex, and moving up in social rank increases an individual's access to food (Forrester 1991), mates (Buston 2003a), and habitat (Thompson et al. 2007). Social rank often corresponds to feeding success rates, which is correlated to growth rates, and allows dominant individuals to remain well-fed where food is limited (Gurney and Nisbet 1979). Recently, fish have become a popular vertebrate model to study hierarchy and dominance since they have clear behavior of aggression and can be kept easily in laboratory settings (Chase and Seitz 2011). For example, the coral-dwelling goby *Paragobiodon xanthosomus* exhibits a size-based hierarchy in which members form a queue to inherit breeding status from the dominant pair. Cooperation between subordinates regulates growth and maintains a size ratio between ranks to avoid conflict and punishment (i.e., eviction) (Wong et al. 2007). While many studies examine the causes of rank change and dominance in reef fish by examining growth rates (Wong et al. 2007; Wong et al. 2016; Reed et al. 2019), most are conducted as short-term experiments (Buston 2003a; Buston 2003b; Buston and Cant 2006; Rueger et al. 2018). To date, there have been no studies that examine rank change and growth rates

over a longer time period (> 1 year) in their natural habitat. Longer-term studies can aid in the understanding of population dynamics by providing larger datasets that can be used to predict future population changes and are lacking in the marine environment (Reinke et al. 2019).

Mating behavior plays an essential role in driving, establishing, enforcing, and maintaining social hierarchy. Sexual selection within hierarchical societies elucidates patterns of conflict within as opposed to between sexes. Wong and colleagues determined that food limitation and paternal egg care leads to competition among female coral gobies for males, meaning they are less likely to mate with subordinate males, and this leads to monogamy within social groups (Wong et al. 2008). Most clownfish live in groups comprising one dominant breeding pair and several non-breeding subordinates where the female is the dominant individual. The species *Amphiprion bicinctus* and *A. akallopisos* have been shown to exhibit monogamy based on individual recognition (Fricke 1973) and pair-bonding (Fricke 1974). Fricke and Fricke also found that several pairs of *A. bicinctus* remained on the same anemone without changing partners for at least three years (Fricke and Fricke 1977), revealing that social structures are relatively stable for the female and male.

The orange clownfish, *Amphiprion percula* (Lacepède, 1802), is one of 28 species of clownfish belonging to the subfamily Amphiprioninae within the family Pomacentridae. It is estimated to have a life-span of 30 years (Buston and Garcia 2007) and commonly associates with anemone hosts *Heteractis magnifica* and *Stichodactyla gigantea* (Fautin and Allen 1992). Anemone species may play an important role in the growth and size of *A. percula* individuals. Previous studies found that, on average, females were 10% larger in *H. magnifica* compared to those living on *S. gigantea*, and juveniles that settled on *H. magnifica* had a faster growth rate based on otolith increments (Salles et al. 2016). A recent study (Salis et al. 2021) concluded that juvenile *A. percula* delay the development of their white bars during metamorphosis depending on the anemone species they are hosted by. Additionally, anemone surface area has a significant impact on social structure with larger anemones hosting larger social groups and individuals (Chausson et al. 2018).

Within social groups of *A. percula*, there is a strict size-based ratio between sequentially ranked individuals in which a dominant individual is approximately 1.26 times the size of its immediate subordinate (Buston 2003b). Similar to gobies, subordinates regulate their growth to maintain this ratio or are otherwise evicted or killed (Buston 2003b; Rueger et al. 2018). In theory, individuals that change rank grow faster due to the increase in food they consume as they rise in status. In this study, our aims were to examine rank changes and growth in naturally occurring social groups of *A. percula* clownfish over an eight-year time period on shallow coral reefs in Kimbe Bay, Papua New Guinea. We hypothesize that individuals that are higher ranking will grow faster and climb higher in the social hierarchy compared to those that do not change rank. During this time, individuals were exposed to natural levels of predation risk, food availability, and recruitment.

## 2. Materials And Methods

## (a) Sample Collection

The *Amphiprion percula* population on Kimbe Island (5°12'13.54" S, 150°22'32.69" E), a remote island in Kimbe Bay, was sampled in March 2011 and April 2019. Each time, all individuals sized >25mm (n = 660 in 2011; n = 533 in 2019) were caught with hand nets, occasionally anesthetized with a dilute solution of clove oil (if necessary to facilitate capture), measured to the nearest mm (total length, TL) (Fig. 1S), and their host anemone species (*Stichodactyla gigantea* and *Heteractis magnifica*) recorded (Fig. 1). To genotype all individuals, a tissue sample was taken from the caudal fin before they were released back onto their anemone host. The fin clip is regrown within approximately two weeks and has no negative long-term effects on the fish. Samples were preserved in 96% ethanol. Rank was assigned based on relative total lengths of individuals within each social group. Rank 1 was the largest individual and assumed to be the female; rank 2 was the second largest and assumed to be the male. Any additional individuals were classed as sub-adults.

## (b) Genetic Techniques

Genomic DNA from *A. percula* fin clips ~ 2 mm<sup>2</sup> was extracted using the Macherey-Nagel 96 tissue kits following the manufacturer's protocols. Microsatellite loci were amplified using the QIAGEN Multiplex PCR kit using the protocol (Almany et al. 2017) annealing temperatures were 58°C or 59°C (Table 1). Forward primers were labeled with fluorescent tags and pooled into four multiplex mixes indicated in Table 1. PCR products were analyzed on an ABI 3730x1 genetic analyzer (Applied Biosystems). Alleles sizes for 20 microsatellite loci were successfully amplified and were manually scored in the fragment analysis software *GENEMAPPER* v4.0. Characteristics of the 20 microsatellite markers were analyzed in *GenAlEx* v6.5 (Peakall and Smouse 2012) and are presented in Table 2. Alleles were binned in R (R Core Team 2019) using the package *MsatAllele* (Alberto 2009).

Individuals that survived from 2011 to 2019 were identified in the R package *AlleleMatch* (Galpern et al. 2012). Only individuals classed as females, males, or sub-adults were included in this analysis (n = 660 in 2011, and n = 533 in 2019). A sensitivity analysis indicated that up to 8 genotypic mismatches could confidently identify identical genotypes within the sample.

Table 1: Summary of the 20 microsatellite markers amplified in this study for *A. percula*. The primer sequence, motif, fluorescent dye, number of alleles, size range, and multiplex are indicated below.

Locus	Primer Sequence (5'-3')	Motif	Dye	Number of Alleles	Size (base pair)	Multiplex
CF27	F: TGCAATTATGTTAGCACCTG R: TGGCCAGATTAGATGGTTAC	(TCTA) <sub>16</sub>	PET	15	190 - 240	A
79	F:GCATGGATGGTCAACAGAGGAGCT R: CTCTGAAAGTTCAAGGCTGCAGAC	(GT) <sub>27</sub>	NED	17	210 - 260	A
perc06	F: GTGCTATGAAGAAAGTGGGCG R: CTGCACACACAACCTACCTCC	(AC) <sub>14</sub>	VIC	11	235 - 270	A
perc21	F: TTGTGTGAGTTCCTGACCCG R: AAATGGAGAGGCTGGCGTC	(AC) <sub>11</sub>	6-FAM	11	220 - 270	A
perc41	F: TTTGCTATGTTCTCCTGTGC R: TGACAGGAATGCTGGAGGAG	(ATCC) <sub>12</sub>	6-FAM	9	330 - 380	A
CF9	F: CTCTATGAAGGTGAGATTTTT R: GTACATGTGTGGGTTTCCTC	(TCAA) <sub>8</sub> TGAA(TCAA) <sub>15</sub>	NED	18	270 - 360	B
CF36	F: TTTACAGATGTAACCTACACG R: GGACAAACACACACACTG	(CA) <sub>23</sub>	6-FAM	32	190 - 340	B
perc07	F: TTAAGCTGCAAGGAACACTC R: CGAAAGGCAGGAGAAGACAC	(AGAT) <sub>22</sub>	PET	24	190 - 280	B
perc02	F: CCTGATCCCTGGTGTAAAG R: AGTGTAAAGACTAGCCAGG	(AG) <sub>10</sub>	PET	12	370 - 440	B
perc38	F: TGCTACTGACAGATCTGCC R: ATCTTTGCGGAAACAGGCAG	(ATCC) <sub>10</sub>	VIC	7	300 - 350	B
120	F: TCGATGACATAACACGAAGCAGT R: TGTGTCCGCTCCAGCTCTAC	(GT) <sub>16</sub> Na(GT) <sub>14</sub>	VIC	9	380 - 420	C
70	F: AGATGATTGGGCAACCTCACACT R: GATTATTGTCTTGTGGGAGTCA	(GT) <sub>13</sub> (GT) <sub>8</sub>	6-FAM	14	360 - 380	C
perc17	F: TGAGGGCTTCTAAAGTATGGCTC R: GTACGACACTCCAGAGACCC	(AC) <sub>13</sub>	NED	7	90 - 150	C
perc42	F: TGTGGCTGATTTGTATCGC R: ACCTCCATTGTTCTCTGCC	(AC) <sub>14</sub>	PET	11	130 - 220	C
perc18	F: GCACTCATGTTTACTCGGC R: TGACATCTGCTGACAAAGGC	(AC) <sub>10</sub>	NED	8	100 - 260	C
CF11	F: GCTGGTTACAACACCTTG R: GACAGGCAAGCCATATGAG	(CT) <sub>10</sub> (CA) <sub>16</sub>	PET	13	100 - 300	D
CF3	F: GTTACGCCCTGTATGACATT R: TGCTCTCATTCTCTAGTCC	(CA) <sub>17</sub>	PET	22	190 - 400	D
44	F: TTGGAGCAGCGTACTTAGCT R: ATGTGGCACTCAGCCTCCT	(GT) <sub>13</sub>	6-FAM	15	200 - 340	D
CF39	F: CCGGACAGCCAGAGCAAGA R: CCTAATCGATCGGTGGTACAT	(AC) <sub>10</sub> (GC) <sub>2</sub> (AC) <sub>2</sub> (AGAC) <sub>1</sub> (AGAT)(AGAC) <sub>2</sub> (AC) <sub>1</sub> (AGAC) <sub>2</sub>	VIC	27	310 - 400	D
CF42	F: TGCAATCCAAACCTGAAA R: ATGTGCACAAAGGTCAAA	(AGAT) <sub>1</sub> (AGAC) <sub>1</sub> (AGCC)(AGAC) <sub>2</sub> (AC)(AG) <sub>2</sub>	VIC	20	170 - 260	D

Table 2: Characteristics of the 20 microsatellite markers amplified in this study for *A. percula* for 2011 and 2019. N, number of individuals genotyped; Na, total number of alleles; Ho, observed heterozygosity; He, expected heterozygosity; *F*<sub>i</sub>, fixation index; *p*-value from Hardy-Weinberg Equilibrium.

Locus	Amphiprion percula 2011 population (n = 821)					Amphiprion percula 2019 population (n = 709)				
	Na	Ho	He	Fis	p value	Na	Ho	He	Fis	p value
CF27	10	0.800	0.813	0.16	ns	12	0.812	0.807	-0.006	p < 0.001
79	18	0.661	0.764	0.134	p < 0.001	19	0.633	0.764	0.172	p < 0.001
perc06	4	0.716	0.695	-0.031	ns	4	0.741	0.683	-0.085	p < 0.001
perc21	6	0.593	0.593	0.000	ns	5	0.603	0.622	0.031	ns
perc41	5	0.548	0.538	-0.017	p < 0.001	7	0.606	0.580	-0.045	ns
CF9	17	0.887	0.900	0.014	p < 0.001	17	0.872	0.897	0.028	p < 0.001
CF36	22	0.753	0.821	0.083	p < 0.001	22	0.731	0.827	0.116	p < 0.001
perc07	20	0.744	0.788	0.032	p < 0.05	15	0.788	0.786	-0.028	ns
perc02	7	0.387	0.589	0.343	p < 0.001	5	0.528	0.604	0.125	p < 0.001
perc38	5	0.587	0.579	-0.016	ns	5	0.593	0.584	-0.015	p < 0.05
120	4	0.695	0.685	-0.014	ns	4	0.583	0.669	0.129	p < 0.001
70	9	0.634	0.621	-0.022	p < 0.001	7	0.614	0.600	-0.022	p < 0.001
perc17	5	0.540	0.545	0.009	ns	4	0.553	0.550	-0.005	ns
perc42	7	0.558	0.578	0.035	ns	6	0.583	0.610	0.044	ns
perc16	6	0.529	0.528	-0.001	p < 0.001	6	0.546	0.533	-0.024	ns
CF11	9	0.715	0.725	0.014	ns	9	0.702	0.743	0.055	p < 0.001
CF3	23	0.781	0.815	0.042	p < 0.001	27	0.738	0.893	0.174	p < 0.001
44	9	0.523	0.554	0.056	p < 0.001	8	0.570	0.567	-0.005	p < 0.001
CF39	20	0.890	0.886	-0.004	ns	21	0.887	0.893	0.008	ns
CF42	9	0.847	0.843	-0.005	ns	9	0.826	0.826	0.001	ns

### (c) Statistical Analyses

When an individual was sampled in both 2011 and 2019, we measured growth as the difference in total length between the two time points. New growth was calculated as a percent of the total body length based on how much the individual grew from 2011. Then we analyzed the data using the R package *glmmTMB* (Friedman et al. 2010) to fit linear and generalized linear mixed models using maximum likelihood estimation. Next, we used the R package *emmeans* (Searle et al. 1980) to compute the estimated marginal means.

## 3. Results

134 of the 660 individuals (i.e., 20%) sampled in 2011 were recaptured in 2019, which includes 36 females, 52 males, and 46 sub-adults. Of the 134 survivors, 72 individuals remained within their social group, and were confirmed to have been collected from the same anemone, with 67 individuals changing social rank. Due to the attrition of the tags, not all individuals were able to be confirmed on the same anemone. Of these survivors, we identified 12 breeding pairs that remained together from the original 238

pairs documented in 2011. Additionally, three of those pairs remained on the same anemone with other individuals from their original social group.

All individuals recaptured in 2019 either remained in the same rank or went up in rank, and those that changed rank grew significantly faster than individuals that did not change rank.

The model demonstrated that rank had a strong effect on new growth with individuals that were sub-adults in 2019 grew the fastest. Individuals that changed rank grew 29.4% compared to individuals that did not change rank and grew 13.7%, which is a 15.6% difference ( $df = 117, p = < 0.0001$ ). Anemone species also had a significant effect on new growth, and that on average, individuals grew 17% on *H. magnifica* and 25% on *S. gigantea*. Excluding rank as a factor, there was a 7.6% difference in new growth between individuals living on *H. magnifica* vs. *S. gigantea* ( $df = 117, p = < 0.0001$ ) (Fig. 2).

## 4. Discussion

Our study examined the wild *A. percula* clownfish population on Kimbe Island in Kimbe Bay, Papua New Guinea over an eight-year time period. Tracking a marine organism during a long-term study can be challenging, which is why clownfish and anemones are such a useful model system because they tend not to move. Using this unique system in this long-term study, we were able to analyze growth rates related to rank changes, breeding pair stability (monogamy), and anemone species effects.

Overall, we found that clownfish that changed rank (i.e., sub-adult to male, male to female, or sub-adult to female) grew faster than those that did not change rank. Half of the surviving individuals changed rank and grew significantly more than those that did not change rank. Within groups that changed rank, the smallest sample size of fish was those that went from sub-adults to female ( $n = 12$ ). This is likely not standard growth, but opportunistic growth that occurs when a female or male is removed from the group since *A. percula* have been known to regulate or suppress their growth to decrease the likelihood of being evicted (Buston 2003b). Of those that did not change rank, females ( $n = 36$ ) were the largest sample size which makes sense because they are at the top of the social hierarchy, followed by males ( $n = 19$ ) then sub-adults ( $n = 12$ ).

The 12 breeding pairs that were still found together follows the mating behavior (Wong et al. 2008) that clownfish are monogamous unless their mate is physically removed from the social hierarchy, suggesting that these breeding pairs were monogamous over the eight-year time period. This is incredibly interesting to find since vertebrates that were previously considered monogamous in the wild with long-term pair bonding i.e., birds (Mock and Fujioka 1990) were found not to be monogamous with genetic analysis (Kaplan 2007). A field study in the Red Sea found that several pairs of *A. bicinctus* remained on their host anemone without changing partners over the course of a three-year study (Fricke and Fricke 1977). Our genetic analysis confirming that the same individuals in breeding pairs were stable in wild populations supports the lab studies on the mating behavior of clownfish. Monogamy and breeding stability are often hard to confirm in the field over long-term studies without the adequate genetic analysis of all individuals present making this challenging in many other field study systems.

Additionally, we found that anemone host species had a significant effect on growth. Individuals hosted by *S. gigantea* grew faster than those that were hosted by *H. magnifica*. Previous studies in Kimbe Bay (Salles et al. 2016) had found that juveniles that settled on *H. magnifica* grew faster than those on *S. gigantea* which is slightly different to what we found in our study; our results found sub-adult and adult individuals growing faster on *S. gigantea*. Juveniles that recruited to *S. gigantea* had acquired their white bars faster compared to those who recruited to *H. magnifica* (Salis et al. 2021). This could be due to their environment since most *S. gigantea* individuals were in a sheltered shallow habitat close to shore, compared to *H. magnifica*, which were further offshore and tended to be in slightly deeper water (Fig. 1). Since our study examined wild populations, it would be difficult to determine which factors contributed to faster growth rates without extensive data on environmental variables at a very small scale. For example, variables such as temperature, flow, turbidity, nutrient/ food availability, predation pressure, and intraspecific competition would have to be quantified at each anemone. The scale at which these variables need to be measured to understand their impacts on the physiology and growth of clownfish would be very difficult to achieve as mentioned in other studies (Burgess et al. 2021).

Rank change and growth are important in an ecological context because these metrics are often intertwined and evaluated in other social species (Robbins et al. 2005) to elucidate patterns of group dynamics. Both social and environmental characteristics can influence the outcome of hierarchies in nature. Future work could examine the anemone population stability and how their potential habitat limitation due to climate change e.g. (Hobbs et al. 2013) may influence the clownfish social structure. If there are fewer habitable anemone hosts, then there would be more competition at an intraspecific level. This further highlights the opportunity to develop clownfish and anemones as a model study system given the ability to maintain them in captivity, and their nature in the field itself (they tend not to change host anemones) for detailed in-situ studies.

## Conclusion

This study provides the first long-term evaluation of the social structure and individual growth in a wild population of reef fish. Anemone hosts or anemone host locations potentially impact survivorship, growth rates, and settlement of both adults and recruits. This study has important implications for the many socially complex reef fishes and other organisms that are obligatory symbionts in specific habitats such as anemones or corals. Climate change poses several threats to these hosting organisms; associated mortality of the hosts presents a major habitat limitation for the residents. These shifts may have a disproportionate effect on resident organisms with social hierarchies. In a broader ecological context, this is a good example of how the complex interaction of factors can influence population dynamics.

## Declarations

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Code availability: N/A

Authors' contributions: LMF, HBH, and MLB contributed to the study conception and design. Data collection was performed by all authors. Data analysis was performed by LMF, HBH, DJC, and PS-A. The first draft of the manuscript was written by LMF and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Ethics Approval: All international and institutional guidelines for sampling for the study have been followed and all necessary approvals have been obtained. Details available upon request.

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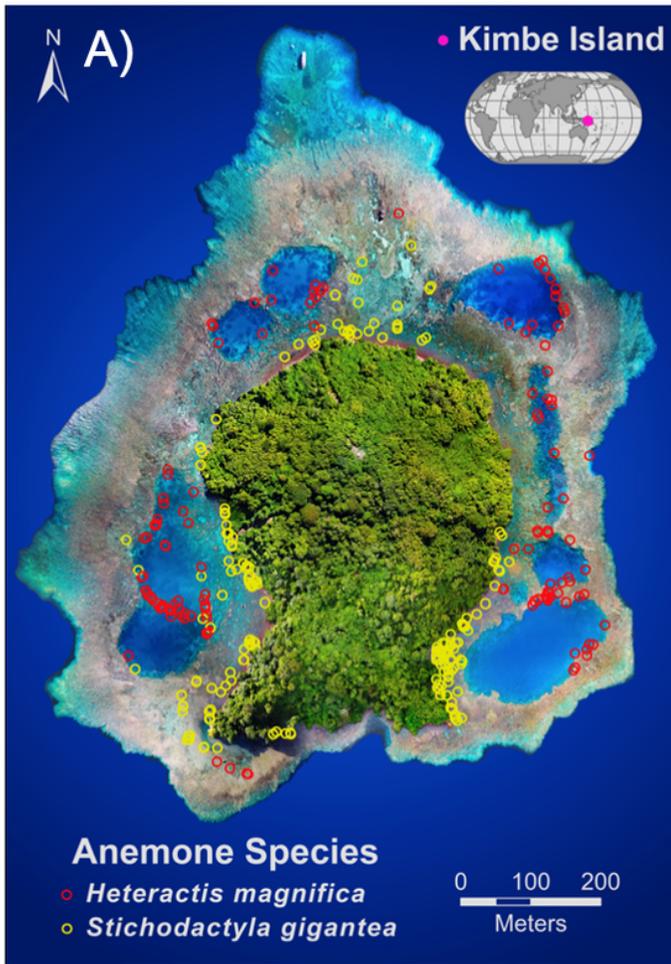
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## Figures



**Figure 1**

(A) Visual of the study site, Kimbe Island (Papua New Guinea), and surrounding lagoon and reef habitats with tagged anemone locations (*Heteractis magnifica* in red and *Stichodactyla gigantea* in yellow). Kimbe Island = green, shallow (< 1 m) hard bottom substrate = grey, lagoons = light blue, and deeper ocean outside of the fringing reef habitat = dark blue. Host anemones *Heteractis magnifica* (B) and *Stichodactyla gigantea* (C) on the right. Aerial image credit to H.B.H., map courtesy U. Langner (RSRC), photographs credit to M.B.S.

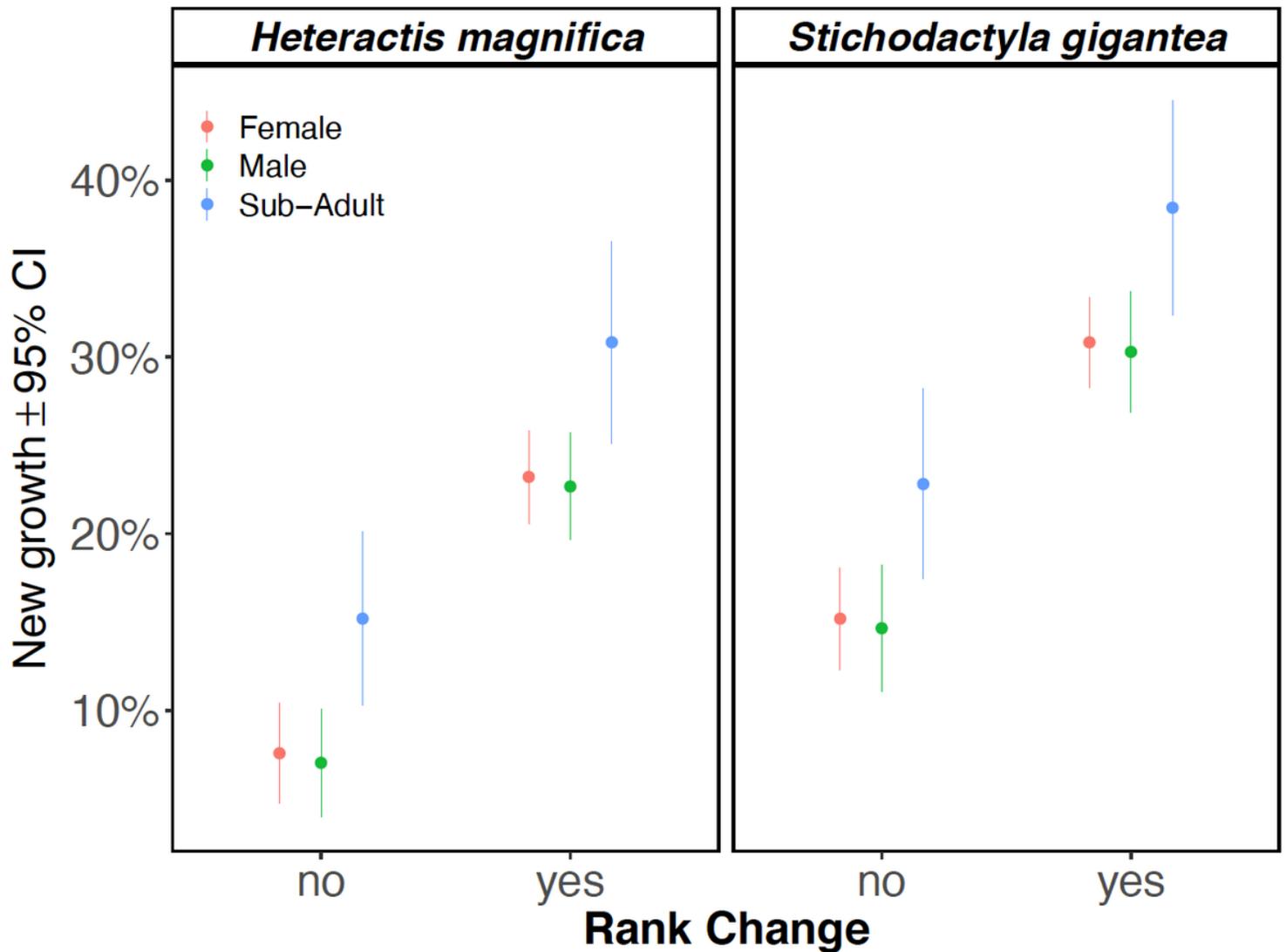


Figure 2

Amphiprion percula rank change by new growth as a percent of the total body length with a 95% confidence interval shown by the whisker length. The left panel denotes individuals residing on *Heteractis magnifica* and the right panel for those on *Stichodactyla gigantea*. The coloration signifies the rank in 2019: sub-adults = blue, males = green, and females = pink.

## Supplementary Files

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