

2009

Injuries inflicted as a predictor of winning in contests between beadlet anemones, *Actinia equina*

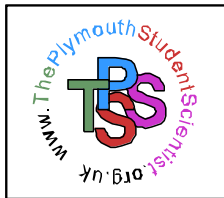
Robinson, L.

Robinson, L., Porter, B., Grocott, J., Harrison, K. (2009) 'Injuries inflicted as a predictor of winning in contests between beadlet anemones, *Actinia equina*', *The Plymouth Student Scientist*, p. 32-49.

<http://hdl.handle.net/10026.1/13852>

The Plymouth Student Scientist
University of Plymouth

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.



Injuries inflicted as a predictor of winning in contests between beadlet anemones, *Actinia equina*

Laura Robinson, Ben Porter, Jennifer Grocott and Kendal Harrison

2009

Project Advisor: [Mark Briffa](#) School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA

Abstract

If the number of individuals in a population oversubscribes a resource then competition can occur and may lead to injurious fighting, if the cost of fighting is lower than the value of the resource. Here we consider how weapon size (nematocyst length), body size (pedal disc diameter, wet weight) and number of injuries inflicted are related to fighting ability in the common intertidal beadlet anemone, *Actinia equina*. 160 anemones were utilised from two sites, within two size classes, to engage in contest behaviour. There was no significant effect on pedal disc diameter, wet weight or nematocyst length of the outcome of a contest. The winners of contests were the anemones found to inflict the greatest number of injuries on their opponents. The results also demonstrated a significant positive relationship between the body size of an anemone and the number of peels inflicted on that individual by their opponent. However, there was no significant relationship between the average nematocyst length of an individual and the number of scars that individual had. As anemone size increased, the number of injuries inflicted on that individual also increased. This may be related to it being more difficult to triumph over a larger anemone and so you have to cause greater injury to it. In this study, individuals appear not to 'size up' their opponents, merely escalate to all out fighting immediately. Further work includes studying whether past encounters affect an anemone's fighting ability in a later contest.

Introduction

Animals need an area to inhabit and have evolved a large range of adaptations to guard and increase this area (Williams 1991). One such method is contest or agonistic behaviour. Defined as “behavior that is adaptive in situations of conflict between members of the same species” (Scott 1966), agonistic behaviour relates to the range of intraspecific fighting or competitive behaviours, including threat, attack, retreat and defensive fighting (Scott & Fredericson 1951). If the number of individuals in a population oversubscribes a resource, such as space, food or water, then competition can occur and may lead to injurious fighting if the cost of fighting is lower than the value of the resource (Just & Morris 2003). Ultimately, the aim of contest behaviour is to induce the opponent to retreat (Briffa & Sneddon 2007).

Parker (1974) defined resource holding potential (RHP) as “a measure of the absolute fighting ability of an individual” and this can be influenced by morphology, physiology and also past experience (Sneddon *et al.* 1997). Body size is usually expected to correlate with fighting ability or RHP of an individual (Just & Morris 2003). Renison *et al.* (2006) reveal how both inflicting injuries and body size are related to fighting ability in male Magellanic penguins; they found that larger males won more fights and that the amount of injuries inflicted by male penguins was positively correlated to the quality of the nest being fought over. However, Lindstrom & Pampoulie (2005) demonstrated that individuals might not necessarily choose the most valuable resource, but the optimum resource, as a compromise between value and dependability.

Previous studies have shown body size and weapon size to be important elements of fighting behaviour. Sneddon *et al.* (1997) used body size and chela length as indicators of RHP in male shore crabs, *Carcinus maenas*. They found that individuals with larger claws won more contests, but that relative body size was not significantly related to fighting ability. In contrast, Briffa (2008) demonstrates how weapon size is not as good a predictor of fight outcomes in house crickets, *Acheta domesticus*, as body size. The author also provides evidence that winners of contests between crickets were heavier or larger and had higher energy levels than losers. Schroeder & Huber (2001) investigated how claw growth is related to fighting ability, and strategies, in the crayfish, *Ornectes rusticus*. They discussed the reasons why larger male crayfish spend longer at each stage of agonistic behaviour, before escalating to the next. These included increased likelihood of injury and the possibility of losing a claw, rendering the crayfish defenceless and less attractive to mates.

Briffa & Elwood (2005) found that in the hermit crab, *Pagurus bernhardus*, energy reserves were closely correlated to fighting behaviour, and physiological change happened before any changes to behaviour. They discuss how contest behaviour is likely to be more costly “in terms of harmful metabolic by-products”, rather than the individual receiving obvious damage. This shows that endurance and energy needed for this type of behaviour could be constraints on the fighting ability of an individual (Briffa & Sneddon 2007).

The current study considers how weapon size (nematocyst length), body size (pedal disc diameter, wet weight) and number of injuries inflicted are related to fighting ability in the common intertidal beadlet anemone, *Actinia equina*. The beadlet anemone is found in the family Actiniidae, within one of the orders, Actiniaria (the true

sea anemones), of the Cnidarian class Hexacorallia (Manuel 1981). The phylum Cnidaria (=Coelenterata, part of the super phylum Radiata (Dunn 1982)) is uniquely characterised by the possession of cnidae in their tissues, and these structures are necessities for their way of life (Watts *et al.* 2000). Cnidae, meaning 'stinging thread' (Daly *et al.* 2003), are intracellular capsules containing "a coiled tubule that may be everted in response to suitable stimulation" (Williams 1996) and the most common type is the nematocyst.

Sea anemones have been established as one of the 'simplest' animals to possess aggressive behaviour (Bigger 1980) and this aggression has been well documented (e.g. Brace & Pavey 1978; Brace & Reynolds 1989; Turner *et al.* 2003). The functional role of this aggression is thought to be to increase the chance of survival through competitive occupation of space (Brace & Santer 1991) and it can be carried out using a range of specialist nematocyst-bearing structures, including the acrorhagi or catch tentacles (Williams 1991).

Acrorhagi are hollow sacs containing numerous holotrichous ("spines over the full length") nematocysts (England 1991), which are located in the 'fosse' (a circular groove enclosed by the parapet), below the outer circle of tentacles on the upper body column (Ayre 1982). These structures are only found in species within the family Actiniidae (Williams 1991). All acrorhagi bearing species studied thus far appear to follow the sequence of behaviours described for *Actinia equina* by Bonnin (1964). There are five phases to aggressive encounters: initiation, inflation of acrorhagi, overtopping, attack and recovery (Francis 1973; Brace *et al.* 1979; Brace 1981; Turner *et al.* 2003). Initiation is when two genetically distinct anemones are brought into tentacular contact, followed by a number of feeding tentacles being withdrawn (Knowlton 1996). The acrorhagi are inflated and moved, by contractions of the oral disc and body column, to touch the adversary (overtopping) (Williams 1978). The aggressor then places its expanded acrorhagi on the other anemone, and the acrorhagi discharge nematocysts into the victim's outer body layer (Francis 1988). Usually pieces of the ectoderm are left behind, termed "acrorhagial peels" by Bigger (1980). These 'peels' continue to discharge nematocysts and can cause necrosis of the tissues, and even the death of the individual (Brace & Reynolds 1989). Recovery of the attacking individual consists of a slow return to the original position (Brace 1981).

In a previous study, Brace & Pavey (1978) discussed how the size of an anemone within the species *Actinia equina* is related to the individual's aggressive response. They found a "size-dependent dominance hierarchy" showing that larger contestants aggress earlier and subsequently win more encounters. Brace (1981) also used asymmetric contests to demonstrate that larger individuals of the species *Phymactis clematis* show evidence of aggressive responses earlier than smaller ones. However, the study also found that there was a distinct lack of individuals assessing their opponent's size and ability before escalating. The author proved this by showing that the onset of aggression is not related to the 'dominance rankings' of individuals. In contrast, Knowlton (1996) showed that the weight of an anemone is not related to the likelihood of winning a contest. However, these studies all failed to look at any other factors that could influence the individual's fighting abilities or confound the results of their work, for example, weapon size. No study has thus far shown a relationship between weapon size or number of injuries inflicted and an anemone's fighting ability.

The objectives of this study were to (1) identify which of the potential correlates of RHP, body size, weapon size and injuries inflicted, differ between winners and losers in *Actinia equina* and (2) determine whether asymmetry between contestants in these parameters changes the outcome of contests. This investigation aims to deduce the key factors of agonistic behaviour in anemones, by eliminating all of the possible confounding factors.

Methods

Collection and Maintenance of Animals

The anemones used in this investigation were collected from two sites, Hannaford Point, Looe (OS grid reference: SX254533) and Whitsands Bay (OS grid reference: SX410513), both in Cornwall. This was to ensure the individuals in a contest could not possibly be clonemates (genetically identical individuals) and so would elicit an aggressive response, as clonemates have been proven to show no indications of aggression (Turner *et al.* 2003). Individuals were collected weekly, at low tide, throughout autumn and winter (September to December 2007) and individuals from both sites were collected during the same low tide on the same day each week. At the same time, individuals from the previous week were replaced in their natural environment.

Individuals were prised away from the substrate gently using a blunt knife, and any animals damaged in this process were discarded. The red/pink pedal disc colour morphs were favoured over the grey/green morph because Brace & Reynolds (1989) demonstrated that the grey/green morph was significantly less aggressive than those animals with light pink to dark red pedal disc colouration. Two size classes were collected; 'large' anemones with a pedal disc diameter of over 20mm and 'small' anemones with a diameter less than 15mm.

Specimens were transported to the University of Plymouth in plastic buckets, with lids, containing fresh seawater. In the laboratory, the anemones were allowed to settle onto individual small, flat rocks and then placed into saltwater aquaria (volume = 20 litres), aerated by air stones. The aquaria were kept in a controlled-temperature facility at 15 °C, under a natural light regime and the individuals were given a minimum of three days to acclimatise. The specimens from the two sites were maintained in separate tanks and so non-experimental contact was kept to a minimum. Tests were carried out during the daytime, with no tests being conducted after the anemones had been housed in excess of seven days.

Observation of Aggressive Encounters

For each experiment, two anemones (one from each site), on their individual rocks, were placed into an experimental tank (volume = 5 litres), filled with pre-aerated saltwater, and allowed a minimum of 10 minutes to acclimate and fully expand their tentacles. Only animals with fully expanded oral discs were used in contests. The two rocks bearing the animals were then pushed together until contact was established between at least three of each anemones' tentacles, as Francis (1973) found that

proximity alone is not enough to initiate an aggressive response; tentacular contact is required for an aggressive encounter to ensue.

The contests were then monitored for three hours, before the outcome of the encounter was decided. The 'winner' was determined to be the anemone that had moved the least distance from the start (centre) point. The winner usually remained expanded and the 'loser' partially closed and sometimes partly detached from its rock. If neither anemone had moved and both remained open and active, the contest was deemed to be a 'no fight'. No anemone was used in more than one contest.

Since, in these experiments, both individuals were firmly fixed to rocks before the contest, the 'residency factor' (Grafen 1987; Kemp & Wiklund 2004) should not have influenced the outcome. Pedal disc diameter was measured using dial callipers and wet weight was recorded. The number of acrorhagial peels or scars each animal had received during the contest was noted.

Tissue samples were taken from each individual, irrespective of the outcome of the encounter, by scraping a small amount of ectoderm from one of the acrorhagi. The tissue sample was placed on a standard 76x26mm glass microscope slide and compressed using a pair of forceps. The nematocysts within the tissues were then stained using 1% methylene blue solution. Nematocysts were viewed using a binocular confocal Leica MZ12 microscope at x8 magnification and a digital image (using a Nikon Coolpix 4500 Digital Camera) of the nematocysts of each individual was taken. The nematocysts were then measured using Image Tool 3.0 software, using a graticule (division = 0.1mm) for calibration. Only undischarged (still capable of being fired) nematocysts were measured since changes in volume may occur after discharge (Godknecht & Tardent 1988). Within randomly selected fields of view, 10 nematocyst lengths were measured and a mean length calculated for each individual.

Contests were carried out within four discrete groups: (a) an individual from Looe against an individual from Whitsands – both large; (b) an individual from Looe against an individual from Whitsands - both small; (c) a large individual from Looe against a small individual from Whitsands; and (d) a small individual from Looe against a large individual from Whitsands. 160 individuals were used in contests overall: 80 from each site within 80 contests. Large individuals always had a pedal disc diameter of over 20mm; small anemones always had a pedal disc diameter under 15mm.

Statistical Analysis

All data were analysed using MINITAB (version 15) or StatView statistical software. Factorial repeated measures ANOVAs were used to analyse the effect on each parameter measured of the outcome of fights. Chi-squared contingency tables were applied to the chance of an anemone from one site winning a contest within each group of fights and across them all. Pearson's correlations were used to look for relationships between the different parameters and paired t-tests were performed to examine differences between the anemones from the two sites.

Results

To determine the effects of winning or losing a fight on the morphological factors, a series of 'one within, two between' repeated measures ANOVAs was performed. The repeated measure was the outcome of the contest, the winner or loser. The between group factors were the size class ('large' or 'small') of the individual from Looe and the individual from Whitsands Bay (WS). The dependent variables were pedal disc diameter, wet weight, average nematocyst length and number of peels inflicted on the individual.

Effect of Body Size

There was no effect on pedal disc diameter of the outcome of a fight ($F_{1,69} = 0.165$, $P = 0.686$) (see Figure 1). There was a highly significant effect of size of anemones from Looe ($F_{1,69} = 63.042$, $P < 0.0001$) and Whitsands Bay ($F_{1,69} = 49.726$, $P < 0.0001$) between the two size classes, which demonstrates that the experiments were carried out correctly. There was no effect on wet weight of an individual caused by its fighting ability ($F_{1,69} = 0.301$, $P = 0.585$) (see Figure 2). There were no interaction effects found connected to wet weight or diameter.

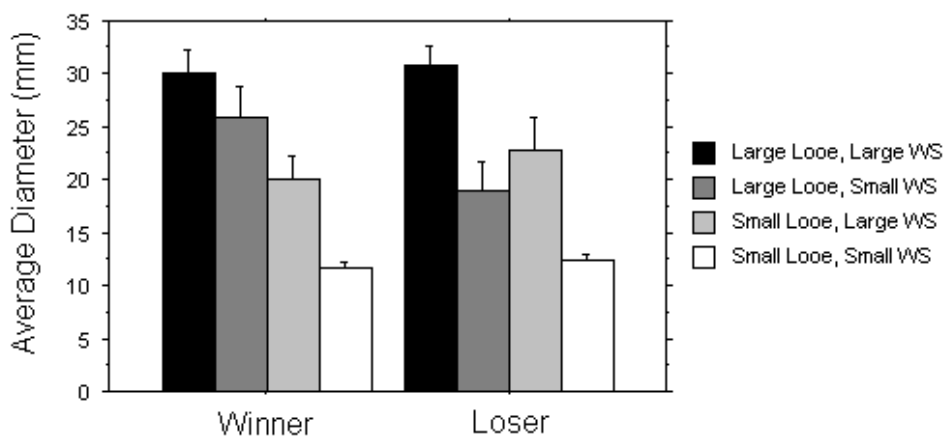


Figure 1. Average (± 1 standard error) pedal disc diameter of the winner and loser anemone within each group of contests.

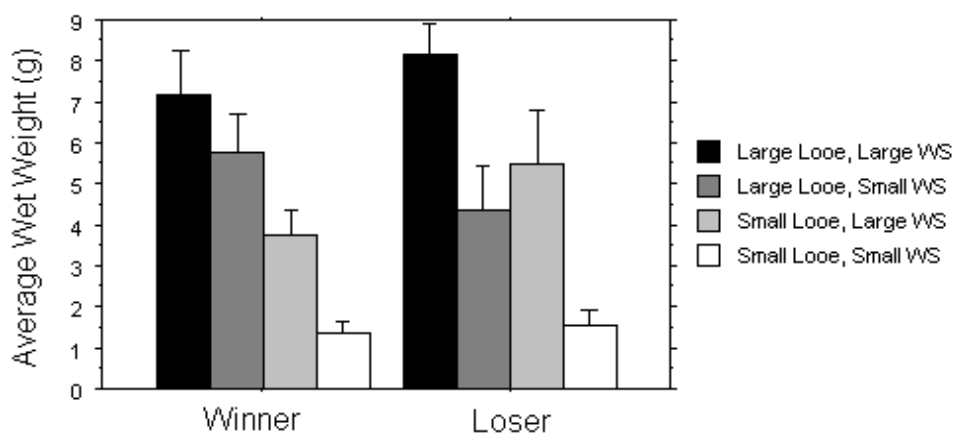


Figure 2. Average (± 1 standard error) wet weight of the winner and loser anemone within each group of contests.

Effect of Weapon Size and Use

There was a near-significant effect on the average nematocyst length of the winner or loser caused by the outcome ($F_{1,67} = 3.646$, $P = 0.061$) (see Figure 3). This trend showed losers had longer nematocysts on average than winners. The data also showed a near-significant trend in nematocyst size between large and small anemones from Looe ($F_{1,67} = 3.803$, $P = 0.055$) with larger individuals having larger nematocysts (see Figure 4). This pattern was not seen in individuals from Whitsands Bay.

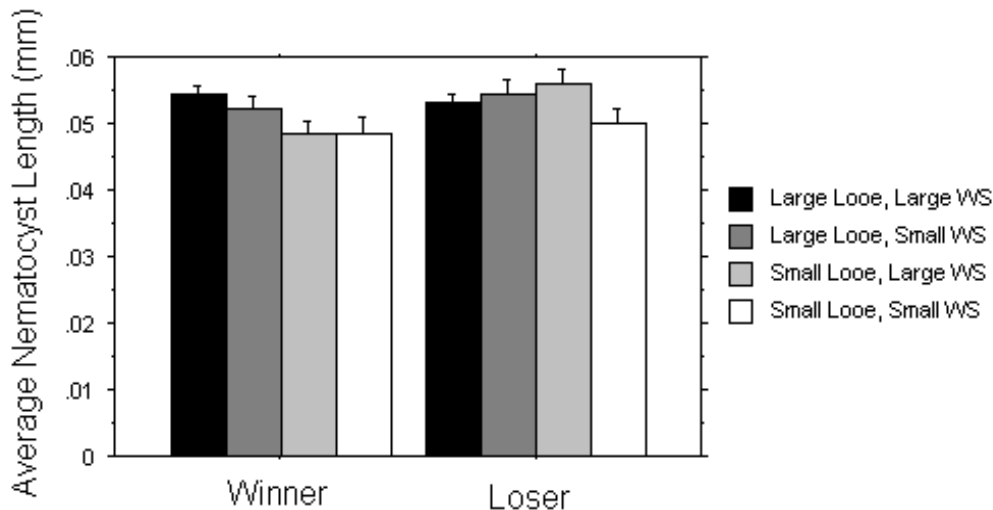


Figure 3. Average (± 1 standard error) nematocyst length of the winner and loser within each group of contests.

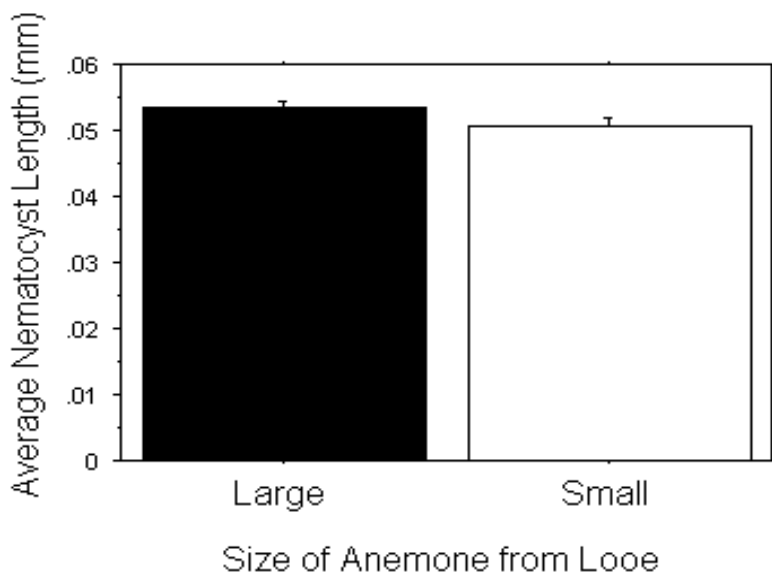


Figure 4. Average (± 1 standard error) nematocyst length of individuals within the two size classes from the Looe site.

There was a significant effect of the outcome of a fight on number of peel scars ($F_{1,69} = 7.053, P < 0.01$) (see Figure 5). Winners were found to inflict a greater number of peels on losers, than losers reciprocated. The data also demonstrated an interaction effect between winning a fight and the size of the anemone from Looe ($F_{1,69} = 3.990, P < 0.05$) (see Figure 6). Large anemones from Looe had a greater number of peels inflicted on them when they lost a fight, than small individuals or winners from Looe.

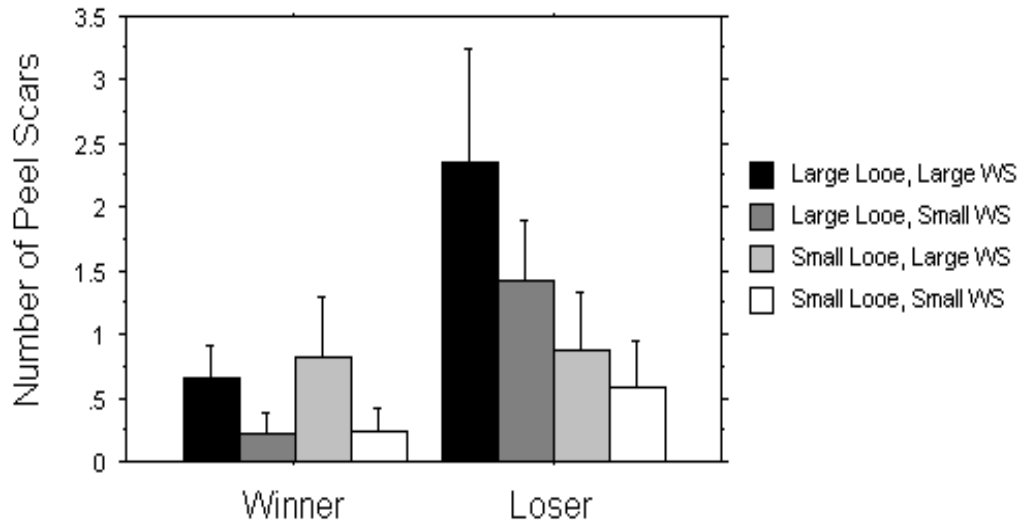


Figure 5. Average (± 1 standard error) number of peels or scars inflicted on the winner and loser within each group of contests.

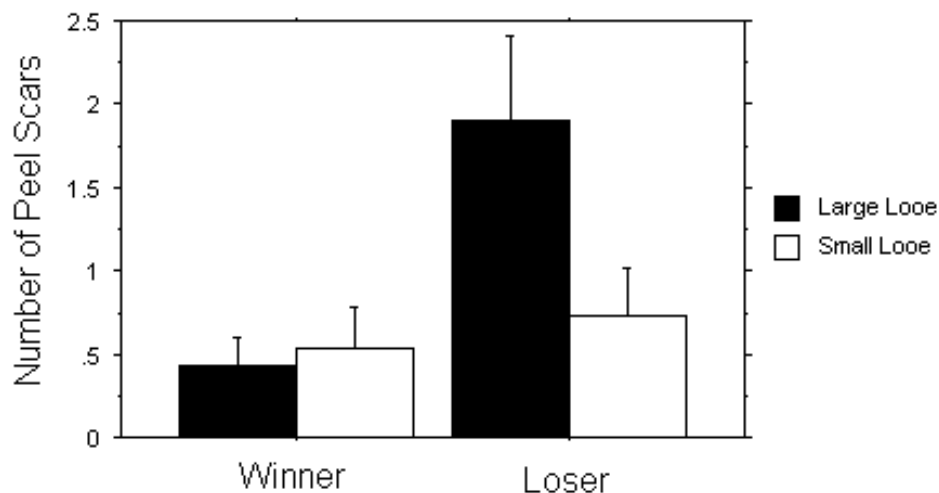


Figure 6. Average (± 1 standard error) number of peels or scars inflicted upon an individual from the Looe site, showing the difference between size classes and the outcome of contests.

Relationships between Factors

A Pearson's correlation demonstrated that the diameter of an individual was highly significantly positively related to its wet weight ($r = 0.899$, 144 d.f, $P < 0.001$) (see Figure 7). The results also demonstrate a significant positive correlation between the pedal disc diameter of an anemone and the number of peels inflicted on that individual ($r = 0.242$, 144 d.f, $P = 0.003$) (see Figure 8). There was also a significant positive correlation between wet weight of an individual and number of peels received ($r = 0.219$, 144 d.f, $P = 0.008$) (See Figure 8). However, there was no significant correlation between the average nematocyst length of an individual and the number of scars that individual had ($r = 0.119$, 144 d.f, $P = 0.160$). The results also show a highly significant positive correlation between wet weight and average nematocyst length ($r = 0.314$, 144 d.f, $P < 0.001$) and between pedal disc diameter and average nematocyst length ($r = 0.348$, 144 d.f, $P < 0.001$) (see Figure 9).

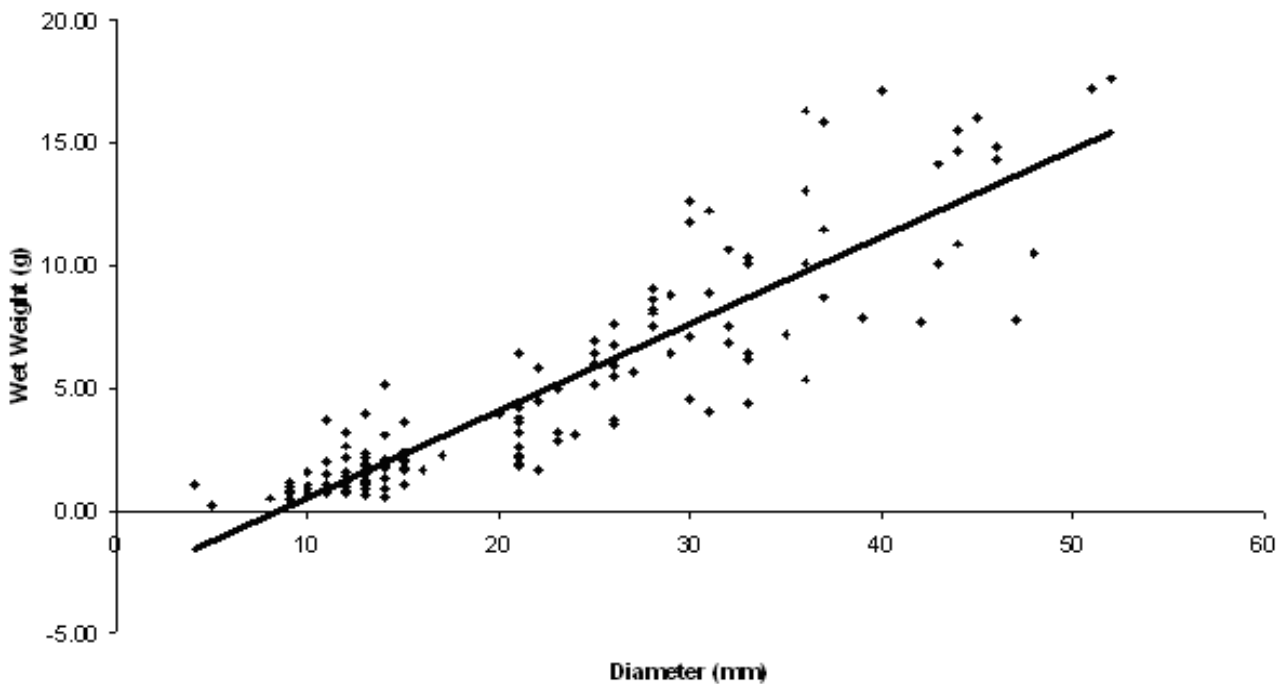


Figure 7. Positive relationship between an anemone's pedal disc diameter and wet weight. Each point is a single anemone.

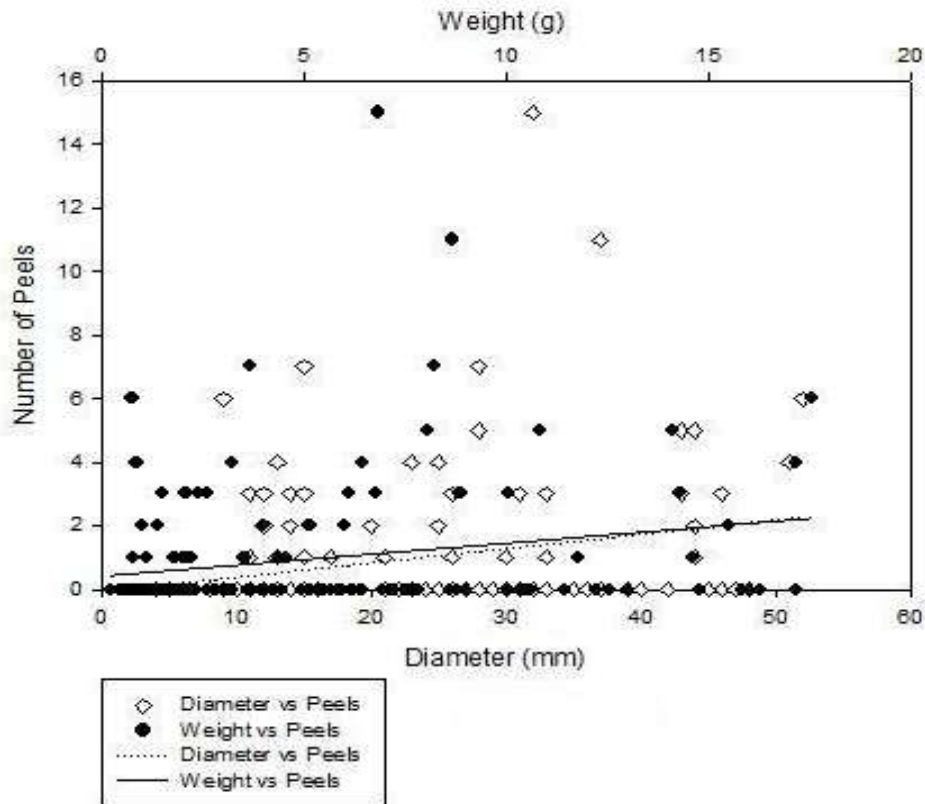


Figure 8. Positive relationship between pedal disc diameter and wet weight with the number of peels inflicted on an individual. Each point is a single anemone.

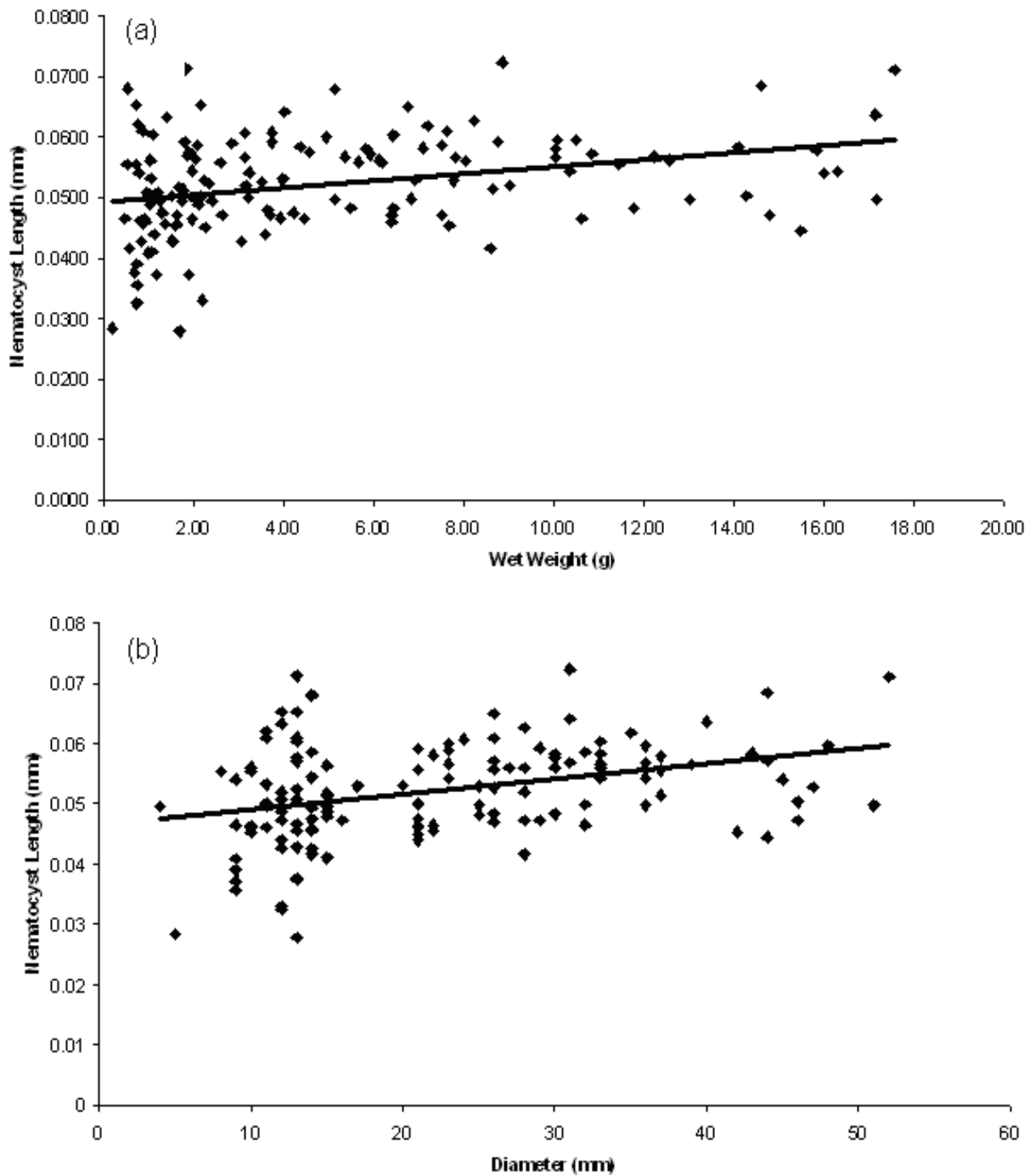


Figure 9. Relationship between the average nematocyst length of an anemone and (a) wet weight, (b) pedal disc diameter. Each point is a single anemone.

Differences between Sites

Paired t-tests showed no significant differences in pedal disc diameter ($t = 0.61$, 138 d.f, $P = 0.543$), wet weight ($t = 0.03$, 138 d.f, $P = 0.979$) or average nematocyst length ($t = 1.04$, 138 d.f, $P = 0.301$) of all individuals between the two sites, Looe and Whitsands Bay. However, there was a significant difference in the number of peels inflicted upon individuals from the two sites ($t = 2.10$, 138 d.f, $P = 0.04$). The total number of peels inflicted on individuals from Whitsands Bay (90) was over twice that received by individuals from Looe (41). Within the large against large contests, there was also a significant difference in the number of peels inflicted on an individual ($t = 2.92$, 38 d.f, $P = 0.009$). There was also a significant difference in the nematocyst lengths of individuals from the two sites, within the large Looe against small Whitsands Bay contests ($t = 1.63$, 34 d.f, $P = 0.014$).

Outcome of Contests

Chi-squared tests were carried out on the data to reveal if the number of fights won by anemones from Looe differed to the number won by individuals from Whitsands. The total number of contests won by each site was random ($\chi^2 = 0.027$, 1 d.f, $P = 0.869$), however in the large against large ($\chi^2 = 6.4$, 1 d.f, $P = 0.011$) and small against small ($\chi^2 = 14.235$, 1 d.f, $P < 0.001$) contests, the number of fights won by each site was significantly not random. In category A, both individuals being large, the individual from Looe won 14 out of 20 fights (70%), but within category B, both small anemones, the anemone from Whitsands Bay won 14 out of the 17 contests (82%). A two-way chi-squared contingency table across all contest groups demonstrated a significantly not random outcome of contests ($\chi^2 = 11.681$, 3 d.f, $P = 0.009$).

Discussion

This study has demonstrated that body size, i.e. wet weight and pedal disc diameter, has no effect on an individual anemone's fighting ability or the outcome of a contest. Other studies have, in the past, found evidence to the contrary (e.g. Brace & Pavey 1978; Brace et al. 1979), however no recent studies have been able to confirm this argument and Stuart-Fox (2006) discussed how body size is a limited 'proxy' for RHP. This could be because older studies (e.g. Brace & Pavey 1978) employed amputated tentacles or rods as the stimulus for an aggressive encounter, whereas more recent studies, including this one, utilise whole individuals, which may cause a different reaction or behaviour to follow. Similarly to previous studies, weapon size was also not proven to be an important element of an anemones' fighting ability in this investigation.

The number of injuries an individual receives, however, is highly significant to the outcome of a contest proving the old adage, 'it's not what you've got; it's what you do with it that matters'. The winners of contests were the anemones that inflicted the greatest number of injuries on their opponents and this was similar across all four groups of contests. It could be disputed that the decision to 'give up' in a contest is related to the cost an individual has acquired during that fight and so the individual with the higher cost would be the 'loser' (Briffa & Elwood 2005). Another theory, proposed by Neat *et al.* (1998) is that the costs relative to those of your opponent are

central to decision making and a loser may assess that their opponent is willing to incur a greater cost than they are, and so choose to give up and minimise physical damage. As a consequence of this, when there is a palpable asymmetry between opponents, the probability of the better fighter winning should increase as the difference between the two individual's fighting ability increases (Leimar & Enquist 1984).

As anemone size increased, the number of injuries inflicted on that individual also increased. This may be because the difficulty of overcoming a larger anemone is greater and so you have to cause further injury to it. Large anemones from the Looe site had a greater number of injuries when they lost a fight, than small individuals or winners from Looe in either size class. Similar results were found in a study by Neat *et al.* (1998), which provides evidence that, in cichlid fish, smaller winners inflicted significantly more damage on their opponents than they received, whereas this was not seen in contests when the larger fish won. The author proposes "winners are inflicting greater costs on their opponents than they receive themselves when they are smaller than their opponent" (Neat *et al.* 1998).

Why does an individual proceed to using an acrorhagial response when it is smaller in body or weapon size than its opponent? This could be dependent on whether anemones assess their adversaries before aggressing. Theory predicts that if two individuals are competing for a resource, and there is an apparent asymmetry, then the outcome of the contest should be determined by this asymmetry (Enquist & Leimar 1983; Grafen 1987).

Some game theory models suggest that opponents compare their own ability to that of their rival before choosing whether or not to compete (Maynard Smith & Parker 1976). This may be because contest behaviour can be very costly to the individual concerned, both energetically, physically due to injury and in terms of lowered reproductive rates (Riechert 1988). The Asymmetric War of Attrition model, as discussed by Hammerstein & Parker (1982), proposes that individuals escalate their behaviours steadily, only ending in all out fighting. This helps the individual to more accurately assess their opponents RHP and decide whether or not to continue. Leiser *et al.* (2004) demonstrated that only when contestants are evenly matched in size, do they escalate to dangerous fighting behaviour. When faced with a 'large' opponent, the smaller individual retreats rather than risking injury. However, in the current study, individuals appeared not to 'size up' their opponents, merely escalated to all out fighting without delay. Alternatively the anemones may assess their opponent and if it is larger than they are, they choose to fight, but recognise that they must inflict a higher number of injuries to win.

Overall, the individuals from Looe were significantly more aggressive, inflicting a greater number of peels on their opponents and subsequently winning more fights overall and in three of the four contest groups. This may be related to the amount of competition the two populations of anemones encounter on a regular basis. There may be a greater number of individuals living at the Looe collection site and therefore competition for space would be more common and more intense.

A small number of contests in this study ended in stalemate and there could be a number of reasons for this. A couple of the specimens may have been of the green morph of the species, which has been shown to be significantly less aggressive than

the red morph (Brace & Reynolds 1989; Allcock *et al.* 1998). 83% (10 of 12) of these 'no fights' involved a large anemone from Looe, and the contest data demonstrated that to win a fight against a large individual from Looe, the opponent would need to inflict a higher number of injuries. This may have been at too high a cost to the individual from Whitsands Bay or this individual may have decided it was better to minimise damage and cohabit with its opponent. Half of these 'no fights' involved at least one anemone with previous acrorhagial scars, which may have caused the individual not to aggress.

One theory suggested by Turner *et al.* (2003) is the possibility that individuals may mistake a conspecific for a clonemate, even when they are not genetically identical. Sauer *et al.* (1986) discussed how glycoprotein recognition molecules, found on the tentacles, could cause the aggressive response in anemones and it has been shown that individuals may share alleles, including those used to determine recognition of other individuals (Bigger 1980). Therefore, an individual may decide not to attack a conspecific mistakenly. Further investigation could focus on whether clonemates have identical glycoproteins and how they differ between clones from a single location and multiple locations. Turner *et al.* (2003) also found that *Actinia equina* only deposits acrorhagial peels onto conspecific individuals, never in interspecific contests. Other species, e.g. *Actinia fragacea*, did not leave a scar on any conspecific individual, but only scarred individuals of a different species. Further studies could explore this genetic relatedness in relation to the acrorhagial response of anemones.

Another factor to consider is why the number of injuries inflicted is the most important element of agonistic behaviour and how these scars affect the anemones. Turner *et al.* (2003) discuss the exceptional healing ability of *Actinia equina*, able to form two smaller individuals when one anemone is cut in half. This capability could be exploited to reveal differences in fighting ability of genetically identical individuals, for example due to environmental factors, as well as the possibility of repeating experiments with the 'same' individual.

Further work includes studying whether past encounters affect an anemone's fighting ability in a later contest. Brace (1981) explained that *Phymactis clematis* does not appear to have a "general memory of past events", however, the study suggested that further investigation is needed. Brace & Santer (1991) proposed more examination into the persistence of habituation to help explain the memory capability of anemones. An additional suggestion is to focus on 'resident' ("non-mobile anemone fastened to the substratum") versus intruder ("mobile") encounters, to determine if the resident anemone had an advantage in a contest.

One limitation of the data in the current study is the number of sites used to collect individuals, and, therefore, the number of clones investigated. The individuals could have been genetically analysed to determine if all individuals from one site were clonemates (i.e. genetically identical) or if a number of clones were used. A further study focussing on the differences in RHP between several genetically distinguished clones is needed to elaborate on the results found in the current study. This could also demonstrate whether fighting ability is hereditary or unrelated to genetics.

The current study also did not account for environmental factors that could be affecting the two populations of anemones. One population may have been coping with pollution, for example, and therefore agonistic behaviour may be affected. South West Observatory Board (2007) has shown that Whitsands Bay should be considered for a Marine Protected Zone due to the high levels of fishing and tourism affecting the beach and the surrounding waters. Hannaford Point, however, is much less of a tourist spot, with fewer aggravations to the sea life inhabiting it. CEFAS (2005) focused on a disposal site in Whitsands Bay and found there to be a number of biological issues raised due to this site, including increased litter and turbidity, which potentially affects the anemones survival at that site.

This study concludes that body size and weapon size are not significant factors in agonistic behaviour in the anemone *Actinia equina*. Acrorhagial aggression, specifically the number of injuries an individual inflicts, is the key element and has a large effect on the outcome of contests. Furthermore, it is possibly controlled by the nerve net or may be immunologically based. However, further information is required on the allogeneic recognition between individuals and the possible consequences of these acrorhagial peels.

Acknowledgements

Jennifer Grocott, Kendal Harrison, Ben Porter and I worked as a group to gather the specimens from the shore and carry out the experiments (in order to guarantee our data sets were accurate and followed the same protocols). Each member of the group carried out a quarter of the data points within each group of fights, to ensure the results were unbiased.

I wish to thank Dr. Mark Briffa, who assisted in this project as my supervisor and for critically reading the draft manuscript. Also the staff of the University of Plymouth and the Marine Biology and Ecology Research Centre for their technical assistance and providing space and equipment for our use.

References

- Allcock, A.L., Watts, P.C. & Thorpe, J.P. 1998. Divergence of nematocysts in two colour morphs of the intertidal beadlet anemone *Actinia equina*. *Journal of the Marine Biological Association of the UK*, **78**, 821-828.
- Ayre, D.J. 1982. Inter-genotype aggression in the solitary sea anemone *Actinia tenebrosa*. *Marine Biology*, **68**, 199-205.
- Bigger, C.H. 1980. Interspecific and intraspecific acrorhagial aggressive behaviour among sea anemones: recognition of self and non-self. *Biological Bulletin*, **159**, 117-134.
- Bonnin, J-P. 1964. Recherches sur la réaction d'agression et sur le fonctionnement des acrorrhages d'*Actinia equina*. *Le Bulletin Biologique de la France et de la Belgique*, **98**, 225-250.

Brace, R.C. 1981. Intraspecific aggression in the colour morphs of the anemone *Phymactis clematis* from Chile. *Marine Biology*, **64**, 85-93.

Brace, R.C. & Pavey, J. 1978. Size-dependent dominance hierarchy in the anemone *Actinia equina*. *Nature*, **273**, 752-753.

Brace, R.C. & Reynolds, H.A. 1989. Relative intraspecific aggressiveness of pedal disc colour phenotypes of the Beadlet anemone, *Actinia equina*. *Journal of the Marine Biological Association of the UK*, **69**, 273-278.

Brace, R.C. & Santer, S-J. 1991. Experimental habituation of aggression in the sea anemone *Actinia equina*. *Hydrobiologia*, **216/217**, 533-537.

Brace, R.C., Pavey, J. & Quicke, D.L.J. 1979. Intraspecific aggression in the colour morphs of the anemone *Actinia equina*: the 'convention' governing dominance ranking. *Animal Behaviour*, **27**, 553-561.

Briffa, M. 2008. Decisions during fights in the house cricket, *Acheta domesticus*: mutual or self assessment of energy, weapons and size? *Animal Behaviour*, **75**, 1053-1062.

Briffa, M. & Elwood, R.W. 2005. Rapid change in energy status in fighting animals: causes and effects of strategic decisions. *Animal Behaviour*, **70**, 119-124.

Briffa, M. & Sneddon, L.U. 2007. Physiological constraints on contest behaviour. *Functional Ecology*, **21**, 627-637.

Centre for Environment, Fisheries and Aquaculture Science (CEFAS). 2005. *Environmental impacts resulting from disposal of dredged material at the Rame Head disposal site, S.W. England: An analysis of existing data and implications for environmental management*. CEFAS Contract BA004.

Daly, M., Fautin, D.G. & Cappola, V.A. 2003. Systematics of the hexacorallia (Cnidaria: Anthozoa). *Zoological Journal of the Linnean Society*, **139**, 419-437.

Dunn, D.G. F. 1982. *Cnidaria*. In *Synopsis and Classification of Living Organisms Vol. 1*, 669-706. Parker, S.B. (ed.), McGraw-Hill Book Company, New York.

England, K.W. 1991. Nematocysts of sea anemones (Actiniaria, Ceriantharia and Corallimorpharia: Cnidaria): nomenclature. *Hydrobiologia*, **216/217**, 691-697.

Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387-410.

Francis, L. 1973. Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related sea anemones. *Biological Bulletin*, **144**, 73-92.

Francis, L. 1988. Cloning and aggression among sea anemones (Coelentera: Actiniaria) of the rocky shore. *Biological Bulletin*, **174**, 241-253.

Godknecht, A. & Tardent, P. 1988. Discharge and mode of action of the tentacular nematocysts of *Anemonia sulcata* (Anthozoa: Cnidaria). *Marine Biology*, **100**, 83-92.

Grafen, A. 1987. The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Animal Behaviour*, **35**, 462-467.

Hammerstein, P. & Parker, G.A. 1982. The asymmetric war of attrition. *Journal of Theoretical Biology*, **96**, 647-682.

Just, W. & Morris, M.R. 2003. The napoleon complex: why smaller males pick fights. *Evolutionary Ecology*, **17**, 509-522.

Kemp, D.J. & Wiklund, C. 2004. Residency effects in animal contests. *Proceedings of the Royal Society of London*, **271**, 1707-1711.

Knowlton, N. 1996. Interclonal warfare. *Trends in Ecology and Evolution*, **11**, 271-272.

Leimar, O. & Enquist, M. 1984. Effects of asymmetries in owner-intruder conflicts. *Journal of Theoretical Biology*, **111**, 475-491.

Leiser, J.K., Gagliardi, J.L. & Itzkowitz, M. 2004. Does size matter? Assessment in fighting in small and large size-matched pairs of adult male convict cichlids. *Journal of Fish Biology*, **64**, 1339-1350.

Lindstrom, K. & Pampoulie, C. 2005. Effects of resource holding potential and resource value on tenure at nest sites in sand gobies. *Behavioural Ecology*, **16**, 70-74.

Manuel, R.L. 1981. *British Anthozoa*. Academic Press, London.

Maynard Smith, J. & Parker, G.A. 1976. The logic of asymmetric contests. *Animal Behaviour*, **24**, 159-175.

Neat, F.C., Taylor, A.C. & Huntingford, F.A. 1998. Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. *Animal Behaviour*, **55**, 875-882.

Parker, G.A. 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, **47**, 223-243.

Renison, D., Boersma, D., Van Buren, A.N. & Martella, M.B. 2006. Agonistic behaviour in wild male Magellanic penguins: when and how do they interact? *Journal of Ethology*, **24**, 189-193.

Riechert, S. 1988. The energetic costs of fighting. *American Zoology*, **28**, 877-884.

Sauer, K.P., Muller, M. & Weber, M. 1986. Alloimmune memory for glycoprotein recognition in sea anemones competing for space. *Marine Biology*, **92**, 73-79.

Schroeder, L. & Huber, R. 2001. Fight strategies differ with size and allometric growth of claws in crayfish *Orconectes rusticus*. *Behaviour*, **138**, 1437-1449.

Scott, J.P. 1966. Agonistic behavior of mice and rats: a review. *American Zoology*, **6**, 683-701.

Scott, J.W. & Fredericson, E. 1951. The causes of fighting in mice and rats. *Physiological Zoology*, **24**, 273-309.

Sneddon, L.U., Huntingford, F.A. & Taylor, A.C. 1997. Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas*. *Behavioural Ecology & Sociobiology*, **41**, 237-242.

South West Observatory Board (SWO). 2007. *State of the South West* [Online]. (Accessed 12/02/08) (Edited by Nick Chase)
<http://www.swo.org.uk/SoSW2007/web/index.html>

Stuart-Fox, D. 2006. Testing game theory models: fighting ability and decision rules in chameleon contests. *Proceedings of the Royal Society of London Series B*, **273**, 1555-1561.

Turner, V.L.G, Lynch, S.M., Paterson, L., Leon-Cortes, J.L. & Thorpe, J.P. 2003. Aggression as a function of genetic relatedness in the sea anemone *Actinia equina* (Anthozoa: Actiniaria). *Marine Ecology Progress Series*, **247**, 85-92.

Watts, P.C., Allcock, A.L., Lynch, S.M. & Thorpe, J.P. 2000. An analysis of the nematocysts of the beadlet anemone *Actinia equina* and the green sea anemone *Actinia prasina*. *Journal of the Marine Biological Association of the UK*, **80**, 719-724.

Williams, R.B. 1978. Some recent observations on the acrorhagi of sea anemones. *Journal of the Marine Biological Association of the UK*, **58**, 787-788.

Williams, R.B. 1991. Acrorhagi, catch tentacles and sweeper tentacles: a synopsis of "aggression" of actinarian and scleractinian Cnidaria. *Hydrobiologia*, **216/217**, 539-545.

Williams, R.B. 1996. Measurements of cnidae from sea anemones (Cnidaria: Actiniaria): statistical parameters and taxonomic relevance. *Scientia Marina*, **60**, 339-351.