Oecologia (2006) 149:362–372
DOI 10.1007/s00442-006-0442-z

BEHAVIORAL ECOLOGY

A new perspective on size hierarchies in nature: patterns, causes, and consequences

Peter M. Buston · Michael A. Cant

Abstract Many plant and animal aggregations have size hierarchies within which a variety of sizes of individuals, from large to small, can be found. Size hierarchies are thought to indicate the existence of competition amongst individuals within the aggregation, but determining their exact cause is difficult. The key to understanding size hierarchies lies in first quantifying the pattern of size and growth of individuals. We conducted a quantitative investigation of pattern in the size hierarchy of the clown anemonefish *Amphiprion percula*, in Madang Lagoon, Papua New Guinea. Here, groups of *A. percula* occupy sea anemones (*Heteractis magnifica*) that provide protection from predators. Within each anemone there is a single group composed of a breeding pair and zero to four non-breeders. Within each group there is a single size hierarchy; the female is largest (rank 1), the male is second largest (rank 2), and the non-breeders get progressively smaller (ranks 3–6). We demonstrate that individuals adjacent in rank are separated by body size ratios whose distribution is significantly different from the distribution expected under a null model—the growth of individuals is regulated such that each dominant ends up being about 1.26 times the size of its immediate subordinate. We show that it is decisions about growth at the individual level that generate the size hierarchy at the group level, and thereby determine maximum group size and population size. This study provides a new perspective on the pattern, causes and consequences of size hierarchies.

Keywords Conflict · Queue · Competition · Limit to similarity · Size ratio

1 Introduction

Size hierarchies are conspicuous features of many plant and animal aggregations (Rubenstein 1981; Forrester 1990; Nagashima et al. 1995; Poulson and Platt 1996). Qualitatively, size hierarchies are described as the presence of a variety of sizes of individuals, from large to small, within an aggregation. Size hierarchies are thought to indicate the existence of competition amongst individuals within the aggregation (Obeid et al. 1967; Rubenstein 1981; Begon 1984; Jones 1987; Nagashima et al. 1995; Booth 1995), but determining the exact cause of size hierarchies is notoriously difficult (Koebele 1985; Schwinning and Weiner 1998). Currently, it is not even known whether the sizes of individuals within such hierarchies are randomly or non-randomly distributed. Quantifying this pattern is a vital first step toward understanding the causes and consequences of size hierarchies.

Communicated by Libby Marschall

Present Address:
P. M. Buston (✉)
Estación Biológica de Doñana, C.S.I.C., Avenida de María
Luisa s/n., Pabellón de Perú, Apdo. 1056,
41013 Sevilla, Spain
e-mail: buston@ebd.csic.es

Present Address:
M. A. Cant
Department of Zoology, University of Cambridge,
Downing Street, Cambridge CB2 3EJ, UK

P. M. Buston · M. A. Cant
Department of Neurobiology and Behavior,
Cornell University, Seeley G. Mudd Hall,
Ithaca, NY 14853, USA

The clown anemonefish *Amphiprion percula* (Pisces: Pomacentridae) has a very simple size hierarchy that could provide a useful baseline for understanding other more complex hierarchies (Buston 2003a, 2004a). In Madang Lagoon, Papua New Guinea, groups of *A. percula* are confined to sea anemones (*Heteractis magnifica*) that afford protection from predators (Mariscal 1970; Fautin 1992; Elliott et al. 1995; Elliott and Mariscal 2001; Buston 2003b, c). Within each anemone, there is a single group of *A. percula* composed of a dominant breeding pair and 0–4 non-breeding subordinates (Fricke 1979; Fautin 1992; Buston 2004a, b). Within each group, there is a single size hierarchy; the female is largest (rank 1), the male is second largest (rank 2), and the non-breeders get progressively smaller (rank 3–6) (Fricke and Fricke 1977; Fricke 1979; Ochi 1986; Hattori 1991; Buston 2003a). *A. percula* are protandrous hermaphrodites (Fricke and Fricke 1977; Moyer and Nakazano 1978); if the female of a group dies, the male changes sex and assumes the position vacated by the female, and the largest non-breeder from within the anemone inherits the position vacated by the sex-changing male (Fricke 1979; Ochi 1989; Hattori 1994; Buston 2004a; Mitchell 2005). The size hierarchy represents a queue to attain dominant status; individuals only ascend in rank when a higher rank individual disappears, and the smallest fish in the groups is always the most recent recruit (Buston 2003a, 2004a).

A rigorous methodology has been developed to investigate pattern in interspecific size hierarchies (Hutchinson 1959; MacArthur and Levins 1967; Horn and May 1977; Strong et al. 1979; Roff 1981; Wiens 1981; Gotelli and Graves 1996). Here, we co-opt this methodology to conduct a quantitative investigation of the pattern, causes, and consequences of the intraspecific size hierarchies of *A. percula*. We test five hypotheses:

1. The body size ratios of individuals adjacent in rank will be non-randomly distributed (Hutchinson 1959; MacArthur and Levins 1967; Horn and May 1977; Strong et al. 1979; Gotelli and Graves 1996).
2. Variation in these body size ratios will be related to social and ecological factors (Roff 1981).
3. Variation in these body size ratios will decline over time, as individuals converge on an intermediate body size ratio (Roff 1981; Wiens 1981).
4. Convergence on an intermediate body size ratio will be caused by the regulation of growth.
5. Understanding these body size ratios will enable us to predict maximum group size (Hutchinson 1959; MacArthur and Levins 1967).

Our analyses provide a new perspective on the pattern, causes and consequences of size hierarchies.

2 Materials and methods

2.1 Study population

This study was conducted using data collected from a population of clown anemonefish, *Amphiprion percula*, studied for 12 months (January 1997–December 1997), in Madang Lagoon (5°09’S, 145°48’E), Papua New Guinea (Buston 2002). All fieldwork was conducted using SCUBA, at depths of less than 15 m. Ninety-seven anemones (*Heteractis magnifica*) were located on three reefs: Sinub (reef 1), $n = 40$; Wongad (reef 2), $n = 31$; Masamoz (reef 3), $n = 26$ (see Jebb and Lowry 1995, for a description of Madang Lagoon and its reefs). This study utilizes 70 groups found on reef 1 and reef 2. (The 26 groups on reef 3 were not used for this study because they could not be regularly censused, and they were subject to an experimental manipulation for another study). On each reef, anemones were an average of 30 m apart. Each anemone was occupied by a single group of *A. percula*. Groups consisted of a breeding pair and from zero to four non-breeders (mean number of individuals in each group ± SD = 3.4 ± 0.9, $n = 97$).

A dive computer was used to measure the depth of each anemone to 0.1 m (mean depth ± SD = 6.9 ± 2.3 m, $n = 97$). Depths were measured on ten occasions throughout 1997, and the depth assigned to each anemone in the analyses was the mean of these depths. The mean diameter of each anemone’s oral disc was used as a measure of anemone size (mean anemone diameter ± SD = 49 ± 8 cm, $n = 97$). The diameter of the anemone was measured to the nearest 5 cm, and the mean was calculated 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. No anemone growth was detected over the year.

2.2 Size, growth, rank, and ratios

In January 1997, all fish ($n = 334$) were captured using hand nets and taken to the surface in plastic bags. There, the standard length (SL) of each individual was measured to 0.1 mm using calipers. A fish’s SL is the straight-line distance from the tip of the snout to the base of the caudal fin (Caillet et al. 1986). We used SL as our metric, rather than mass, because SL is unlikely to vary day to day. In December 1997, all surviving fish were re-captured and re-measured. All fish survived these procedures, without any sign of harm, and were returned to the anemone from which they were captured within 3 h, where they remained.

Individuals were ranked (1–6) based on their size relative to other individuals within the same group, with the largest being ranked 1. We considered an individual of rank *N* to be dominant to all individuals with ranks greater than *N*, and subordinate to all individuals with ranks less than *N*. Rank assigned in this way perfectly predicted the order in which individuals inherited breeding positions within an anemone (Buston 2002, 2004a).

We determined the ratio of SL of individuals adjacent in rank within each group: (SL rank *N*/SL rank *N* + 1). We used the ratio as our measure of similarity, rather than absolute size difference, because the ratio controls for absolute SL. We assigned ratios at different positions in the size hierarchy a ‘‘ratio number’’. For example, the SL ratio of individuals at ranks 1 and 2 was called ‘‘ratio 1’’, that between ranks 2 and 3 was ‘‘ratio 2’’, and so on. Further, we called the ratio between the two smallest individuals in the group the ‘‘terminal ratio’’, and all other ratios were called ‘‘non-terminal’’. When only two individuals were present in the group ($n = 4$) the ratio between them was identified as a terminal ratio.

2.3 Group dynamics

Settlement, recruitment, migration, and disappearance of individuals were monitored by conducting a thorough census of each group every 1–2 days (Buston 2002, 2003b). Following the logic of previous investigators (Williams and Sale 1981; Keough and Downes 1982), individuals were assigned to one of five classes: (1) settlers, if they were less than 18 mm in SL when they were first observed in an anemone; (2) recruits, if they reached ≥ 18 mm in SL after settling in an anemone; (3) residents (rank 1–6), if they were ≥ 18 mm in SL and were present in the anemone at the beginning of the study; (4) migrants, if they were ≥ 18 mm in SL and moved between anemones; or (5) disappearances, if they had been ≥ 18 mm in SL but could not be found in their anemone or any of the other anemones on the reef after a thorough search.

The transition from settler to recruit marked the point (18 mm SL) at which a settler was deemed to have joined a group. Although the 18 mm SL transition point was arbitrary, it was chosen for two reasons: (1) fish greater than 18 mm SL ($n = 334$) could be recognized individually on the basis of natural variation in their color markings, when regularly censused (Nelson et al. 1994; Buston 2002, 2003b, c); and (2) fish greater than 18 mm SL could be reliably censused without continual disturbance of the anemone (Elliott and Mariscal 2001; Buston 2002, 2003b, c). Residents did not migrate between anemones, and individuals that disappeared probably died (Buston 2002, 2003b, c).

3 Results

3.1 Hypothesis 1: the body size ratios of individuals adjacent in rank will be non-randomly distributed

We tested the hypothesis that the body size ratios of individuals adjacent in rank will be non-randomly distributed (Hutchinson 1959; MacArthur and Levins 1967; Horn and May 1977), by comparing the observed distribution of size ratios to the distribution of size ratios expected under a null model (Strong et al. 1979; Gotelli and Graves 1996).

We obtained an observed distribution of 177 ratios, from 70 groups, in January 1997. We created a null distribution of 17,700 ratios using a Monte Carlo procedure, programmed in MATLAB. To do this we randomly selected individuals from the pool of 247 available individuals (the same 70 groups) and combined them into groups according to the natural distribution of group sizes found in our sample. We then ranked the individuals in these random groups on the basis of relative size, and calculated the ratio of the size of individuals adjacent in rank. The procedure was iterated 100 times, generating an expected random distribution of ratios against which our observed distribution could be compared. This null model design is appropriate because it excludes only the factor of interest (naturally occurring interactions between individuals adjacent in rank) while incorporating other realistic factors (naturally occurring distribution of body sizes and group sizes) that might influence the results (Gotelli and Graves 1996).

The observed distribution of ratios differed significantly from the distribution of ratios generated by the null model (Fig. 1; Kolmogorov–Smirnov test: $df = 2$, $\chi^2 = 71.427$, $P < 0.0001$). The most striking differences between the distributions are the lack of small ratios (e.g., ratios less than 1.1) and the overabundance of intermediate ratios (e.g., ratios from 1.2 to 1.3) in the observed distribution (Fig. 1). We conclude that the size hierarchies have a non-random structure.

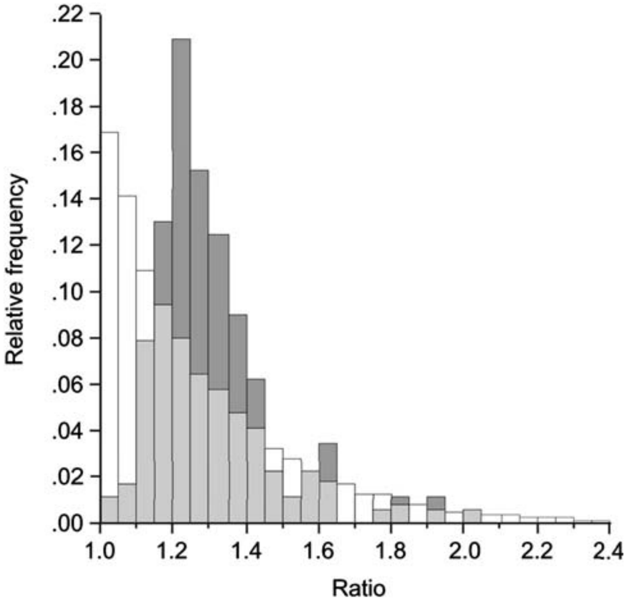

Fig. 1 The observed distribution of ratios of standard lengths (SLs) of clown anemonefish (*Amphiprion percula*) individuals adjacent in rank within each group (*dark gray* and *light gray*; mean = 1.30, SD = 0.17, n = 177), and the distribution of ratios expected under a null model generated using Monte Carlo procedure (*white* and *light gray*; mean = 1.28, SD = 0.27, n = 17700). *Light gray* represents area where two distributions overlap

3.2 Hypothesis 2: variation in these body size ratios will be related to social and ecological factors

The preceding analysis demonstrated that although these body size ratios are non-randomly distributed they are not invariant. To better understand this pattern, we tested the hypothesis that variation in these size ratios will be related to social and ecological factors (Roff 1981).

We conducted a mixed model analysis with "ratio" as the dependent variable (n = 177 ratios), six independent variables, and "group identification number" (1–70) entered as a random effect (SAS Mixed Procedure). We investigated the effect of six independent variables: "ratio number" (five fixed levels), "terminal ratio" (two fixed levels; terminal and non-terminal), "number of individuals" (six fixed levels), "anemone diameter" (centimeter, covariate), "depth" (meter, covariate), and "reef" (two fixed levels). Independent variables were removed from the model in a backward 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.

The only factor that was significantly related to "ratio" was the comparison between "terminal ratios" and all other "non-terminal ratios" (Fig. 2; SAS Mixed Procedure: df = 1, 106, F = 22.16, P < 0.0001). The terminal ratio is the ratio between the two smallest individuals in the group, and all other ratios are non-terminal. Terminal ratios tend to be larger than all other ratios. We conclude that some of the variation in the size ratio is attributable to variation in the size of the smallest member of the group. Because the smallest member of the group is always the most recent recruit (Buston 2003b, 2004a), this result suggests that the length of time individuals spend together might influence the size ratio.

3.3 Hypothesis 3: variation in these body size ratios will decline over time

The preceding analyses suggested that there might be convergence on intermediate body size ratios over time. To better understand this pattern, we tested the hypothesis that there will be convergence on intermediate size ratios over time in groups whose membership was stable (Roff 1981; Wiens 1981).

We compared the variance in the ratios of January 1997 (n = 116 ratios) to the variance in the ratios of December 1997 (n = 116 ratios). Only groups whose membership was stable, (i.e., groups that experienced no losses of intermediate or high-rank individuals for the entire study period), were included in this analysis (n = 47 groups). The variance in the ratio was less in December 1997 than in January 1997

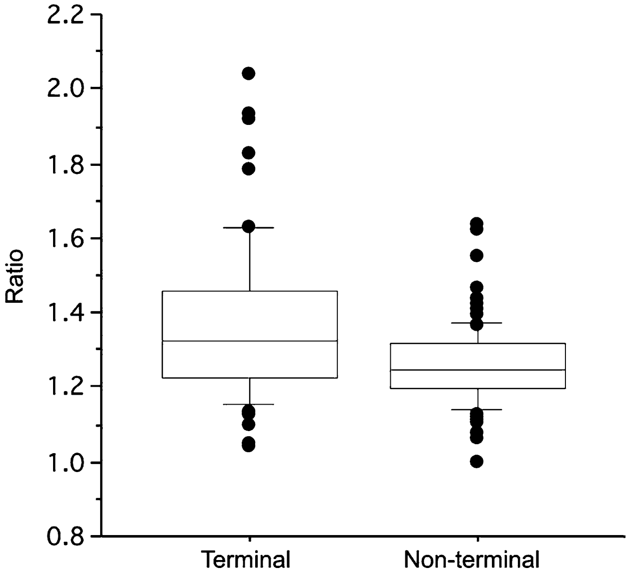

Fig. 2 The magnitude of "terminal ratios", the ratio of SL of the two smallest individuals in each group (mean ± SE = 1.37 ± 0.03, n = 70), and all other "non-terminal ratios" (mean ± SE = 1.26 ± 0.01, n = 107). *Horizontal lines* in box plot display the 10th, 25th, 50th, 75th, and 90th percentile. All values above the 90th percentile and below the 10th percentile are plotted separately

(Fig. 3; equality of variances F-test: $df = 115$, $F = 2.77$, $P < 0.0001$). This reduction in variance occurs both as a result of small ratios increasing and large ratios decreasing (Fig. 3). We conclude that there is convergence on intermediate body size ratios over time.

3.4 Hypothesis 4: convergence on an intermediate size ratio will be caused by regulation of growth

The preceding analysis demonstrated that there was convergence on intermediate body size ratios over time. To better understand the cause of this pattern, we tested the hypothesis that convergence will be caused by the differential regulation of growth above and below a specific body size ratio.

We began by considering several possible estimates of a specific body size ratio on which convergence might be occurring: (1) the mean of the observed distribution of ratios (mean ± SD = 1.30 ± 0.17, $n = 177$, Fig. 1); (2) the mean of the non-terminal ratios (mean ± SD = 1.26 ± 0.10, $n = 107$, Fig. 2); and (3) the mean of the ratios found in stable groups in December 1997 (mean ± SD = 1.27 ± 0.11, $n = 116$, Fig. 3). Of these alternatives, we considered the smallest with the least variation (1.26 ± 0.10) to be the best estimate of the ratio of convergence—the ratio upon which individuals would converge given sufficient time.

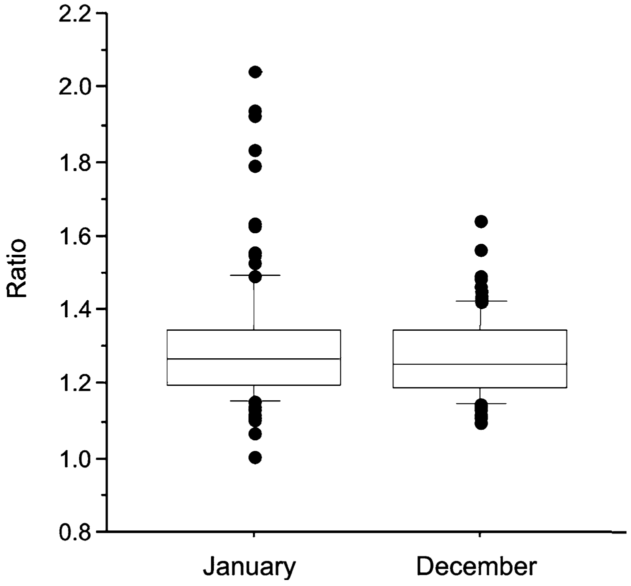

Fig. 3 The ratio of SLs in January 1997 (mean = 1.30, variance = 0.03, $n = 116$) and December 1997 (mean = 1.27, variance = 0.01, $n = 116$). Only the 47 groups with stable memberships were included. *Horizontal lines* in box plot display the 10th, 25th, 50th, 75th, and 90th percentile. All values above the 90th percentile and below the 10th percentile are plotted separately

The body size ratio of individuals adjacent in rank will change if the individuals show a different percentage increase in SL. We compared the percent change in SL of rank N (dominants) to the percent change in SL of rank $N + 1$ (subordinates) over four size intervals, defined by the ratio of convergence (1.26) and its SD (± 0.10): (1) initial size ratio of the pair was less than 1.16; (2) initial size ratio of the pair was greater than 1.16 but less than 1.26; (3) initial size ratio of the pair was greater than 1.26 but less than 1.36; and (4) initial size ratio of the pair was greater than 1.36.

Dominants grew relatively more than their immediate subordinates when the initial size ratio of the pair was less than 1.16 (Fig. 4; paired t-test: $df = 12$, $t = 2.21$, $P = 0.0470$), and slightly though not significantly more when the initial size ratio of the pair was between 1.16 and 1.26 (Fig. 4; paired t-test: $df = 43$, $t = 0.24$, $P = 0.8101$). Conversely, subordinates grew relatively more than their immediate dominants when the initial size ratio of the pair was greater than 1.36 (Fig. 4; paired t-test: $df = 22$, $t = 4.01$, $P = 0.0006$), and slightly though not significantly more when the initial size ratio of the pair was between 1.26 and 1.36 (Fig. 4;

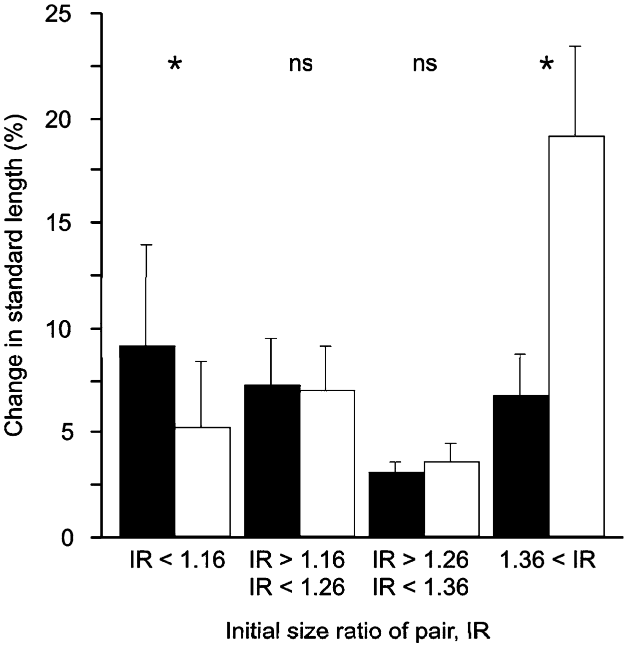

Fig. 4 The percentage change in SL (mean ± SE) of dominants, rank N (*black*), and subordinates, rank $N + 1$ (*white*), when the initial size ratio (*IR*) of the pair was: less than 1.16 (dominant, $n = 13$; subordinate, $n = 13$); greater than 1.16 but less than 1.26 (dominant, $n = 44$; subordinate, $n = 44$); greater than 1.26 but less than 1.36 (dominant, $n = 36$; subordinate, $n = 36$); and greater than 1.36 (dominant, $n = 23$; subordinate, $n = 23$). *Horizontal lines* in bar chart represent the mean and *bars* are SEs. * Difference significant, where $\alpha = 0.05$; *ns* not significant

paired t-test: $df = 35$, $t = 0.89$, $P = 0.3798$). We conclude that convergence on a specific body size ratio is caused by the differential regulation of growth above and below this ratio.

3.5 Hypothesis 5: understanding these body size ratios will enable us to predict maximum group size

The preceding analyses indicated that there might be convergence on a ratio of 1.26 over time (Figs. 2, 3, 4). If there is convergence on a specific body size ratio over time then we should be able to predict maximum group size (Hutchinson 1959; MacArthur and Levins 1967). To better understand the consequences of this pattern, we tested the hypothesis that maximum group size will be predicted by the size of the largest individual and this particular body size ratio.

We assumed that there was convergence on a body size ratio of 1.26 between individuals adjacent in rank and that the smallest group members were 18 mm in SL (see Materials and methods). These two assumptions enabled us to predict maximum group size, over a range of SLs of rank 1 individuals [range of rank 1 SL (millimeter), and maximum group size ($g_{\max}$): 18.0–22.6 mm, $g_{\max} = 1$; 22.7–28.5 mm, $g_{\max} = 2$; 28.6–35.9 mm, $g_{\max} = 3$; 36.0–45.3 mm, $g_{\max} = 4$; 45.4–57.1 mm, $g_{\max} = 5$; 57.2–71.9 mm, $g_{\max} = 6$; 72.0–90.7 mm, $g_{\max} = 7$).

We compared the observed group size to the predicted maximum group size, for 71 groups. There is a perfect correlation between predicted maximum group size and observed maximum group size (Fig. 5; correlation coefficient: $df = 2$; $r = 1$; $P < 0.05$; Zar 1984). We do not place much weight on the statistic itself. The most important result is that all observed group sizes fall at, or below, the predicted maximum. We conclude that knowing that there is convergence on a specific body size ratio enables us to effectively predict maximum group size.

4 Discussion

4.1 Patterns, causes, and consequences of size hierarchies

Size hierarchies are conspicuous features of many plant and animal aggregations, yet no study has quantified their pattern. To gain a better understanding of size hierarchies, we conducted a quantitative description of the pattern found in the simple hierarchy of *A. percula*. We show that the size hierarchy of *A. percula* has a non-random structure; the distribution of body size ratios of individuals adjacent in rank lacks small ratios and has an overabundance of intermediate ratios (Fig. 1). We demonstrate that there is convergence on intermediate ratios (ratios between 1.2 and 1.3) over time; more specifically, we provide evidence that there is convergence on the ratio of 1.26 (Figs. 2, 3). Our analysis indicates that convergence on this specific ratio is caused by the differential regulation of growth above and below this ratio; initially large ratios decrease over time because when the ratio is large the subordinate grows relatively more than its immediate dominant, whereas initially small ratios increase over time because when the ratio is small the dominant grows relatively more than its immediate subordinate (Fig. 4). On the basis of the body size ratio of convergence (1.26) and the body size of the largest group member we are able to accurately predict maximum group size (Fig. 5).

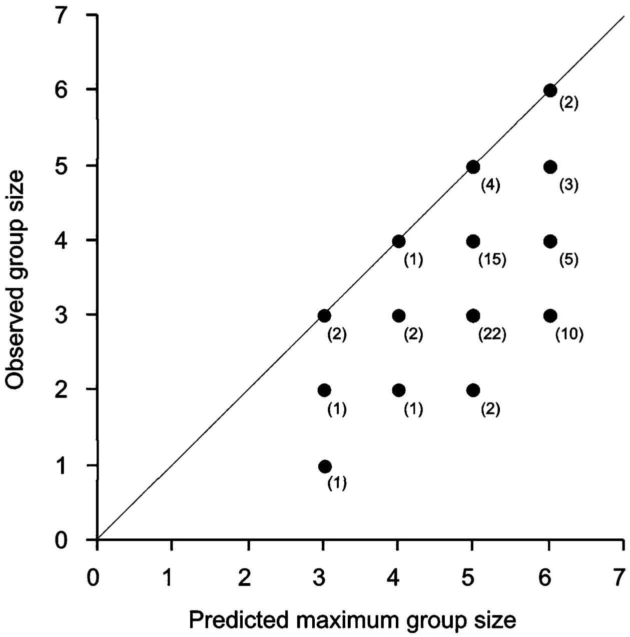

Fig. 5 The relationship between the observed group size and the predicted maximum group size (n = 71 groups). Maximum group size was predicted assuming that there was convergence on a body size ratio of 1.26. The *line* represents the 1:1 relationship between observed group size and predicted maximum group size. *Points* represent the existence of groups, and *numbers in parentheses* indicate the number of groups at each point

This study clearly demonstrates that size hierarchies can have a non-random structure, which is caused by the precise regulation of the growth of individuals. Recognizing these facts opens up a whole series of interesting questions. First, how and why is the growth of individuals regulated? This question can be answered in terms of ultimate and proximate causation (Mayr 1961; Tinbergen 1964; Sherman 1988), and from the perspective of both the dominant and the subordinate. Second, what are the implications of the non-random structure for group dynamics and population dynamics? Here we consider preliminary answers to these questions.

4.2 Ultimate causes of growth regulation

To understand the ultimate causes, or adaptive significance, of growth regulation it is necessary to have some measure of the fitness consequences of changes in size. For *A. percula* these fitness effects are quite well understood. Subordinate individuals benefit from settling in an anemone and queuing for breeding positions (Buston 2004a), and thus a subordinate's rank is the key predictor of whether or not it will obtain a breeding position (Field et al. 1999; Kokko and Johnstone 1999; Ragsdale 1999; Buston 2004a; Cant et al. 2006). Dominant individuals, however, gain no measurable benefits from the presence of their subordinates, and subordinates are always potential challengers for a dominant's rank and the access to reproduction that it confers (Buston 2004b). This asymmetry in the benefits of group living generates potential evolutionary conflict over group membership between individuals adjacent in rank, and dominants occasionally evict or kill subordinates of similar size (Allen 1972; Buston 2003b). The regulation of growth resolves the potential evolutionary conflict over group membership between individuals adjacent in rank (Buston 2003a). Dominants benefit from regulating the growth of their subordinates because in doing so they prevent challenges to their rank. Subordinates benefit from regulating their own growth because in doing so they avoid becoming a threat to their immediate dominant, and thereby avoid being evicted. In *A. percula* the fitness effects of regulating growth are understood from both the dominants' and subordinates' perspectives.

We expect that adaptive regulation of growth and non-random size hierarchies will be found in other fish species. Some likely candidates include other members of the genus *Amphiprion* (Allen 1972; Fricke 1979; Ochi 1986; Hattori 1991; Mitchell and Dill 2005), and members of the goby genera *Gobiodon* and *Paragobiodon* (Lassig 1976, 1977; Hobbs and Munday 2004), which are sex changers that form groups composed of a dominant breeding pair and a number of subordinate non-breeders. Also, members of the damselfish genus *Dascyllus* (Coates 1980; Sweatman 1983; Forrester 1990; Booth 1995; Schmitt and Holbrook 1999), which are sex changers but form groups composed of a dominant male and a number of subordinate females. Additionally, members of the cichlid genus *Neolamprologus* (Taborsky 1984; Balshine-Earn et al. 1998; Heg et al. 2004), which have separate sexes but form groups composed of a dominant breeding pair and a number of subordinate non-breeders. Common to all these species are potential benefits for subordinates that remain in a territory, in terms of gaining access to better breeding positions, and potential costs to a dominant of tolerating a subordinate, in terms of having their rank challenged, which together generate evolutionary conflict. We suggest that the regulation of growth may help to resolve this conflict in all of these species.

4.3 Proximate causes of growth regulation

Turning to the proximate mechanisms of growth regulation, many investigations of size hierarchies have suggested that dominants regulate the growth of their subordinates either by using aggression (Brown 1946; Allen 1972; Fricke 1974; Koebele 1985; Ochi 1986; Hattori 1991; Booth 1995) or by intercepting food resources (Magnuson 1962; Coates 1980; Forrester 1991). Aggression by dominants is thought to regulate subordinate growth either because subordinates expend energy fleeing from attacks, such that less energy is available for growth, or because subordinates become stressed in response to attacks, such that available energy is not converted into growth (Brown 1946; Allen 1972; Koebele 1985; Booth 1995). In these size hierarchies aggression directed from dominants to subordinates is relatively common; there are more than 40 aggressive events per hour in *Amphiprion perideraion* (Allen 1972) and more than 12 aggressive events per individual per hour in *Amphiprion akallopisos* (Fricke 1979) and *Dascyllys albisella* (Booth 1995). In *A. percula* aggression is relatively rare; there is less than one aggressive event per individual per hour (P.M. Buston, unpublished data), suggesting that dominants are not using aggression to suppress their subordinates in this species. Instead we suggest that the presence of the dominant and the threat of eviction by the dominant are sufficient to regulate subordinate growth. Comparing across groups within species, or across species, we predict that dominants will have to employ more aggression to regulate subordinate growth when they are less able to control group membership.

Although most previous studies of size hierarchies have focused on the role of the dominant in the regulation of subordinate growth, we suggest that the role of the subordinate in regulating its own growth must also be considered. The dominant's actions will elicit behavioral, hormonal, and neuronal response mechanisms in the subordinate by which the subordinate regulates its own growth. That is to say, the growth regulation mechanisms of dominants and subordinates should both be viewed as products of natural selection that enable the individuals to produce best responses to each other. A subordinate might regulate its own growth by reducing its food intake (Allee et al 1948; Yamigashi et al. 1974; Koebele 1985), increasing its level of the stress hormone cortisol, or increasing the size of its somatostatin containing neurons (Fox et al. 1997; Hofman and Fernald 2000). The mechanisms that subordinates use to regulate their own growth might be conserved across species, but we suggest that the cues required to elicit them might vary. For example, in species like *A. percula* where each dominant is able to evict its subordinate (Buston 2003b), the subordinate might reduce its food intake or increase its level of cortisol in response to the presence of the dominant and convergence on a specific size ratio. In species like *A. perideraion* where each dominant is apparently less able to evict its subordinate (P. M. Buston, personal observation), the subordinate might employ similar mechanisms but only in response to increases in the level of aggression from the dominant. Comparing across groups within species, or across species, we predict that the behavioral, hormonal, and neuronal mechanisms that the subordinate uses to regulate its growth will require less aggression from the dominant when the dominant is more able to control group membership.

4.4 Implications for group dynamics and population dynamics

This study increases our understanding of the factors that influence group size in *A. percula* and other territorial fishes. In territorial fishes there are often correlations between territory size and the size of the dominant, the size of the dominant and the size of the group, and the size of the group and the size of the territory [anemonefishes (Allen 1972; Ross 1978; Fricke 1979; Hattori 1991; Fautin 1992; Elliott and Mariscal 2001; Buston 2003b; Mitchell and Dill 2005); hawkfishes (Donaldson 1989); gobies (Kuwamura et al. 1994); cichlid fishes (Balshine et al. 2001)]. This triangle of correlates has made it difficult to determine the cause and effect of these relationships. Here, we demonstrate that the body size of the dominant sets a limit on group size (Fig. 5), which would generate the commonly observed correlation between the size of the dominant and group size (e.g., Fig. 1b in Mitchell and Dill 2005). Why does the body size of the dominant set the limit on group size? When the dominant is large, it is possible to fit more fish in the anemone while maintaining the required size ratio between individuals adjacent in rank. Thus maximum group size, and the relationship between dominant size and group size, can be a product of the way in which reproductive conflict is resolved.

This study complements our growing understanding of the factors that influence population size in the anemonefishes—model systems for marine population ecology. Taking the triangle of correlates between the size of the dominant, group size, and anemone size as our framework, we have shown that the size of the dominant can have a direct causal impact on group size. Elsewhere, it has been shown that group size does not directly influence the size of the dominant; the presence of non-breeders does not influence the survival, growth or reproduction of breeders (Buston 2004b). Recent studies have shown that the growth of anemones can be dependent on the number of fish present (Porat and Chadwick-Furman 2004; Holbrook and Schmitt 2005). This effect can be caused by the fish defending the anemone against predators, influencing the photosynthetic behavior of the anemone, and providing ammonia to the anemone, all of which might enhance tissue growth, regeneration, and indeed reproduction (Porat and Chadwick-Furman 2004, 2005; Holbrook and Schmitt 2005). To date there is no evidence that anemone size has a direct effect on group size. Anemone size, however, can have a direct causal effect on the size of the dominant. Buston (2002) has documented that the growth of the dominant is dependent on the anemone size, once other variables are statistically controlled. Presumably, this occurs because there is more food available in larger anemones. To date there is no evidence that dominant size has a direct effect on anemone size. Thus it seems that increases in the size of the dominant can cause increases in group size, increases in group size can cause increases in anemone size, and increases in anemone size can cause increases in the size of the dominant. Since there is only one group per anemone (Fricke 1979; Buston 2004b), and groups do not occur outside of anemones (Mariscal 1970; Fautin 1992; Elliott et al. 1995; Elliott and Mariscal 2001; Buston 2003b), population size of this species will be critically dependent on the direct and indirect interactions between dominant size, group size, and anemone size.

4.5 Plant size hierarchies

Some of the most intriguing parallels to the size hierarchies found within groups of fish are found within neighborhoods of plants. In both fishes and plants, the growth of individuals (Marks and Gardescu 1998; Poulson and Platt 1996; Buston 2003a) and the size of individuals within the aggregation (Rubenstein 1981; Ochi 1986; Nagashima et al. 1995; Poulson and Platt 1996) seem to follow a similar pattern. In both, the hierarchies are thought to indicate the existence of competition among individuals within the aggregation (Obeid et al 1967; Rubenstein 1981; Begon 1984; Jones 1987; Booth 1995; Nagashima et al. 1995).

The proximate mechanisms causing the regulation of subordinate growth in fish and plant size hierarchies are thought to be similar (Koebele 1985; Schwinning and Weiner 1998). Dominant individuals may suppress subordinates either by intercepting food/light energy (Magnusson 1962; Coates 1980; Weiner 1988; Geber 1989; Forrester 1991; Schwinning 1996) or by being physically/chemically aggressive (Rose 1960; Allen 1972; Fricke 1974; Franco 1986; Jones and Harper 1987a, b; Mahall and Callaway 1991, 1992; Booth 1995). Subordinates may grow mainly in response to changes in social cues, and not necessarily in response to changes in resource availability (Rose 1960; Koebele 1985; Ballare et al. 1990; Forrester 1990; Ballare and Scopel 1997).

The ultimate fitness effects causing the regulation of subordinate growth in fish and plant size hierarchies might also be similar. The cost to subordinates of growing large may be increased conflict with their local dominant, which can result in damage or the death of the subordinate (Allen 1972; Barlow et al. 1986; Franco 1986; Rowland 1989; Brunkow and Collins 1998). Natural selection can favor the strategy of remaining small and waiting for the local dominant to die in any organism where this strategy maximizes the subordinate's chances of attaining positions that confer high reproductive success (Kokko and Johnstone 1999; Ragsdale 1999; Shreeves and Field 2002; Falster and Westoby 2003; Buston 2004a; Cant et al. 2006).

4.6 Challenges facing investigations of size hierarchies

This study sheds light on three issues that should be considered in future investigations of size hierarchies. First, such investigations should account for the possibility that the underlying pattern can be obscured in disturbed populations. Long-term studies of marked individuals would help to account for this possibility. Second, investigations should clearly define which individuals are involved in each size hierarchy. In *A. percula*, this is relatively easy because there is only one hierarchy in each anemone and anemones are separated by inhospitable terrain. In other fishes and plants with overlapping territories and sub-territories, it will be necessary to determine the set of subordinates that each dominant influences and the set of dominants that each subordinate is influenced by before pattern and process in the size hierarchy can be investigated. Finally, investigations should bear in mind that the ultimate hypothesis for the regulation of growth, (presented earlier), is that it resolves conflict within a queue for breeding positions. This being the case, then there may be a single queue within groups of hermaphrodites such as *A. percula*, but there may be two queues within groups of gonochores such as *Neolamprologus pulcher* (a male queue and a female queue). Analyzing the male and female queue together likely will obscure any pattern that is predicted to exist within each queue.

4.7 Conclusions

This study demonstrates that size hierarchies can have a non-random pattern. The growth of individuals can be strictly regulated such that a specific size ratio is maintained between individuals adjacent in rank. This pattern can reflect the resolution of potential evolutionary conflict between dominants and their immediate subordinates. Resolution of conflict at the individual level can generate the well-defined size hierarchy at the group level, determine maximum group size and influence population size. The framework presented here provides a new perspective on pattern, causes and consequences of size hierarchies.

Acknowledgements This work comprises a portion of P. M. B.'s doctoral thesis requirements (Cornell University). P. M. B. thanks his Ph.D. advisors, S. Emlen, P. Sherman, A. McCune, K. Reeve, and A. Bass for incredible support; J. Mizeu, M. Black, C. Norris, M. Moore, and the staffs of the Christensen Research Institute and the Jais Aben Resort for their assistance in Papua New Guinea; the landowners of Riwo village, the Madang Provincial Government, and the Papua New Guinea Government for permission to work on the reefs of Wongad, Sinub and Masamoz in Madang Lagoon. Further, we thank J. Dale, N. Hairston, F. Huntingford, D. Heg, J. von Fischer, L. Marschall, P. Munday, C. Petersen, R. Warner, C. Webb, M. Wong, and several anonymous reviewers for helpful comments and discussion. B. Ledvina (a.k.a. James Dean) helped with the Monte Carlo simulation. P. M. B. was supported by D. Christensen and the Christensen Fund, a National Science Foundation Doctoral Dissertation Improvement Grant, the Andrew W. Mellon Fund of the Cornell College of Agriculture and Life Sciences, the Cornell and National Chapters of Sigma Xi, the International Women's Fishing Association, and the Cornell University Department of Neurobiology and Behavior. P. M. B. is currently funded by a Ramón y Cajal Fellowship of the Consejo Superior de Investigaciones Científicas. M. A. C. was supported by a Royal Commission for the Exhibition of 1851 Research Fellowship. M. A. C. is currently funded by a Royal Society University Research Fellowship.

References

Allee WC, Greenberg B, Rosenthal GM, Frank P (1948) Some effects of social organization on growth in the green sunfish, *Lepomis cyanellus*. J Exp Zool 108:1–9

Allen GR (1972) The anemonefishes: their classification and biology, 2nd edn. T.F.H., Neptune City

Ballare CL, Scopel AL (1997) Phytochrome signaling in plant canopies: testing its population level implications with photoreceptor mutants of *Arabidopsis*. Funct Ecol 11:441–450

Ballare CL, Scopel AL, Sanchez RA (1990) Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. Science 247:329–332

Balshine-Earn S, Neat FC, Reid H, Taborsky M (1998) Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. Behav Ecol 9:432–438

Balshine S, Leach B, Neat F, Reid H, Taborsky M, Werner N (2001) Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). Behav Ecol Sociobiol 50:134–140

Barlow GW, Rogers W, Fraley N (1986) Do Midas cichlids win through prowess or daring? It depends. Behav Ecol Sociobiol 19:1–8

Begon M (1984) Density and individual fitness: asymmetric competition. In: Shorrocks B (ed) Evolutionary ecology. Blackwell, London, pp 175–194

Booth DJ (1995) Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. Ecology 76:91–106

Brown ME (1946) The growth of brown trout (*Salmo trutta* Linn.). I. Factors influencing the growth of trout fry. J Exp Biol 22:118–129

Brunkow PE, Collins JP (1998) Group structure affects patterns of aggression in larval salamanders. Behav Ecol 9:508–514

Buston PM (2002) Group structure of the clown anemonefish, *Amphiprion percula*. PhD dissertation, Cornell University

Buston PM (2003a) Size and growth modification in clownfish. Nature 424:145–146

Buston PM (2003b) Forcible eviction and prevention of recruitment in the clown anemonefish. Behav Ecol 14:576–582

Buston PM (2003c) Mortality is associated with social rank in the clown anemonefish (*Amphiprion percula*). Mar Biol 143:811–815

Buston PM (2004a) Territory inheritance in the clown anemonefish. Proc R Soc Ser B 271 [Suppl]:S252–S254

Buston PM (2004b) Does the presence of non-breeders enhance the fitness of breeders? An experimental analysis in the clown anemonefish. Behav Ecol Sociobiol 57:23–31

Caillet GM, Love MS, Ebeling AW (1986) Fishes: a field and laboratory manual on the structure, identification, and natural history. Wadsworth, Belmont

Cant MA, Llop JB, Field J (2006) Individual variation in social aggression and the probability of inheritance: theory and a field test. Am Nat 167:837–852

Coates D (1980) Prey-size intake in humbug damselfish, *Dascyllus aruanus* (Pisces, Pomacentridae) living within social groups. J Anim Ecol 49:335–340

Donaldson TJ (1989) Facultative monogamy in obligate coral dwelling hawkfishes (Cirrhitidae). Environ Biol Fish 26:295–302

Elliott JK, Mariscal RN (2001) Coexistence of nine anemonefish species: differential host and habitat utilization, size and recruitment. Mar Biol 138:23–36

Elliott JK, Elliott JM, Mariscal RN (1995) Host selection, location, and association behaviors of anemonefishes in field settlement experiments. Mar Biol 122:377–389

Falster DS, Westoby M (2003) Plant height and evolutionary games. Trees 18:337–343

Fautin DG (1992) Anemonefish recruitment: the roles of order and chance. Symbiosis 14:143–160

Field J, Shreeves G, Sumner S (1999) Group size, queuing, and helping decisions in facultatively eusocial hover wasps. Behav Ecol Sociobiol 45:378–385

Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish. Ecology 71:1666–1681

Forrester GE (1991) Social rank, individual size, and group composition as determinants of food consumption by humbug damselfish, *Dascyllus aruanus*. Anim Behav 42:701–711

Fox HE, White SA, Kao MHF, Fernald RD (1997) Stress and dominance in a social fish. J Neurosci 17:6453–6469

Franco M (1986) The influence of neighbours on the growth of modular organisms with an example from trees. Philos Trans R Soc Lond Ser B Biol Sci 313:209–225

Fricke H (1974) Oko-ethologie des monogamen Anemonefisches *Amphiprion bicinctus* (Freiwasseruntersuchung aus dem Roten Meer). Z Tierpsychol 32:225–256

Fricke HW (1979) Mating system, resource defense and sex change in the anemonefish *Amphiprion akallopisos*. Z Tierpsychol 50:313–326

Fricke H, Fricke S (1977) Monogamy and sex change by aggressive dominance in coral reef fish. Nature 266:830–832

Geber MA (1989) Interplay of morphology and development on size inequality: a *Poygonum* greenhouse study. Ecol Monogr 59:267–288

Gotelli NJ, Graves GR (1996) Null models in ecology. Smithsonian Institution Press, Washington, D.C.

Hattori A (1991) Socially controlled growth and size-dependent sex change in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. Jpn J Ichthyol 38:165–177

Hattori A (1994) Inter-group movement and mate acquisition tactics of the protandrous anemonefish, *Amphiprion clarkii*, on a coral reef, Okinawa. Jpn J Ichthyol 41:159–165

Heg D, Bender N, Hamilton I (2004) Strategic growth decisions in helper cichlids. Proc R Soc Lond Ser B 271 [Suppl]:S505–S508

Hobbs JPA, Munday PL (2004) Intraspecific competition controls spatial distribution and social organization of the coral-dwelling goby *Gobiodon histrio*. Mar Ecol Prog Ser 278:253–259

Hofman HA, Fernald RD (2000) Social status controls somatostatin neuron size and growth. J Neurosci 20:4740–4744

Holbrook SJ, Schmitt RJ (2005) Growth, reproduction, and survival of a tropical sea anemone (Actinaria): benefits of hosting anemonefish. Coral Reefs 24:67–73

Horn HS, May RM (1977) Limits to similarity among coexisting competitors. Nature 270:660–661

Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals. Am Nat 93:145–159

Jebb MHP, Lowry JK (1995) Natural history of Madang Lagoon with an appendix of collecting localities. Rec Aust Mus 22 [Suppl]:1–24

Jones GP (1987) Competitive interactions among adults and juveniles in a coral reef fish. Ecology 68:1534–1547

Jones M, Harper JL (1987a) The influence of neighbours on the growth of trees. I. the demography of buds in *Betula pendula*. Proc R Soc Lond Ser B Biol Sci 232:1–18

Jones M, Harper JL (1987b) The influence of neighbours on the growth of trees. II. the fate of buds on long and short shoots in *Betula pendula*. Proc R Soc Lond Ser B Biol Sci 232:19–33

Keough JJ, Downes BJ (1982) Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia 54:348–352

Koebele BP (1985) Growth and the size hierarchy effect: an experimental assessment of three proposed mechanisms; activity differences, disproportional food acquisition, physiological stress. Environ Biol Fish 12:181–188

Kokko H, Johnstone R (1999) Social queuing in animal societies: a dynamic model of reproductive skew. Proc R Soc Biol Sci Ser B 266:571–578

Kuwamura T, Yogo Y, Nakashima Y (1994) Population dynamics of goby *Paragobiodon echinocephalus* and host coral *Stylophora pistillata*. Mar Ecol Prog Ser 103:17–23

Lassig BR (1976) Field observations on the reproductive behaviour of Paragobiodon spp. (Osteichthyes Gobiidae) at Heron Island Great Barrier Reef. Mar Behav Physiol 3:283–293

Lassig BR (1977) Socioecological strategies adopted by obligate coral-dwelling fishes. In: Proceedings of the 3rd International Coral Reef Symposium, pp 565–570

MacArthur R, Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. Am Nat 101:377–385

Magnusson JJ (1962) An analysis of aggressive behavior, growth, and competition for food and space in medaka [*Oryzias latipes* (Pisces, Cyprinodontidae)]. Can J Zool 40:313–363

Mahall BE, Callaway RM (1991) Root communication among desert shrubs. Proc Natl Acad Sci USA 88:874–876

Mahall BE, Callaway RM (1992) Root communication mechanisms and intracommunity distributions of two desert shrubs. Ecology 73:2145–2151

Mariscal RN (1970) The nature of the symbiosis between Indo-Pacific anemonefishes and sea anemones. Mar Biol 6:58–65

Marks PL, Gardescu S (1998) A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. J Torrey Bot Soc 125:287–296

Mayr E (1961) Cause and effect in biology. Science 134:1501–1506

Mitchell JS (2005) Queue selection and switching by false clown anemonefish, *Amphiprion ocellaris*. Anim Behav 69:643–652

Mitchell JS, Dill LM (2005) Why is group size correlated with the size of the host sea anemone in the false clown anemonefish? Can J Zool 83:372–376

Moyer JT, Nakazano A (1978) Protandrous hermaphroditism in six species of the anemonefish genus *Amphiprion* in Japan. Jpn J Ichthyol 25:101–106

Nagashima H, Terashima I, Katoh S (1995) Effects of plant density on frequency distributions on plant height in *Chenopdium album* stands: analysis based on continual monitoring of height growth of individual plants. Ann Bot 75:173–180

Nelson JS, Chou LM, Phang Violet PE (1994) Pigmentation variation in the anemonefish *Amphiprion ocellaris* (Teleostei: Pomacentridae): type, stability and its usefulness for individual identification. Raffles Bull Zool 42: 927–930

Obeid M, Machin D, Harper JL (1967) Influence of density on plant to plant variation in fiber flax, *Linum usitatissimum*. Crop Sci 7:471–473

Ochi H (1986) Growth of the anemonefish *Amphiprion clarkii* in temperate waters, with special reference to the influence of settling time on the growth of 0-year olds. Mar Biol 92:223–229

Ochi H (1989) Acquisition of breeding space by non-breeders in the anemonefish *Amphiprion clarkii* in temperate waters of southern Japan. Ethology 83:279–294

Porat D, Chadwick-Furman NE (2004) Effects of anemonefish on giant sea anemones: expansion behavior, growth and survival. Hydrobiologia 530/531:513–520

Porat D, Chadwick-Furman NE (2005) Effects of anemonefish on giant sea anemones: ammonium uptake, zooxanthellae content and tissue regeneration. Mar Freshwater Behav Physiol 38:43–51

Poulson TL, Platt WJ (1996) Replacement patterns of beech and sugar maple in Warren Woods, Michigan. Ecology 77:1234–1253

Ragsdale JE (1999) Reproductive skew extended: the effect of resource inheritance on social organization. Evol Ecol Res 1:859–874

Roff VL (1981) Constancy in the size ratios of sympatric species. Am Nat 118:394–404

Rose SM (1960) A feedback mechanism of growth control in tadpoles. Ecology 41:188–199

Ross RM (1978) Territorial behavior and ecology of the anemonefish *Amphiprion melanopus* on Guam. Z Tierpsychol 36:71–83

Rowland WJ (1989) The effects of body size, aggression, and nuptial coloration on competition for territories in male threespine sticklebacks, *Gasterosteus aculeatus*. Anim Behav 37:282–289

Rubenstein DI (1981) Individual variation and competition in the everglades pygmy sunfish. J Anim Ecol 50:337–350

Schmitt RJ, Holbrook SJ (1999) Mortality of juvenile damselfish: implications for assessing processes that determine abundance. Ecology 80:35–50

Shreeves G, Field J (2002) Group size and direct fitness in social queues.Am Nat 159:81–95

Schwinning S (1996) Decomposition analysis of competitive symmetry and size structure dynamics. Ann Bot 77:47–57

Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447–455

Sherman PW (1988) The levels of analysis. Anim Behav 36:616–619

Strong DR, Szyska LA, Simberloff DS (1979) Tests of community-wide character displacement against null hypotheses. Evolution 33:897–913

Sweatman HPA (1983) Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *Dascyllus reticulatus*) on coral reefs. Mar Biol 75:225–229

Taborsky M (1984) Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. Anim Behav 32:1236–1252

Tinbergen N (1964) On aims and methods of ethology. Z Tierpsychol 20:410–433

Weiner J (1988) Variation in the performance of individuals in plant populations. In: Davy AJ, Hutchings MJ, Watkinson AR (eds) Plant population ecology. Blackwell, Oxford, pp 59–81

Wiens JA (1981) Single-sample surveys of communities: are the revealed patterns real? Am Nat 117: 90–98

Williams DM, Sale PF (1981) Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within One Tree Lagoon, Great Barrier Reef. Mar Biol 65:245–253

Yamigashi H, Maruyama T, Mashiko K (1974) Social relation in small experimental population of *Odonobutis obscurus* (Temminck et Schlegel) as related to individual growth and food intake. Oecologia 17:187–202

Zar JH (1984) Biostatistical analysis, 2nd edn. Prentice Hall, Englewood Cliffs, N.J.