

NOTE

Boom-or-bust growth in coral reef lagoons

Kathryn D. Kavanagh*

Department of Marine Biology, James Cook University, Townsville, Queensland 4811, Australia

Present address: Evolution and Development Unit, Institute of Biotechnology, PO Box 56, University of Helsinki 00014, Finland

ABSTRACT: This study reports the results of a natural experiment demonstrating that wind-mediated growth compensation occurs in wild juvenile damselfishes *Acanthochromis polyacanthus* Bleeker, 1855 (Pomacentridae) living in a coral reef lagoon. Strong wind conditions are thought to bring additional oceanic plankton into the lagoon through increased wave height and water movement. The strong winds and presumed burst of food were found to rapidly increase growth rate in lagoon juveniles beyond that of exposed-reef conspecifics. Under calm conditions, lagoon juveniles grew more slowly than exposed-reef juveniles, and analysis of foregut fullness indicated that lagoon juveniles under calm conditions ate significantly less than exposed-reef juveniles. These results fit the definition of compensatory growth and provide some of the first evidence of this phenomenon in wild fish populations. Eye growth was also measured and found to be less responsive than growth in length.

KEY WORDS: Growth compensation · Coral reef · Habitat

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

The observation of compensatory growth in animals (faster-than-routine growth rates in response to growth depression) is puzzling to ecologists and evolutionary biologists because it goes against the prediction that animals, which are often subject to size-selective pressures, would always grow at the maximum rate physiologically possible (Ali et al. 2003). If food is not limited and faster growth is possible, why not grow faster routinely? Growth compensation has also been known as 'catch-up' growth, because the growth-rate-depressed fish accelerate growth rate when food becomes abundant again, and thus can 'catch up' in size with fish that were growing at routine rates all along. Over the past decade, researchers have realized that this 'catch-up' growth may have important consequences for population and ecological dynamics. For example, growth compensation would tend to canalize ontogenetic changes in size, buffer the effects of environmental variability, offset maternal allocation differences, as well as

incur significant short- and long-term physiological 'costs of rapid growth' (Metcalf & Monaghan 2001, Ali et al. 2003). However, due to the lack of clear control groups, growth compensation is difficult to identify in wild populations—the majority of observations of growth compensation have been made on domesticated endotherms or aquacultured coldwater fishes; thus, the prevalence and significance of growth compensation in wild populations is unknown (Ali et al. 2003). Here I report the results of an experiment demonstrating wind-mediated compensatory growth in wild hatchlings of a coral reef fish. Furthermore, in the same growth-compensating individuals, I detected concurrent growth stability (lack of compensation) in eye growth, suggesting decoupling of body parts during this unusually rapid growth response. These field-based results provide the first demonstration of growth compensation in early stages of wild fishes living at high temperatures (~29°C) and further indicate that growth compensation may facilitate some level of environmentally mediated morphological differences among populations.

*Email: kathryn.kavanagh@helsinki.fi

The spiny damselfish *Acanthochromis polyacanthus* Bleeker, 1855 (Pomacentridae) is a small planktivorous reef fish and is unusual in that it broods its young for relatively long periods, such that sibling juveniles can be repeatedly sampled from the same site (<1 m³) to measure growth rates in particular reef habitats (Kavanagh 2000). Because wind-driven currents provide oceanic plankton to the reefs, broods produced on the reef zones exposed to oceanic waters have consistent access to this replenishment of plankton, but the lagoon broods do not. The ocean water can only reach the lagoon by passing through narrow cuts in the reef structure or as a thin veneer passing across the reef flat, where the plankton is essentially sieved by a phenomenon called the 'wall of mouths' (Hamner et al. 1988), in which a high density of planktivores reduces the plankton available to the lagoon community. During periods of strong winds, however, increased wave height and water volume passing over the reef would conduct more plankton into the lagoon.

Several previous observations from the literature on coral-reef biology have led to the hypothesis that lagoon-dwelling planktivorous fishes may have a more variable food supply than fishes living outside the lagoon. This hypothesis is based on several facts about

the biotic structuring of reef environments, particularly the distinct patterns of coral reef habitat zonation that are most obvious between exposed and lagoonal reefs (Myers 1989). These 2 reef zones differ in various aspects of their physical, chemical, and biotic environment (Leis 1986, Eckert 1987, Gladstone & Westoby 1988, Hamner et al. 1988, Beukers 1996). Growth rates and average sizes of fishes inhabiting lagoonal zones have often been reported to be lower than those in exposed-reef zones (Thresher 1985, Gladstone & Westoby 1988, Kavanagh 1998). Furthermore, growth rate and abundance of planktivorous reef fishes have been correlated with local current speed, often leading to the suggestion of a causal relationship (Hobson & Chess 1978, Thresher 1983). Several experimental studies have shown that growth rates and maturation of coral-reef fishes can be increased by supplemental feeding (Jones 1986, Forrester 1990), while others found no effect of supplemental feeding (K.D. Kavanagh unpubl. data). These contrasting results suggest that food-limitation may be variable among locations and times.

In this study, the results of periods of calm and strong winds on growth rates in hatchling *Acanthochromis polyacanthus* in these habitats were compared.

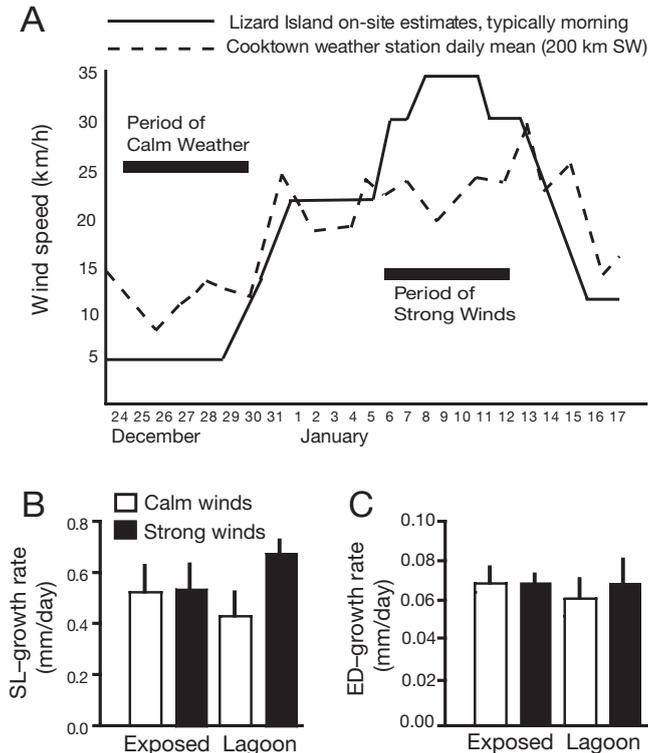


Fig. 1. (A) Daily wind measurements and (B,C) growth responses of *Acanthochromis polyacanthus* hatchlings in Exposed and Lagoon reef habitats during the study period. SL: standard length; ED: eye diameter

MATERIALS AND METHODS

Forty-five recently hatched *Acanthochromis polyacanthus* broods were selected haphazardly from lagoon and exposed reef habitats at Lizard Island, northern Great Barrier Reef (14° 40' S, 145° 27' E), during a period when, coincidentally, calm weather was followed by strong winds (Fig. 1A). Using a small hand-net, an initial collection of 10 individuals was taken from each brood, then placed alive in a small plastic bag. These juveniles were fixed shortly after collection in 10% seawater-buffered formalin. For each collection, within-brood size variation was low (1 to 3%). Ten more individuals were sampled from each brood one or more times, over 3 to 5 d periods. Daily wind conditions were estimated (e.g. by observing waves and from research station staff's assessments of wind strength) and recorded on site for the entire experimental period, then confirmed with regional weather reports recorded at the closest Bureau of Meteorology weather station (Cooktown, 200 km SW) (Fig. 1A). A period of steady calm winds and a period of steady high winds were identified *a priori* (after the sampling period was over, but before analysis of growth rate data). These wind conditions were treated as a factor for analytical purposes when comparing growth rates over these periods.

The subset of broods sampled from the beginning and end of the period of either calm or strong winds were used in the comparative analysis ($n = 10$, Exposed–Calm; 2, Exposed–Strong Wind; 13, Lagoon–Calm; and 7, Lagoon–Strong Winds). Only 2 broods could be used for the Exposed–Strong Winds treatment group because rough weather and dangerous diving conditions limited the ability to sample more broods during this period. Using an ocular micrometer calibrated on a dissecting scope, standard length (SL) and eye diameter (ED) of each juvenile collected were measured. Means and standard deviations were calculated for each sample (5 juveniles per brood per collection) for both measurements. Growth rates were calculated using the equation $(L_d - L_i)/d$, where L_d is the length (either SL or ED) at Day d after start, L_i is the initial length, and d is the number of days since initial collection, e.g. since the beginning of the period of calm or strong winds.

Brood-mean growth rates were analyzed for differences between reef zones and wind-strength treatments. To test for differences, 2-factor ANCOVAs were used with brood-mean initial size as a covariate and reef-zone and wind-strength as factors.

To look for changes in feeding level in different environments, gut fullness was estimated from similar-sized (7.2 to 8.2 mm SL) individuals (3 or 4 ind. brood⁻¹). These collections had been made in the afternoon in all cases, reducing the effect of feeding variation due to time of day. Guts were dissected from the gut cavity and percent fullness was estimated based on the presence of any identifiable zooplankton body part in sections of the fore- and midgut. Hindgut fullness was not assessed in order to reduce effects of capture-related gut evacuation.

RESULTS

Over the size range of the juveniles examined, SL growth rates were quite variable and no consistent effect of initial SL was apparent (among treatments, some individuals slightly increase in SL growth rate as initial size increases and others decrease in SL growth rate as initial size increases; overall $F_{1,31} = 2.82$, $p = 0.105$). In the overall model, there was a significant effect of wind strength ($F_{1,31} = 14.47$, $p = 0.0006$), and a significant interaction between wind strength and zone ($F_{1,31} = 13.12$, $p = 0.001$), but no significant effect of zone ($F_{1,31} = 0.314$, $p = 0.5788$). Zone-specific differences in growth responses to wind conditions were revealed by post-hoc examination of these data (Scheffé test; Fig. 1B): (1) exposed-reef juveniles grew similarly in calm and strong winds; (2) lagoon juveniles in strong winds had higher growth rates and lower

variability than the other treatments; and (3) lagoon juveniles in calm winds had lower growth rates than the other treatments. A power analysis indicated that the ANOVA had a 92% power to detect significant differences among treatment factors.

In contrast to the SL growth rate pattern, the analysis of ED growth rate indicated no significant differences among zones ($F_{1,31} = 0.994$, $p = 0.326$) or wind conditions ($F_{1,31} = 1.007$, $p = 0.323$) (Fig. 1B). Again, no consistent directional effect of initial SL on ED growth rate was observed in all treatments ($F_{1,31} = 0.28$, $p = 0.6$). Power analysis indicated that the test had the ability to detect differences among treatment factors with 49% certainty.

To determine whether growth rate was related to feeding level, percent gut fullness was also estimated and found to be statistically similar in individuals from Exposed–Calm (mean = 58.6%), Exposed–Strong Wind (48.0%) and Lagoon–Strong Wind (50.2%) broods. However, fish from Lagoon–Calm broods had significantly lower gut fullness (16.5%; ANOVA: $F_{3,67} = 13.27$; $p < 0.001$; Scheffé: $p < 0.001$).

DISCUSSION

The lower gut fullness of the lagoon fish in calm weather indicates that the slower SL growth rates of these broods were likely due to food deprivation, as would be expected by the lack of plankton-rich water movement into the lagoon in calm weather. The exposed-reef broods in this comparison thus essentially act as a control for the growth depression/compensation response of the lagoon broods. The observation that fish in exposed reefs did not grow faster in strong winds suggests that exposed-reef fish were already growing at maximum routine rates. These fish were at least able to consume enough to maintain or surpass the calm period growth rates, suggesting that they were not significantly impeded from feeding during strong winds. Previous observations of smaller body size of adult *Acanthochromis polyacanthus* and other fishes in the lagoon habitats may be a result of the inconsistent and/or generally lower level of plankton supply to this reef zone (Thresher 1985, Gladstone & Westoby 1988, Kavanagh 1998).

Although the eye growth data were variable and thus the test had low power, it is nonetheless clear that ED growth rate responded differently than SL growth rate in this comparison. The relative stability in ED growth rate suggests that the somatic (primarily musculoskeletal) growth rate is more responsive than ED growth rate to short-term variability under environmental conditions. Previous studies report that somatic growth and ED growth may be dissociated during

ontogeny and particularly that ED growth may be less sensitive to food deprivation even over long periods (Pankhurst 1992, Reichling & German 2000). Eyes are complex organs composed of many different tissue types that must be precisely coordinated in order to function well. Thus, animals may find it advantageous to have a steady ontogenetic rate for this organ, for which internal regulation of organogenesis is more important than integration with surrounding tissues, at least in the short term. If eyes (or other organs) grow steadily while musculoskeletal systems vary in growth rate, then differences in morphology among local reef fish populations may be detectable.

It appears that the peaceful paradise of the coral reef lagoon may in fact be a place of boom-or-bust growth for juvenile fishes. The ecological and physiological consequences of such growth patterns in wild animals, including their short- and long-term benefits and costs, are just beginning to be recognized. This study found differences in growth rate responses to local weather among fish subpopulations within a single reef formation; such local structuring of critical rates may help explain demographic and ecological patterns in the coral reef community.

Acknowledgements. I am grateful to J. H. Choat, D. Bellwood, J. Leis and J. Jernvall for helpful comments. This research was funded by the Overseas Postgraduate Research Award from the Australian Government.

LITERATURE CITED

- Ali M, Nicieza A, Wootton RJ (2003) Compensatory growth in fishes: a response to growth depression. *Fish Fish Ser* 4: 147–190
- Beukers JS (1996) The relative roles of recruitment and postrecruitment in the population regulation of a coral reef damselfish. PhD thesis, James Cook University of North Queensland, Townsville
- Eckert GJ (1987). Estimates of adult and juvenile mortality for labrid fishes at One Tree Island, Great Barrier Reef. *Mar Biol* 95:167–171
- Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish population. *Ecology* 71: 1666–1681
- Gladstone W, Westoby M (1988) Growth and reproduction in *Canthigaster valentini* (Pisces: Tetraodontidae): a comparison of a toxic reef fish with other reef fishes. *Environ Biol Fish* 21(3):207–221
- Hamner WM, Jones MS, Carleton JH, Hauri IR, Williams DM (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bull Mar Sci* 42:459–479
- Hobson ES, Chess JR (1978) Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. *Fish Bull* 76:133–153
- Jones GP (1986) Food availability affects growth in a coral reef fish. *Oecologia* 70:136–139
- Kavanagh KD (1998) The early life history of the brooding damselfish *Acanthochromis polyacanthus*: effects of ancestry and environment. PhD dissertation, James Cook University of North Queensland, Townsville
- Kavanagh KD (2000) Larval brooding in the marine damselfish *Acanthochromis polyacanthus* (Pomacentridae) is correlated with highly divergent morphology, ontogeny, and life history traits. *Bull Mar Sci* 66(2):321–337
- Leis JM (1986) Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. *Mar Biol* 90:505–516
- Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends Ecol Evol* 16(5):254–260
- Myers RF (1989) Micronesian reef fishes. Coral Reef Graphics, Barrigada, Guam
- Pankhurst NW (1992) Ocular morphology of the sweep *Scorpius lineolatus* and the spotty *Notolabrus celidotus* (Pisces: Teleostei) grown in low intensity light. *Brain Behav Evol* 39:116–123
- Reichling TD, German RZ (2000) Bones, muscles and visceral organs of protein-malnourished rats (*Rattus norvegicus*) grow more slowly but for longer durations to reach normal final size. *J Nutrition* 130:2326–2332
- Thresher RE (1983) Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef Lagoon. *Mar Ecol Prog Ser* 10:137–145
- Thresher RE (1985) Distribution, abundance, and reproductive success in the coral reef fish *Acanthochromis polyacanthus*. *Ecology* 66:1139–1150

*Submitted: March 22, 2004; Accepted: December 14, 2004
Proofs received from author(s): January 20, 2005*

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany