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REPORT

Influence of depth on sex-specific energy allocation patterns in a tropical reef fish

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Abstract The effect of depth on the distribution and sex-specific energy allocation patterns of a common coral reef fish, *Chrysiptera rollandi* (Pomacentridae), was investigated using depth-stratified collections over a broad depth range (5–39 m) and a translocation experiment. *C. rollandi* consistently selected rubble habitats at each depth, however abundance patterns did not reflect the availability of the preferred microhabitat suggesting a preference for depth as well as microhabitat. Reproductive investment (gonado-somatic index), energy stores (liver cell density and hepatocyte vacuolation), and overall body condition (hepato-somatic index and Fulton's *K*) of female fish varied significantly among depths and among the three reefs sampled. Male conspecifics displayed no variation between depth or reef. Depth influenced growth dynamics, with faster initial growth rates and smaller mean asymptotic lengths with decreasing depth. In female fish, relative gonad weight and overall body condition (Fulton's *K* and hepato-somatic index) were generally higher in shallower depths (≤ 10 m). Hepatic lipid storage was highest at the deepest sites sampled on each reef, whereas hepatic glycogen stores tended to decrease with depth. Depth was found to influence energy allocation dynamics in *C. rollandi*. While it is unclear what processes directly influenced the depth-related patterns in energy allocation, this study shows that individuals across a broad depth gradient are not all in the same physiological state and may contribute differentially to the population reproductive output.

Keywords Depth effects · Body condition · Energy allocation · Coral reef fish · Pomacentridae

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Introduction

Life history traits of terrestrial and aquatic vertebrates vary markedly among locations (Adams 1979; Berven 1982). While phylogeny generally determines the template of an organism, the boundaries of life history traits can be extensively modified by environmental factors (Hutchings 1993). Environmental variables, such as temperature and food availability, can influence the partitioning of energy to growth and reproduction, and in doing so affect the fitness of an organism (Roff 1992; Stearns 1992). The relationship between environmental variables and life history traits therefore, is central to understanding the evolution of life-history strategies.

Altitude, depth, latitude, and distance from the coast, are some of the ecologically significant axes along which environmental conditions vary, both gradually and in some cases abruptly (e.g. among habitats) (Rowe 1994; Badayev 1997; Maravelias et al. 2000; Meekan et al. 2001; Gust et al. 2002). Varying environmental conditions may lead to changes in community composition (Lecchini et al. 2003), as species enter and leave communities based on their

physiological tolerances and biological interactions (Rowe 1994; Mark et al. 2001). In the terrestrial environment, elevation has long been considered an important environmental variable influencing life history traits in many animals (e.g. lizards: Mathies and Andrews 1995; birds: Badayev 1997; amphibians: Morrison and Hero 2003; mammals: Gillis et al. 2005). Birds and mammals at lower elevations have shown a general trend of higher reproductive output, earlier age of first reproduction, and lower adult survival compared to those at higher elevations (Badayev 1997; Badayev and Ghalambor 2001; Gillis et al. 2005).

In the marine environment, variations in life history traits along a depth cline have received less attention, especially for mobile organisms (for exceptions see Srinivasan 2003), with most work concentrating on sedentary organisms (e.g. corals: Mundy and Babcock 2000; Edmunds et al. 2004). In mobile marine animals, such as reef fish, the behavioural tendency to forage over varying distances may obscure the influence of a depth gradient. However, irrespective of the distance travelled, both site specific and roving species are faced with energetic trade-offs at different depths. Species with small home ranges must locate a preferable habitat, and hence depth, to sustain them for their entire life. Roving species, on the contrary, may traverse a range of depths and habitats during a 24-h period, some of which may not provide the resources needed.

Distribution patterns along a depth gradient may also be influenced by developmental stage, body size and gender. Many reef fish undergo ontogenetic shifts in their depth distribution over various scales, ranging from a few metres over several weeks (e.g. Lecchini and Galzin 2005) to tens of metres over many months (e.g. McCormick 1989a). Differential size and sex distribution patterns have also been reported over a range of depths, for both temperate (e.g. Choat and Ayling 1987; McCormick 1989a, b) and tropical (e.g. Sale 1969; Johannes 1978) species, with a general trend of increasing body size with depth (for exceptions see Davis and Farley 2001; Wilson 2001). These distribution patterns may reflect a preference for a specific environment that satisfies the energy requirements and maximises the fitness of the various developmental stages.

In the marine reef environment many environmental and biological variables co-vary with depth. Substratum or microhabitat type is an integration of many of these variables and has been demonstrated to be a major factor in the distribution patterns of marine fishes on a variety of spatial scales (e.g. Waldner and Robertson 1980; Russ 1984; Levin 1993). Due to the relationship between habitat and depth, it is often difficult to divorce depth from the influence of substratum characteristics. This study investigated the impact of depth on gender specific life history traits of *Chrysiptera rollandi* (Pomacentridae), a site attached tropical reef fish that exhibits a broad depth range. This contrasts with the only other study of the effect of depth on life history traits of tropical species, which examined species with very narrow depth distributions (Srinivasan 2003). To determine whether a covariance of habitat type and depth would confound depth-related life history trends, this study first examined the role that habitat selectivity played in the distribution patterns of the fish. Once the importance of microhabitat had been determined, depth-related trends in energy partitioning to reproduction, energy storage and growth were explored for each sex. Descriptive information is augmented by an experiment that directly tests the effects of depth on energy storage and growth through the translocation of individuals between depths.

Materials and methods

Study species and location

The model species used in the present study was the tropical damselfish *C. rollandi*, a common member of the coral reef fish communities in the Indo-Pacific. *C. rollandi* displays a very broad depth distribution, extending from just below the reef crest (~2 m) down to at least 40 m on the reef slope. *C. rollandi* is a protogynous hermaphrodite and a benthic serial spawner (Thresher 1984). A recent study at the present study location found that 50% or more of all female *C. rollandi* sampled were in breeding condition throughout the year (Srinivasan and Jones 2006).

The study was conducted in Kimbe Bay, West New Britain, Papua New Guinea (5°25′S, 150°06′E) over a 6-week period during March and April 2001. The bay has a well-developed fringing reef around its margin and numerous small coral reefs that typically have steep reef slopes that extend beyond 60 m in depth. The mean tidal range in Kimbe Bay is ~0.1–0.6 m, therefore the depth ranges on concurrent dives were operationally consistent. The three reefs used in this study (Maya's Reef, Mark's Reef and Malane Huva Reef) were separated by 1–2 km and located within 1 km of the western coast of Kimbe Bay.

Distribution, abundance and habitat selectivity

To examine the distribution patterns of different life stages with respect to depth and habitat availability, a series of visual censuses were conducted. The number of *C. rollandi* and the availability of different habitat types was censused along five haphazardly placed 20×2 m^2 visual belt

transects at three depths (5, 10 and 20 m), at two sites (~500 m apart) within each of three reefs. Each fish was categorised as recruit (8–12 mm standard length, SL), juvenile (13–19 mm SL), or adult (≥20 mm SL) life stage, and the habitat they were associated with was recorded. Preliminary collections indicated that 20 mm SL was the approximate size of sexual maturation. Differences in colouration and behaviour also assisted in the assignment of individuals to life stage categories (e.g. recruits have fluorescent blue head markings that juveniles do not). The substratum under each of 38 random points along the 20 m transects was recorded and placed into one of four categories: coral rubble, sand and rubble, dead coral and algae and live coral.

The selectivity by *C. rollandi* for specific benthic habitats at 5, 10 and 20 m was calculated for juveniles and adults using a resource selection ratio (‘‘ the forage ratio’’: Savage 1931 in Manly et al. 2002). The low numbers of recruits censused precluded analysis for this category. The forage ratio revealed the proportion of each habitat type used compared to the proportion of that habitat type available at each depth. To determine if selection was significant, Bonferroni-corrected 95% confidence limits around the selection ratio estimates were calculated using the following equation:

$$se(\hat{w}_i) = \sqrt{o_i(1-o_i)/(u_+\pi_i^2)},$$

where o_i is (the number of used resource units in category i)/(the total number of used resource units in the population); π_i is (the number of resource units in category i)/(the total number of resource units); and u_+ specifies the total number of used resource units in the population (Manly et al. 2002). When the benthic category was used in proportion to its availability the selection ratio ±95% confidence interval (CI) encompassed one; when used more than its availability the ratio ±95% CI was greater than one; and when the benthic category was avoided the ratio ±95% CI was less than one.

Site fidelity

To determine whether *C. rollandi* are site faithful and the extent to which they changed their depth distribution, 20 individuals were collected from the three depths (5, 10 and 20 m), at each of two sites (separated by ~500 m) on two reefs (total $n = 240$) using the fish anaesthetic clove oil and hand nets. Tagged fish were a random sample of fish present at each depth and spanned the size range from new recruits through to adults. This allowed us to determine whether site fidelity over an 18-day period differed with fish size. Fish were collected and placed into a small plastic click-seal bag, measured to the nearest 0.1 mm using callipers (SL), and tagged in situ with a unique fluorescent elastomer tattoo (Northwest Marine Technologies Inc., Shaw Island, WA, USA) using a 29-gauge hypodermic needle. This tagging method has been used extensively on small pomacentrids and a detailed aquaria study has shown that it has minimal or no effect on growth or survival (Hoey and McCormick 2006). After tagging, fish were allowed to recover from the anaesthetic in water filled plastic bags at the exact site of capture for ~10 min. The location where each fish was captured and released was individually marked with a numbered tag for subsequent reference. An area of ~5 m radius surrounding each marked location was searched every second day for 18 days and the position of tagged fish in relation to these reference points recorded.

Energy partitioning and life history traits

A minimum of 20 *C. rollandi* individuals were collected from each of the three depths (5, 10 and 20 m) at two sites (~500 m apart) within each of three reefs using clove oil and hand nets. Only adult and juvenile fish were targeted. In addition, at one site at two of the reefs, fish were also collected from a depth of 39 m (49 individuals) (total $n = 409$). Fish were euthanized by immersion in an ice water slurry, weighed to the nearest 0.1 mg (blotted wet weight) and standard length measured to the nearest 0.1 mm using callipers. The gonads and livers were removed and preserved in formaldehyde acetic-acid calcium-carbonate (Formaldehyde 37%, 10 ml; Glacial Acetic Acid, 5 ml; Calcium Chloride dihydrate, 1.3 g). The sagittal otoliths were removed, cleaned in ethanol and stored dry for later ageing.

Condition and reproductive investment

Overall condition and the partitioning of energy between reproduction and storage in the liver was compared among depths using five measures: (1) relative gonad weight or gonado-somatic index (GSI), (2) liver hepatocyte vacuolation, (3) liver cell density, (4) relative liver weight or hepato-somatic index (HSI, Nanton et al. 2001), and (5) Fulton’s condition index (K = [wet weight, kg]/[SL, m]^3). GSI provided an instantaneous measure of relative reproductive potential at the time of collection by providing an insight into the amount of investment into reproduction, while Fulton’s K is a morphometric index of fish ‘‘bulk’’. Gonads were weighed to the nearest 0.1 mg and sectioned to determine the sex of each individual. Each fish was classified as being female, male, or transitional (containing both female and male sex cells), allowing sex specific energy allocation to be examined.

The physiological condition of *C. rollandi* was quantified using liver cell density and hepatocyte vacuolation. Liver cells store glycogen and lipids within their cytoplasm and several studies have shown that their size and density responds rapidly to variations in energy demands and diet, such that lower liver cell density represents higher glycogen stores (e.g. Storch and Juario 1983; Ostaszewska et al. 2005). Excess lipids are stored in hepatocyte vacuoles, and Pratchett et al. (2004) showed that hepatocyte vacuolation was directly proportional to liver lipid content in a tropical butterflyfish. In the present study, livers were weighed to the nearest 0.1 mg, prepared for histology in accordance with Green and McCormick (1999), and serially sectioned. Densities of liver cells were counted within randomly placed 189 × 189 μm^2 quadrats at 400× magnification. The proportion of vacuoles in hepatic tissues was estimated using a Weibel eyepiece, recording the proportion of points (out of 42) that intersected vacuoles at 400× magnification. Three counts of liver cell density and hepatocyte vacuolation were made per section from three randomly chosen sections for each fish.

All reproductive and condition measures for female and male *C. rollandi* were analysed using a series of two-way fixed factor ANOVAs to determine if the measures differed among reefs, depths or the interaction factors. Type IV sums of squares were used to adjust for missing data at the 39 m depth at some sites. Assumptions of the ANOVA were examined by residual analysis. The GSI and hepatocyte vacuolation were Log_{10} transformed to satisfy the assumptions of normality and homoscedasticity.

Growth

The age of fish was determined by counting regular growth bands on transverse sections of the sagittal otoliths. These growth bands have been shown to be deposited annually for several tropical pomacentrids (e.g. Meekan et al. 1999) and are assumed to be deposited annually for *C. rollandi*. The preparation of otoliths followed Wilson and McCormick (1997). Two separate counts of the number of opaque bands were made for each individual. If the outermost band was approximately half the width of the previous band it was recorded as a half-yearly age. The Von Bertalanffy Growth Function (VBGF, Schnute 1981) provided the best fit for the size-at-age data from three of the four depths and was subsequently used for comparative purposes across all depths. This growth model may be represented by the equation:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}),$$

where L_t is the length at age t, L_∞ the mean asymptotic length, k the growth coefficient that describes the rate at which the asymptotic length (L_∞) is approached, and t_0 is the theoretical age when length is zero. The parameter t_0 was constrained to pass through zero for all depths. Ninety-five percent confidence ellipses were calculated around k and L_∞ (Kimura 1980; Meekan et al. 2001). As there was considerable overlap in the confidence ellipses of males and females for each depth, the size-at-age data was combined to increase power.

Summary of overall depth effects on life history traits

A canonical discriminant analysis (CDA) was performed to display how female *C. rollandi* differed among depths in their measures of energy allocation (GSI, HSI, Fulton's *K*, liver cell density, hepatocyte vacuolation and growth). Ninety-five percent confidence ellipses were plotted around the depth centroids (Seber 1984). The assumption of multivariate normality was examined prior to analysis.

Experimental isolation of depth effects

Any depth related trends in life history traits of adult fish could be the result of differential settlement or survival of fish with different life history characteristics, or differences in growth and resource allocation. A translocation experiment was used to assess the influence of depth on growth and body condition, whilst keeping history as similar as possible. Sixty *C. rollandi* juveniles were collected from 10 m at each of two reefs. These reefs were the same reefs used to determine the distribution patterns and differences in life history traits of *C. rollandi*. Fish were caught using clove oil and hand nets and placed into separate clipseal plastic bags. Fish were randomly assigned to a depth treatment (5, 10 or 20 m) and batch tagged with a fluorescent elastomer tattoo (Northwest Marine Technologies Inc.), using a different colour for each depth.

At each depth, 20 individuals were released from the plastic bags into a fine mesh cage (0.8 m^3, 3 mm mesh), which had been previously erected over a small patch of coral rubble at each depth with its skirt secured below the rubble. The cage was left over the fish for 24 h to allow acclimation to conditions at the translocated site and reduce predation during this period. Fish that died prior to removal of the cage were replaced with another tagged juvenile.

Twenty-four days after the start of the experiment two divers systematically searched an area of ~1,200 m^2 centred on the experimental coral rubble sites at each depth. Two searches of each site were made on consecutive days. All tagged fish were collected, euthanized, and their size and condition assessed as described above.

The condition and growth of translocated juveniles was compared among depths using three measures: hepatocyte vacuolation, liver cell density and relative growth rate. The

hepatocyte vacuolation and liver cell density were quantified following the methods described previously. Cross-sections of the sagittal otoliths were produced following the protocol of Wilson and McCormick (1997). The width of daily growth increments 11 days before translocation and 24-day post-translocation were measured along the succal groove axis of the sagittal otolith using the image analysis software ImageTool. The relative growth rate was calculated as the proportional change in the mean daily increment width from pre- to post-translocation. These condition and growth measures were analysed using one-way ANOVAs. Reefs were pooled as the number of recovered individuals was low.

Results

Distribution, abundance and habitat selectivity

The distribution patterns displayed by both adults and juveniles indicated a positive selection of coral rubble, and sand and rubble habitats at all depths (Fig. 1). Live coral, and dead coral with algae were avoided by adults and juveniles at most depths. The abundance of *C. rollandi* differed significantly among depths ($F_{2,87} = 4.06$, $P = 0.021$), with the highest abundance recorded at 10 m (0.794 ± 0.071 individual m^{-2}, mean ± SE). The 5 and 20 m depth habitats exhibited similar abundances of fish (0.596 ± 0.050 and 0.595 ± 0.048 individual m^{-2}, respectively). The abundances did not reflect the availability of their preferred habitat (i.e. coral rubble and sand and rubble), which was greatest at 5 m (43.8 ± 2.8%, mean ± SE) and decreased with depth (10 m, 33.2 ± 2.6% and 20 m, 23.8 ± 2.5%).

Site fidelity

Chrysiptera rollandi displayed a high degree of site fidelity, with 71% of all individuals remaining within 0.5 m of their initial capture site, and 82% remaining within a 1 m radius for the 18-day duration of the study. The maximum distance that a fish was found from the marked benthic site was 4 m. There was no significant correlation between the distance moved and fish length.

Energy partitioning and life history traits

Condition and reproductive investment

Female *C. rollandi* exhibited a significant interaction between reef and depth for all five measures examined: GSI ($F_{5,285} = 2.736$, $P = 0.020$), hepatocyte vacuolation ($F_{5,292} = 3.394$, $P = 0.005$), liver cell density ($F_{5,286} = 5.256$, $P < 0.001$), hepato-somatic index (HSI; $F_{5,295} = 3.683$, $P = 0.003$) and Fulton's K ($F_{5,297} = 3.436$, $P = 0.005$). In contrast, there were no significant differences among reefs or depths for male or transitional (i.e. changing from female to male) fish. Further details of the ANOVA results and Tukey's HSD groupings (for significant results) can be found in the electronic supplementary material accompanying this paper.

Generally, the GSI of female *C. rollandi* was lowest at 20 m and highest at 5 or 10 m, depending upon reef identity (Fig. 2a). GSI also showed a significant increase

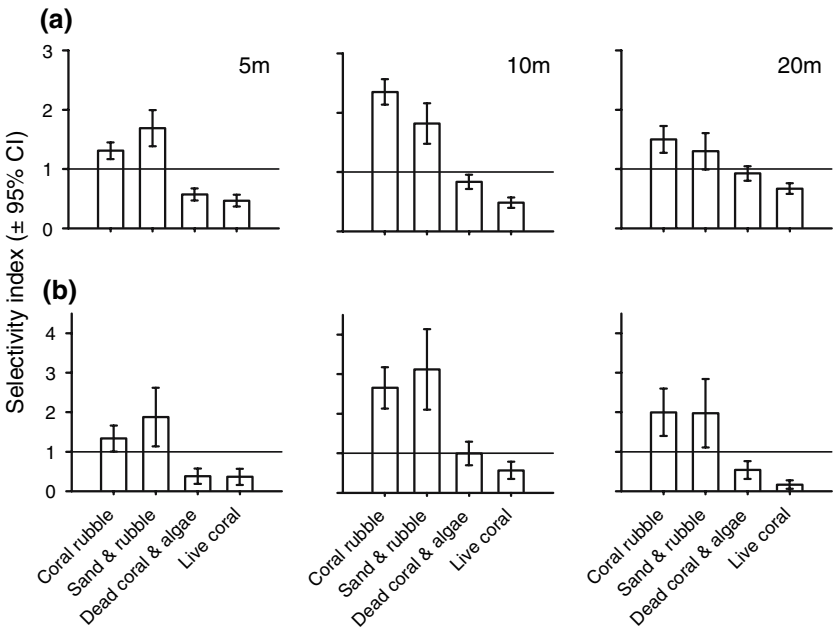

Fig. 1 The habitat selectivity of **a** adult, and **b** juvenile *Chyrsiptera rollandi* across three depths in Kimbe Bay, West New Britain, Papua New Guinea. A selection index of one indicates that the habitat was used in proportion to its availability. Values greater than one indicate positive selection and values less than one indicate negative selection, or avoidance

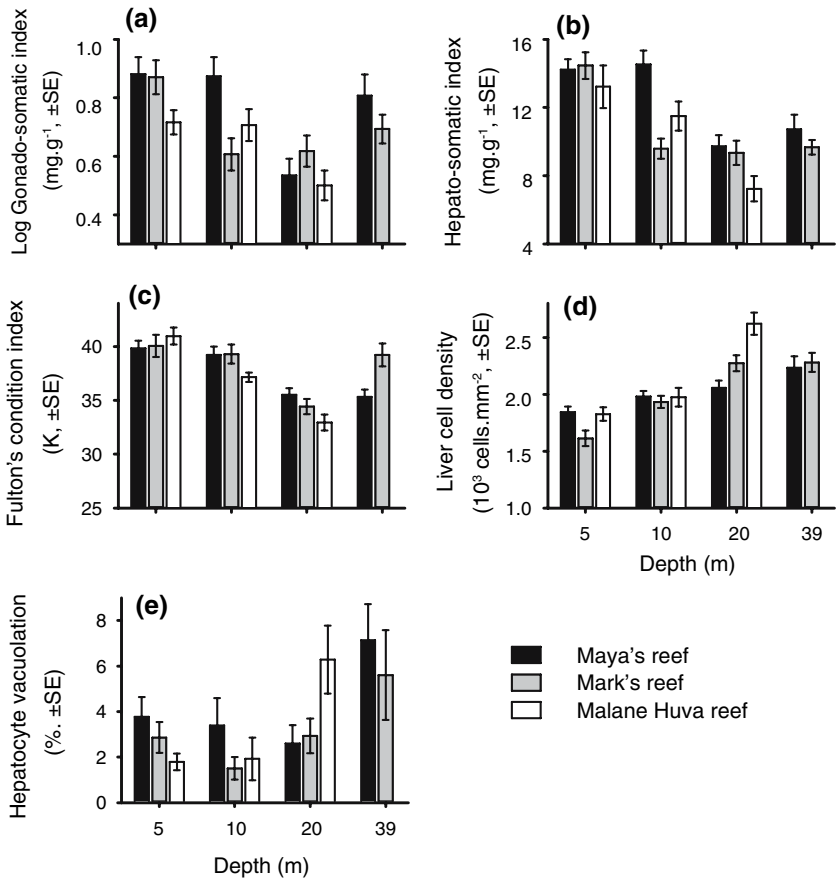

Fig. 2 Comparison of five measures of energy allocation and overall body condition and for female *Chrysiptera rollandi* across four depths and three reefs in Kimbe Bay, West New Britain, Papua New Guinea: **a** gonado-somatic index (*GSI*, mg g^{-1}); **b** hepato-somatic index (*HSI*, mg g^{-1}); **c** Fulton's condition index (*K*, kg m^{-3}); **d** liver cell density; **e** hepatocyte vacuole density

from 20 to 39 m at Maya's Reef. GSIs showed significant differences in magnitude among reefs at 10 m, giving rise to a significant Reef × Depth interaction. HSI of female *C. rollandi* exhibited a very similar pattern among depths and reefs to that for GSI, with the lowest means again being found at 20 m (Fig. 2b). HSI did not differ significantly between reefs at 5 and 39 m, but significant variation occurred at 10 and 20 m. Fulton's *K* also showed a similar pattern of decreasing values to 20 m, together with a marked increase in condition factor of females from Mark's Reef at 39 m (Fig. 2c). The low variance around means meant that there were significant differences among reefs at 10, 20 and 39 m (Fig. 2c).

In contrast, the liver cell density of female *C. rollandi* showed a pattern of increase with depth (i.e. glycogen stores decreased with increasing depth), with females from Mark's Reef and Malane Huva Reef at 20 m having significantly greater densities than those from 5 and 10 m (Fig. 2d), and both Maya's Reef and Mark's Reef at 39 m greater than 5 m. Hepatocyte vacuolation (Fig. 2e) was significantly higher at 39 m compared to 10 and 20 m for Maya's Reef, and compared to 10 m for Mark's Reef, whilst there were no differences between the 5, 10 and 20 m depths at either site. At Malane Huva, vacuolation was significantly higher at 20 m compared to 5 and 10 m.

Growth

Chrysiptera rollandi exhibited rapid growth in their first year, attaining two-thirds of their maximum asymptotic length, and a maximum longevity of 4 years across all depths (Fig. 3a). The fitted Von Bertalanffy Growth Functions suggest that fish from 5 m exhibited faster initial growth and may reach a smaller asymptotic length than fish from 39 m, with fish from 10 to 20 m displaying intermediate growth. This is supported by the 95% confidence ellipses around the growth parameters that indicate that fish from 39 m have a significantly lower growth coefficient (*k*, i.e. rate at which individuals reach maximum length) than fish from 5 m (Fig. 3b).

Summary of overall depth effects on life history traits

The CDA summarizes how energy partitioning was influenced by depth in female *C. rollandi* (Fig. 4). The first two canonical variates explained 83.1 and 14.1% of the total variation, respectively. There was a clear separation of females from deeper (20 and 39 m) and shallower (5 and 10 m) depths along the first canonical variate. This pattern was driven by deep residing females having higher liver cell densities (i.e. lower glycogen stores) and higher

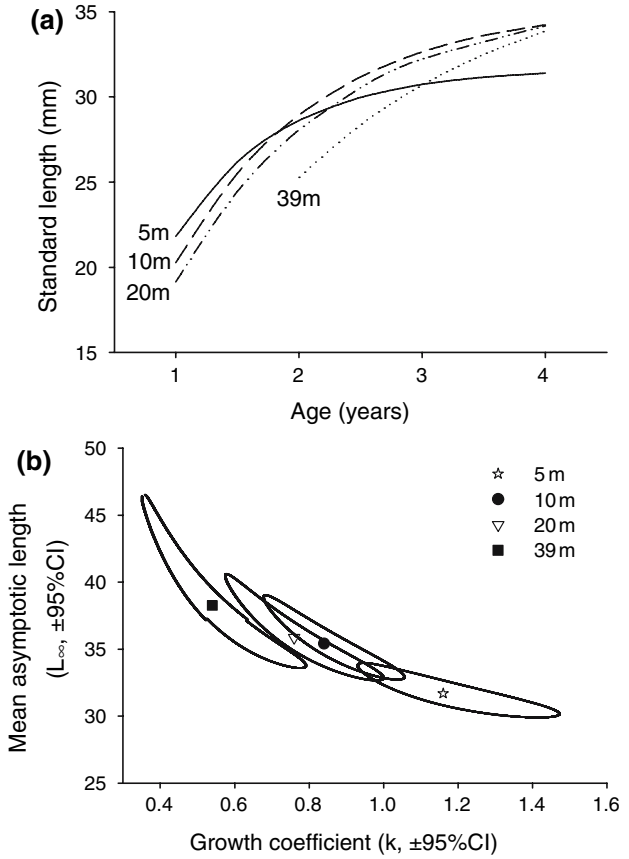

Fig. 3 Comparison of growth and longevity of *Chrysiptera rollandi* collected from four depths in Kimbe Bay, West New Britain, Papua New Guinea: **a** von Bertalanffy growth functions fitted to size-at-age data; **b** Ninety-five percent confidence ellipses generated for estimates of the growth coefficient (k) and the mean asymptotic length (L_∞) from the von Bertalanffy growth functions

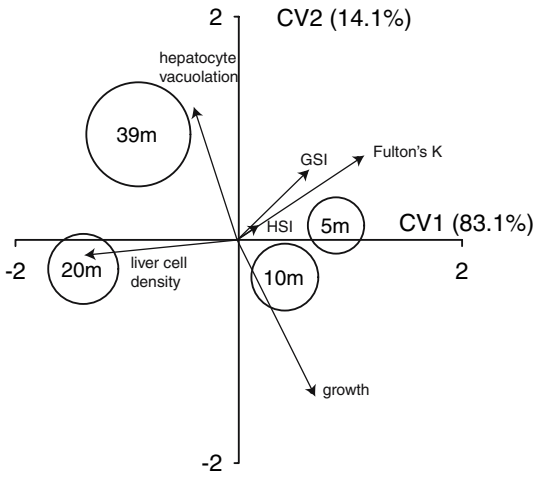

Fig. 4 A canonical discriminant analysis showing a comparison of energy allocation metrics associated with female *Chrysiptera rollandi* from four depths in Kimbe Bay, West New Britain, Papua New Guinea. The ellipses represent 95% confidence intervals

hepatocyte vacuolation, but lower Fulton's K, growth and GSI than their shallow water counterparts. The two deep sites were separated along the second canonical variate, with females from 39 m having higher hepatocyte vacuolation and Fulton's K and lower growth than females at 20 m.

Experimental isolation of depth effects

Of the 120 fish tagged and translocated only 44 were located and retrieved after 24 days. Retrieval at each depth varied, with 12 individuals retrieved from 5 m, 28 from 10 m and 4 individuals from 20 m. Despite the low sample sizes recovered from all but the 10 m depth, liver cell density varied significantly among depths ($F_{2,\ 41} = 6.270$, $P = 0.004$). Further details of the Tukey's HSD groupings can be found in the electronic supplementary material. Fish translocated to 5 m had significantly lower liver cell densities, hence higher glycogen stores, than the control fish (10 m) or those translocated to 20 m (Fig. 5). Hepatocyte vacuolation and growth rate did not significantly differ among depths over the 24-day period.

Discussion

Previous studies have highlighted strong depth-related trends in the spatial distribution of fish (Gosline 1965; Hyndes et al. 1999; Spina 2000), however few have examined how depth influences energy allocation. The present study demonstrates that depth can have a marked influence on fitness characteristics such as growth, energy storage and reproductive potential of fish. It also shows that, whilst there are some general patterns in condition-related measures with depth, there is considerable

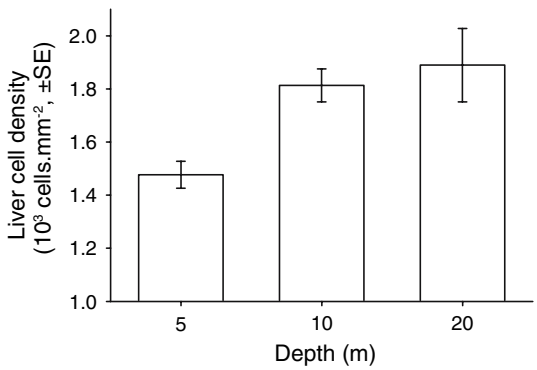

Fig. 5 Comparison among depths of liver cell density for juvenile *Chrysiptera rollandi* that were translocated from ten metres for 24 days

variability amongst reefs within a geographic locality. Such patterns need to be accounted for if realistic estimates of population reproductive output are to be obtained for species that have wide depth distributions.

Chrysiptera rollandi was an ideal species with which to study the influence of depth on energy allocation since it actively selected coral rubble and sand and rubble habitats, which were common down a broad depth gradient. Abundances of *C. rollandi* at each depth did not reflect the availability of the preferred habitat suggesting a preference for depth as well as habitat. The consistent use of the same microhabitat type across depths and life-stages meant that depth effects could be effectively divorced from many of the habitat-related characteristics that are known to influence energy storage and growth (e.g. topography, microhabitat composition; Clarke 1992; Van Rooij et al. 1995).

In the present study, depth was found to affect the growth dynamics of *C. rollandi* with faster initial growth rates and smaller mean asymptotic lengths with decreasing depth. A similar reduction in growth rate with depth was observed in one of two species of damselfish experimentally manipulated by Srinivasan (2003), with the second species showing no significant trend in growth rate over the naturally occurring depth range. Growth represents the end product of many lower-level physiological processes, some of which are quantified by the morphological and histological indices used in the present study. Since growth has been shown to be linked to the timing of many life-history processes (e.g. maturation, sex-change; Roff 1984; Stearns 1992) and mortality schedules (Stearns 1992; Gust et al. 2002), the findings of the present study suggest that depth may have a major, though presently unmeasured, influence on local population dynamics of *C. rollandi* through its influence on growth.

The present study found that the short-term reproductive potential, as measured by the GSI, of *C. rollandi* differed with depth. Since the spawning periodicity of the species is unknown, it is unclear whether the instantaneous view of reproductive potential obtained in this study represents a temporal difference in the spawning cycle among depths, or a real difference in the reproductive output with depth. However, ripe females and males were found at all depths indicating active spawning potential across the depth range at the time of sampling. Differences in reproductive potential amongst habitats have been linked to variations in food availability (Ruttenberg et. al. 2005), predation (Ghalambor et. al. 2004) and competition (Thresher 1983). In *C. rollandi*, given that there was almost twice the amount of preferred habitat at 5 m than at 20 m, lower levels of GSI at 20 m may be reflective of higher competition and lower food availability in this deeper habitat.

The liver is one of the primary sites of lipid storage in fishes, where lipids are stored mainly in vacuoles (Mommsen 1998). The hepatocyte vacuolation of female *C. rollandi* was highly variable amongst reefs and depths. At each of the three reefs sampled females from the deepest sites sampled had the highest mean levels of vacuolation, however there were high levels of variability amongst individuals. In contrast, males showed no depth variation. Little is known of what influences vacuolation in tropical fishes, although in salmonids the amount of lipid within the liver has been found to be dependent upon the gender, feeding regime of the fish and reproductive state (Mommsen 1998). During the peak feeding periods lipids are moved preferentially from the liver to adipose tissue, while during the later stages of vitellogenesis lipids are shunted from the liver to the ovary, with adipose tissue serving as the source of lipoproteins (Mommsen and Walsh 1988). Medford and Mackay (1978) found that the amount of lipid in the liver of the pike (*Esox lucius*) was more influenced by gender and recrudescence of the gonad than by feeding levels. In the present study, levels of lipids (i.e. vacuolation) in the liver may be linked to differences in the breeding cycles among depths, feeding environment or both. Certainly, the differences in the GSI with depth suggest differential allocation to ovaries with depth. Unfortunately information is not available on the maturation state of these ovaries that would allow the link between liver condition (expressed as either vacuolation or cell density) and gametogenesis to be explored.

Interestingly, liver cell densities of female *C. rollandi* showed a general increase with depth, indicating that glycogen storage was greatest at the shallower depths. A fish with high liver cell density has lower glycogen storage, as some depletion or shrinkage of nuclear material has taken place, resulting in cells being packed closer together (Strussman and Takishima 1990). Juvenile *C. rollandi* translocated from 10 m also expressed significantly lower liver cell densities at 5 m than those at 10 and 20 m after 24 days, suggesting that depth may have had a direct influence on glycogen storage within the liver. Glycogen stored in the liver is indicative of excess glucose in the diet (Cowley and Sargent 1979), and it is believed that glycogen in the liver is the most liable deposit in the body (the muscles and brain being the main sites of other deposits; Shul'man 1974). Glycogen is primarily used when there is a need for rapid mobilization associated with bursting movements (prey pursuit or predator evasion) and glycogen reserves in the muscles are continuously replenished from stores in the liver (Shul'man 1974). Differences in glycogen stores with depth may represent depth-related differences in the amount or quality of food ingested or fish activity levels. Indeed the potentially higher levels of predation at depth, indicated by the high loss of translocated fish at 20 m, may lead to higher activity by *C. rollandi* associated with

predator vigilance and avoidance. While the role of glycogen in the metabolism of *C. rollandi* is uncertain it appears to respond relatively quickly (within 24 days) to changes in an individual's depth regime.

While there were some general patterns with depth, there were marked differences in the magnitude of the different indices of condition among the three reefs within a single geographic locality and high levels of individual variability. This is due to the inter-relationships between indices and the complex determinants of lipid and carbohydrate metabolism and storage. Measures of condition that represent overall ''well-being'' (e.g. Fulton's *K*) are more buffered from subtle changes in environmental conditions than measures that reflect cellular level processes (e.g. hepatocyte cell density) (Suthers 1998). In the pike-perch, *Sander lucioperca*, glucose metabolism is first to be affected by feeding followed secondarily by fat deposition (Ostaszewska et al. 2005), suggesting that glycogen present in the cytoplasm of the liver is utilised prior to lipid stores. Glycogen is used for the ''instantaneous switching-on of the motor reaction'' while lipids are the main source of energy for prolonged muscular effort (Shul'man 1974). The relative use of lipid versus glycogen depends upon general activity levels, the amount of red muscle and the level of acclimation to recent activity levels (Storey 2004). Thus, depending upon the activity levels of the fish, liver lipid and carbohydrate levels can be expected to display different trends among individuals or through time.

Chrysiptera rollandi conforms to the generally found trend of larger individuals occurring in deeper water compared to smaller conspecifics (Sale 1969; McCormick 1989a; Gillanders 1995). However, most species that conform to this general trend are large, mobile fish species with large home ranges and who undergo an ontogenetic migration to deeper water; not small sedentary species such as *C. rollandi*. Evidence suggests that the trend for larger size with depth in *C. rollandi* is, at least in part, the product of growth dynamics changing with depth. These findings contrast with those for the small-headed clingfish (*Apletodon dentatus*, maximum size of 4 cm), whose size frequency changes with depth due to an ontogenetic shift in preference for microhabitat that are depth specific (Gonçalves et al. 2002).

Changes in condition indices with depth may be the results of mortality selective for various components of body condition. The high site fidelity of *C. rollandi* and the low number of translocated juveniles recovered from the 20 m depth suggests that mortality rates may change with depth. Hoey and McCormick (2004) found that juveniles of another rubble-dwelling tropical damselfish, *Pomacentrus amboinensis*, which had low levels of total lipids and low growth in their late larval phase had low survival. Moreover, depth was found to influence mortality of juveniles of this species, with higher mortality in shallow rubble areas (McCormick and Hoey 2004). Although liver cell density of translocated fish responded to depth with a pattern that matched depth stratified collections, the change in mortality rates of translocated fish with depth means that the role of selective mortality in influencing these patterns cannot be discounted.

The distribution ranges of all marine species span environmental gradients and these will influence life processes as the organism's physiology interacts with prevailing environmental conditions. Organisms that inhabit areas under sub-optimal conditions may grow more slowly, reproduce less, or sustain higher mortality than those living in more suitable conditions. The present study has identified sex-specific differences in energy allocation along a broad depth cline in a tropical reef fish, indicating that the selection of a particular depth at settlement has important ramifications for subsequent growth, reproductive investment and energy storage in female *C. rollandi*, though has little effect on energy allocation in conspecific males. The results suggest that selection of a depth zone may not only be important in energy allocation dynamics but also have ramifications for the timing of key life history events in *C. rollandi* (e.g. maturation or sex change) and the reproductive output of local populations. This study highlights the importance of incorporating depth as a factor when studying species with broad depth distributions if realistic descriptions of population dynamics are to be ascertained.

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