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Mortality is associated with social rank in the clown anemonefish (*Amphiprion percula*)

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Abstract Elucidating the causes of post-recruitment mortality is a vital step toward understanding the population dynamics of coral reef fishes. Predation is often considered to be the primary proximate cause of mortality. It has, however, proven difficult to discern the relative contributions of predation and other processes, such as competition for food, shelter, or mates, to patterns of mortality. To determine which other processes might be important drivers of mortality patterns, factors related to mortality in the clown anemonefish *Amphiprion percula* (Lacepède, 1802) were examined. Patterns of mortality will not be driven by predation in *A. percula*, because these fish are well protected from predators by their close association with sea anemones. Mortality rates were based on the disappearance of known individuals from a population of 201, in 57 groups, during a 1-year field study (in 1997), in Madang Lagoon, Papua New Guinea. Mortality rate of *A. percula* was low (14% per annum) compared to other coral reef fish, probably due to the protection from predators afforded by the anemone. Six factors (reef, depth, anemone diameter, number of individuals, density, and standard length) showed no association with the probability of mortality ($P > 0.05$). Rank was the only factor associated with the probability of mortality ($P < 0.03$); low-rank individuals (ranks 4–6) suffered a higher mortality rate than high-rank individuals (ranks 1–3) ($P < 0.01$). The most likely explanation for this pattern was that competition for rank, amongst individuals within an anemone,

resulted in some individuals evicting their subordinates. Individuals probably competed for rank because it conferred access to reproduction, and not because it conferred access to food or shelter. Such competition for reproduction will be intense whenever some individuals obtain a greater share of reproduction than others do, and it may be an important process influencing the dynamics of coral reef fish populations.

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Introduction

A central question of coral reef fish population ecology is, what causes post-recruitment mortality? Elucidating the causes of variation in this mortality is a critical step toward understanding a population's dynamics (Warner and Hughes 1988; Caley et al. 1996; Hixon 1998). A wide variety of factors have been related to post-recruitment mortality of reef fishes, and these factors have been linked to a number of causal processes. At a large spatial scale, differences in mortality rate among reefs have been attributed to differences in levels of predation (Aldehoven 1986; Connell 1996; Beukers and Jones 1997; Hixon and Carr 1997). At a smaller spatial scale, differences in mortality rate among substrates have been linked to variation in the quality and quantity of shelters from predators the substrates provide (Jones 1988; Hixon and Beets 1993). Competition for shelters may result in the predation of individuals that do not gain shelter, and could be the underlying cause of positive relationships between density and mortality (Forrester 1995; Tupper and Boutillier 1995; Beukers and Jones 1997; Hixon and Carr 1997; Steele 1997). A positive relationship between density and mortality could also be caused by an increase in the number of agonistic interactions during the establishment of dominance

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hierarchies at high densities, which may lead to increased susceptibility to predation (Shima 2001). Smaller fish may be more susceptible to predation, either because predators target smaller fish (Booth 1995), or because smaller fish lose out in competition for shelter and are then subject to predation (Tupper and Boutilier 1995; Schmitt and Holbrook 1999). While predation is thought to be the main proximate cause of mortality, determining the relative contribution of this and other processes (e.g. competition for shelter) to patterns of mortality has been difficult (Hixon 1991). This difficulty arises because most correlations can reasonably be explained by multiple processes, because the processes may interact in complex ways, and because there have been few multi-factorial experiments specifically designed to disentangle the effects of multiple processes (Sih et al. 1985; Caley et al. 1996; Hixon and Carr 1997).

Anemonefishes (Pomacentridae: *Amphiprion* spp.) provide opportunities for natural experiments in which the contributions of predation and other processes to patterns of mortality can be disentangled. This is because anemonefishes form obligate associations with sea anemones, which provide the fish with protection from predators (Allen 1972; Fautin and Allen 1992). Of anemonefishes, *Amphiprion percula* is one of the most site-attached, rarely straying more than a few centimeters beyond the periphery of its anemone (Elliott and Mariscal 2001; Buston 2003). *A. percula* are never attacked within the anemone, but they are rapidly preyed upon if removed from the safety of the anemone's tentacles (Mariscal 1970; Elliott et al. 1995). Thus, in *A. percula*, the direct cause of mortality is likely to be predation once individuals have left the anemone. But the indirect causes of mortality will be processes, other than predation, that cause individuals to leave the anemone. It is the indirect causes of mortality that will drive patterns of mortality in this species, because variation in mortality among individuals will derive from these processes.

In the present study, I investigated the mortality rate, and the factors related to the mortality rate, of the clown anemonefish *A. percula*, in Madang Lagoon, Papua New Guinea. This study complements previous studies of settlement, recruitment, and migration already conducted on this population (Fautin 1992; Elliott et al. 1995; Elliott and Mariscal 2001; Buston 2003), thus providing a very complete description of the parameters influencing this population's dynamics.

Materials and methods

Study population

I studied the clown anemonefish *Amphiprion percula* (Lacepède, 1802), for 12 months (January 1997–December 1997), in Madang Lagoon, Papua New Guinea (5°09'S; 145°48'E). I conducted all fieldwork using SCUBA, at depths of up to 13 m. I located 97 groups on three reefs: Sinub (reef 1), Wongad (reef 2), and Masamoz (reef 3) [see Jebb and Lowry (1995) for a description of Madang Lagoon and its reefs; Buston 2002]. This study utilized only 57 groups, which were observed without experimental manipulation

for the entire study period. Each group occupied a single anemone [*Heteractis magnifica* (Quoy and Gaimard, 1833; see Appendix 1)]. Natural variation in the color markings enabled me to recognize individual fish > 18 mm in standard length (SL; Caillet et al. 1986; e.g. Appendices 2–10), when they were regularly censused (Nelson et al. 1994; Elliott and Mariscal 2001). Individuals > 18 mm in SL were defined as group members or residents (Buston 2003).

Mortality

I monitored the disappearance of residents by conducting a thorough census of each group every 1–2 days, for 10 lunar months (7 February–5 December 1997). If individuals disappeared from their anemone, I assumed that they had died, rather than migrated. I based this assumption on two empirical results (Buston 2003): (1) no individuals that disappeared could be found after a thorough search of all anemones within the study population, indicating that short-distance migration did not occur; and (2) no migrants came into the study population from outside, indicating that long-distance migration did not occur. This assumption, that disappearance was equivalent to mortality, gave rise to higher estimates of mortality rate than any other assumption.

Factors related to mortality

A wide variety of factors have been related to post-recruitment mortality of reef fishes. To determine which effects might be related to mortality in *A. percula*, I investigated the relationship between mortality of residents and six independent variables analogous to those previously investigated: "reef" (two fixed levels), as a proxy for site; "depth" (m, covariate); "anemone diameter" (cm, covariate), as a proxy for shelter availability; "standard length" (mm, covariate); "number of individuals" (covariate); and "rank" (covariate). The inclusion of "anemone diameter" and "number of individuals" in the same multivariate analysis (below) enabled me to test for an effect of "density".

The 57 groups used in this study were located on reef 1 ($n=33$) and reef 2 ($n=24$). I used a dive computer to measure the depth of each anemone to 0.1 m (mean depth \pm SD: 7.0 ± 2.3 m, $n=57$). Depths were measured on ten occasions throughout 1997, and the depth assigned to each anemone in the analyses was the mean of these depths.

I used the mean diameter of each anemone's oral disc (Fautin and Allen 1992) as a measure of the amount of available shelter (mean anemone diameter \pm SD: 48 ± 8 cm, $n=57$). I measured the diameter of each anemone to the nearest 5 cm, and calculated the mean from 15 separate measures of the oral disc taken throughout 1997. Each anemone was measured multiple times over the year, because anemones varied slightly in size from day to day.

In January 1997, I captured all fish using hand nets, and took them to the surface in plastic bags. There, I used calipers to measure the standard length of each individual to 0.1 mm (mean SL \pm SD: 39.8 ± 11.8 mm, $n=201$). All fish survived these procedures without any sign of harm, and were returned to their anemone within 3 h, where in all cases they remained.

Groups were composed of one to six residents (mean number of individuals in each group \pm SD: 3.5 ± 1.0 , $n=57$). I ranked residents on the basis of their size relative to others within the same group, with the largest being ranked 1. Rank assigned in this way perfectly predicted the order in which individuals inherited breeding positions within an anemone (Buston 2002). It was possible, however, for fish of the same size on different anemones to have different ranks, because there was variation among groups in the structure of the size hierarchy (Buston 2002).

Statistical analysis

I investigated which factors were related to the probability of mortality by using a logistic regression analysis, with the occurrence of mortality (0 or 1) as the dependent variable, and group

identification number (1–57) entered as a random effect (SAS GENMOD). This approach enabled me to test for the effects of multiple independent variables, while controlling for the lack of independence among individuals within the same group. I removed independent variables from the analysis in a backwards stepwise fashion if they did not have a significant effect ($P > 0.05$). Interaction effects were not investigated statistically, because of low sample sizes for some of the effects.

Results

Out of 201 specimens, 23 *Amphiprion percula* died during the study period (7 February–5 December 1997). In order to calculate the finite annual mortality rate for the population, I first estimated the instantaneous mortality rate (m) as $[\ln(178/201)]/302 = -4.02 \times 10^{-4}$. I subsequently estimated the number of fish expected to be alive after 1 year using the formula $N_t = N_0 e^{(m)(t)}$, where N_t was the number of individuals surviving at time t , N_0 was the number of individuals at time zero: $N^{365} = 201 e^{(-0.0004)(365)} = 173.5$. The finite annual mortality rate for the population was estimated to be $(201 - 173.5)/201 = 13.7\%$.

In the logistic regression analysis, rank was the only significant predictor of mortality (Chi-squared test: $df = 1$; $\chi^2 = 4.75$, $P = 0.0293$; Table 1). The other five independent variables (“reef”, “depth”, “anemone diameter”, “standard length”, “number of individuals”) were removed from the logistic model in a stepwise fashion because they did not have significant effects (Table 1). The observation that both “anemone diameter” and “number of individuals” dropped from the analysis indicated that there was no effect of density. The probability of mortality increased as rank increased (Table 2), i.e. rank 1 individuals (the largest in any given anemone) had the lowest probability of mortality, while rank 6 individuals had the highest probability of mortality (Fig. 1).

The outcome of multivariate logistic regression analyses can be influenced by co-linearity of independent variables. In the analysis above, co-linearity of “rank” and “SL” could have been an issue, because they were highly correlated ($r = 0.82$). All other correlation coeffi-

Table 1 *Amphiprion percula*. Probability of mortality of 201 individuals in 57 groups: fixed effects in step prior to their removal from the logistic model. Summary of results of stepwise logistic regression analysis (SAS GENMOD procedure) investigating the effects of multiple independent variables on mortality of resident *A. percula*. Independent variables were removed, one at a time, from the complete model in a backwards stepwise fashion if $P > 0.05$

Order of removal	Effect	df	Chi-squared	P-value
–	Rank	1	4.75	0.0293
5	Number of individuals	1	3.08	0.0794
4	Depth	1	1.96	0.1619
3	Reef	1	1.63	0.2016
2	Standard length	1	1.04	0.3071
1	Anemone diameter	1	0.81	0.3690

Table 2 *Amphiprion percula*. Probability of mortality of 201 individuals in 57 groups: parameter estimates from significant logistic model

Parameter	Estimate	Standard error	95% Confidence limits	Z	Pr > Z
Intercept	–3.6937	0.7373	–5.1387 –2.2487	–5.01	<0.0001
Rank	0.6035	0.2099	0.1920 1.0150	2.87	0.0040

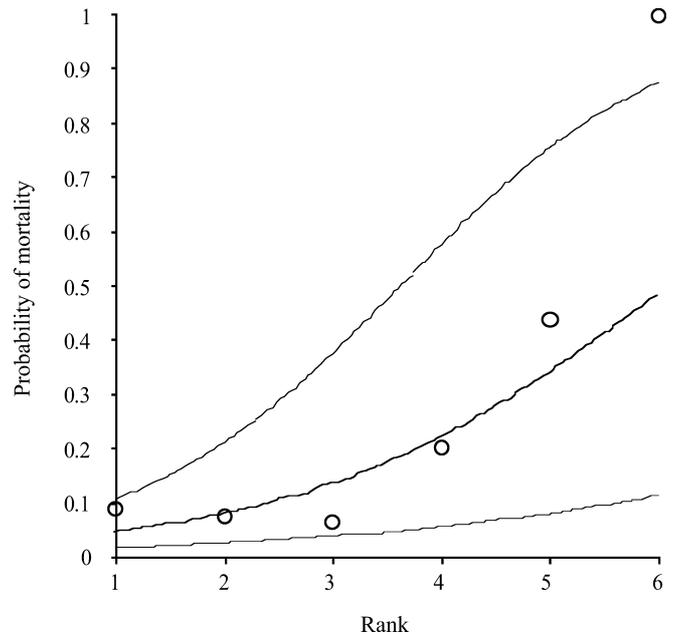


Fig. 1 *Amphiprion percula*. The probability of mortality, in 10 lunar months, increases as the hierarchy is descended. Points are the observed mean probability of mortality for each rank: rank 1 = 5/57, rank 2 = 4/56, rank 3 = 3/52, rank 4 = 5/25, rank 5 = 4/9, and rank 6 = 2/2. Heavy line represents relationship between probability of mortality and rank estimated from coefficients of the logistic model (Table 1): probability of mortality = $1/[1 + e^{-(\text{intercept} + \text{slope} \times \text{rank})}]$. Light lines represent SE of estimated regression

cients were < 0.5 . Therefore, I repeated the logistic regression analysis omitting “rank” from the full model (SAS GENMOD). In this case “SL” was the only significant predictor of mortality (Chi-squared test: $df = 1$; $\chi^2 = 4.00$, $P = 0.0454$), raising the possibility that mortality might be related to “SL” rather than “rank” per se. To determine which of these effects was the better predictor of mortality, I compared the goodness of fit of the “rank” model to the goodness of fit of the “SL” model, by conducting a likelihood ratio test. The “rank” model had a significantly better fit (Chi-squared test: $df = 1$; $\chi^2 = 4.40$, $P < 0.05$), indicating that “rank” was a much better predictor of mortality than “SL”.

I investigated whether or not there was a qualitative shift in mortality rate within the dominance hierarchy, by conducting Chi-squared tests contrasting the mortality rate of higher rank individuals to the mortality rate of lower rank individuals, e.g. rank 1 versus ranks 2–6, ranks 1–2 versus ranks 3–6, and ranks 1–3

versus ranks 4–6. All observed and expected values were ≥ 5 , and the Yates' correction was deemed unnecessary (Zar 1999). There was no difference when the mortality rate of rank 1 individuals was contrasted with the rest (Chi-squared test: $df=1$; $\chi^2=2.7$, $P>0.10$), or when the mortality rate of individuals ranked 1 and 2 was contrasted with the rest (Chi-squared test: $df=1$; $\chi^2=3.3$, $P>0.05$). But the mortality rate of individuals ranked 1–3 was lower than the mortality rate of individuals ranked 4–6 (Chi-squared test: $df=1$; $\chi^2=14.1$, $P<0.001$), indicating that the mortality of high rank (1–3) individuals was qualitatively different from the mortality of low rank (4–6) individuals.

Discussion and conclusions

The mortality rate for the population as a whole ($<14\%$ per annum), and especially for rank 1 individuals ($<5\%$ per annum), is on the lower end of mortality rates documented for adult coral reef fish (12–100% per annum, Munro and Williams 1985; 5–70% per annum, Eckert 1987). It has been suggested that other fishes (e.g. one-lined wrasse, *Labrichthys unilineatus*) may have low mortality because of their association with invertebrate hosts, such as branching corals, which provide protection from predators (Eckert 1987). It is probably the protection from predators provided by the anemone that accounts for the low mortality rate of *Amphiprion percula* (Mariscal 1970; Allen 1972; Elliott et al. 1995).

I detected a strong association between rank and the probability of mortality, with lower rank individuals experiencing higher mortality. It is remarkable that rank but no other factors (reef, depth, anemone diameter, number of individuals, density, or standard length) had a significant association with mortality, especially given that analogous factors have been related to mortality in other coral reef fishes [reef (Aldenhoven 1986; Connell 1996; Beukers and Jones 1997; Hixon and Carr 1997); depth (Jones 1986; Booth 1995); shelter availability (Jones 1988; Hixon and Beets 1993; Booth 1995; Beukers and Jones 1997); number of individuals (Booth 1995; Shima 2001); density (Forrester 1995; Tupper and Boutilier 1995; Hixon and Carr 1997; Steele 1997; Shima 2001); standard length (Booth 1995; Tupper and Boutilier 1995; Schmitt and Holbrook 1999)]. The relationship between these factors and mortality is often thought to be driven by predation. The absence of all these effects in *A. percula* is plausibly the result of the anemone, and the protection from predators that it affords, preventing predation from driving patterns of mortality.

There are several possible causes for the higher mortality rate of lower rank residents: competition, starvation, parasites and disease, and abiotic disturbance. My daily observations produced no indications that starvation, parasites and disease, or abiotic disturbance might underlie this aspect of the pattern of mortality. The most likely explanation for the pattern of mortality is that competition, amongst individuals

within an anemone, results in some individuals evicting their subordinates. Under this eviction hypothesis it is competition that causes individuals to leave the anemone, thereby driving the pattern of mortality, even though it is the action of predators that eventually causes the individuals' demise. Consistent with this hypothesis, other studies have suggested that subordinate anemonefish are sometimes evicted (Allen 1972; Ochi 1985), and I observed attempted evictions of low rank individuals on several occasions (Buston 2003). Evictions have also been observed in *Dascyllus* spp., whose ecology is similar to that of *Amphiprion* spp. in many respects (Sweatman 1983; Schmitt and Holbrook 1999). Further, in *Dascyllus* spp. mortality has been shown to be size related, with the smallest (lowest rank) subordinates suffering the highest mortality, and it is possible that the indirect cause of this mortality was competition, even if its direct cause was predation (Forrester 1990; Booth 1995; Schmitt and Holbrook 1999).

What might individuals be competing for, within an anemone? Given the pattern of mortality, perhaps the simplest answer is that these fish are competing for rank itself. Rank may confer access to better food, better shelter, or a greater share of reproduction. Thus, competing for rank may be favored by natural selection if one (or more) of these resources is limiting. There is no evidence that food was limiting. There was no association between reef or depth and mortality, which would be predicted if food availability varied among sites. Further, there was no association between anemone diameter and/or the number of individuals and mortality, which would be predicted if food was limiting. In general, competition for food is not viewed as a common cause of mortality in reef fishes (Jones 1986, 1991; Forrester 1995), and the present study supports this view. There is no evidence that shelter was limiting, because anemones were large (mean diameter \pm SD: 48 ± 8 cm, $n=57$) relative to the size of the fish (mean SL \pm SD: 39.8 mm, $n=201$). Further, there was no association between anemone diameter and/or the number of individuals and mortality, which would be predicted if shelter were limiting. The conclusion that competition for shelter is not driving mortality is somewhat surprising, because such competition is often viewed as an indirect cause of mortality in reef fishes (Forrester 1995; Tupper and Boutilier 1995; Beukers and Jones 1997; Hixon and Carr 1997; Steele 1997).

It is most likely that *A. percula* compete for rank because rank confers access to reproduction. In *Amphiprion* spp. only the dominant pair breeds, and the non-breeding subordinates form a strict queue for breeding positions (Fricke 1979; Buston 2002). Within the subordinate queue, higher rank individuals are more likely to inherit breeding positions than lower rank individuals, and thus competition over rank, for access to reproduction, will be intense. The idea that competition for rank can occur because it confers access to reproduction, rather than food or shelter, is rarely

considered in the marine ecology literature (but see Shima 2001 for another possible example), indeed there is no mention of it in reviews of post-recruitment mortality (Hixon 1991; Jones 1991). Such competition will occur whenever some individuals obtain a greater share of reproduction than others do. Competition for access to reproduction may be an important process influencing the size and the dynamics of coral reef fish populations.

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