

A deep nursery for juveniles of the zebra angelfish *Genicanthus caudovittatus*

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Abstract Juveniles of many coral reef fish species are thought to either follow the same bathymetric distribution patterns as the adults, or to occupy shallower waters. However, our knowledge base suffers a dearth of data from the deep reefs (>40 m). In a recent survey of the deep reefs of the northern Gulf of Aqaba (<65 m), we examined the bathymetric distribution of 26 diurnal zooplanktivorous species. In sharp contrast to the general trend known from the

literature and from this research, the abundance of juvenile zebra angelfish, *Genicanthus caudovittatus*, peaked at deeper waters (60–65 m) compared with the adults (30 m). This suggests that the deeper reefs may serve as nursery grounds for the zebra angelfish. Peak juvenile abundance coincided with relatively low predator abundances. This raises the question, which factors constrain the bathymetric distribution of the remaining species. Our findings stress the potential importance of deep coral reef research for understanding the ecological patterns and processes that govern reef community structure.

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Introduction

Zooplanktivorous fish play a major role in the ecology of the reef and are the most abundant functional group in many coral reefs (Williams and Hatcher 1983; Rilov and Benayahu 1998; Rossier and Kulbicki 2000). Yet, data regarding their bathymetric distribution patterns (as well as of other taxa) is lacking beyond 30 m (Lesser 2004).

Analyses of spatial distributions and population dynamics of members of ecological guilds that rely solely on total abundance, as oppose to

size structure, may well fail to detect major interspecific interactions (Robertson 1998). Studies of the bathymetric range of adult, juveniles and new recruits of coral reef fish species generally show that the young inhabit either shallower depths than the adults (Rosland and Giske 1994; Zeller and Pauly 2001; Letourneur et al. 2003; Methven et al. 2003; Sassa et al. 2004; Koczaja et al. 2005) or share the same depths (Bean et al. 2002).

The 10 species of Angelfish of the genus *Genicanthus* (Swainson 1839) are often seen in deep reefs and although they are not common above 20 m (Randall 1975), *G. caudovittatus*, *G. lamarck* and *G. semicinctus* occasionally occur at 10 m depth. The zooplanktivorous *G. caudovittatus* is reported to reach depths of 60–70 m (Khalaf and Disi 1997; Allen et al. 1998; Froese and Pauly 2006), yet different studies reported a variety of shallow depth preferences, potentially biased by incomplete sampling of the deeper reefs. For example, in Eilat (northern Gulf of Aqaba; Red Sea), Rilov and Benayahu (2000) found that *G. caudovittatus* (Günther, 1860) are abundant at depths of ca. 20 m (their deepest transects), while Brokovich (2001) found that they are rare in shallow reefs (depths of up to 15 m). This same species was reported in Aqaba (10 km east of Eilat) as abundant at 12 m and rare at 6 m (Khalaf and Kochzius 2002) (their deepest studied depth was 12 m). Unfortunately, in all of the above studies, quantitative data of deep populations (>30 m) was not available, nor was data regarding bathymetrical distribution of the juveniles. The goal of this study was to describe the depth distribution of different size classes of *G. caudovittatus* and to examine whether depth partitioning trends in this species coincide with other, deep and shallow, diurnal zooplankters. We also examined possible interspecific interactions with other functional groups.

Methods

We used advanced technical diving techniques (TRIMIX SCUBA diving, by EB and SE) to quantitatively examine the fish community in the

Red Sea near Eilat between 5 and 65 m. At each of 3 sites, where possible, (Dekel beach, Japanese Gardens and the Interuniversity Institute) we completed a visual census of fishes in 3–6 replicates of 50 m² (25 × 2 m) at each of 5 different depths (total number of transects in parentheses): 5 m (7 transects), 10 m (6 transects), 30 m (10 transects), 45–50 m (12 transects) and 60–65 m (7 transects). Sample sizes deferred due to the absent of a reef at some locations and depths and also due to technical difficulties in reaching some sites as oppose to others. We recorded fish abundance underwater on a plastic slate. We only recorded fish that passed in front of the diver but a whole school was counted if one of its fish crossed the transect (Bortone et al. 1986). We estimated the total lengths (TL) of all fishes in the transect to the nearest centimeter (Bell et al. 1985; Rossier and Kulbicki 2000). We assigned species to functional groups according to their diet using data from the primary literature (Randall 1983; Debelius 1993, 1998; Randall 1995; Khalaf and Disi 1997) and Fishbase (Froese and Pauly 2006). For *G. caudovittatus* we defined juveniles as ≤60 mm TL, adults as larger than 60 mm TL. Juvenile size was defined following Randall's (1975) publication of a photo of a juvenile of ca. 55 mm TL. In addition to *G. caudovittatus*, we surveyed 25 other diurnal zooplanktivore species. Thirteen species (incl. *G. caudovittatus*) had sufficient data for meaningful analyses of the depth partitioning between different size classes. These were: a – *Amblyglyphidodon flavilatus*; b – *Chromis dimidiata*; c – *C. pembae*; d – *C. viridis*; e – *Cirrhilabrus blatteus*; f – *C. rubriventralis*; g – *Dascyllus aruanus*; h – *D. marginatus*; i – *D. trimaculatus*; j – *Genicanthus caudovittatus*; k – *Paracheilinus octotaenia*; l – *Pomacentrus trichourus*; m – *Pseudanthias squamipinnis*. As a possible factor in determining zooplanktivores distribution, we also analyzed piscivores abundance and compared with the above species. One diver (EB) recorded all fish data. Adult and juveniles depth preferences were decided according to the maximal abundance for the species. In cases where there was no clear peak, we averaged the depth range of the species.

Results

Twelve species out of the 13 studied conform to the known trend of juveniles occupying the same or shallower depth as the adults. In contrast, *G. caudovittatus* demonstrate an opposite trend (Fig. 1). We find the highest densities of adults around 30 m, (mean TL of all *G. caudovittatus* at this depth \pm SD: 138 ± 42 , $N = 55$) while juveniles predominate deeper reefs: we find more than 80% of the small juveniles between 60–65 m (mean TL of all fish at this depth \pm SD: 40 ± 3 mm, $N = 63$); we find mid-size fish between 45–50 m (mean TL of all fish at this depth \pm SD: 56 ± 26 mm, $N = 24$) (Fig. 2). These differences in average *G. caudovittatus* size per depth are statistically significant (one way ANOVA, $P < 0.001$). Examining the other 12 species recorded, we find large variances in abundance caused by the tendency of some species to school. Zooplanktivorous fishes, in general, appear to peak (though not significantly) at the same depth of the peak in the abundance of juveniles *G. caudovittatus* (65 m differ from 30 m in *G. caudovittatus*, post hoc tests to one way

ANOVA, $P < 0.05$; Fig. 3). However, piscivorous fishes were significantly less abundant in the deeper habitats (post hoc to one way ANOVA, $P < 0.05$; Fig. 3).

Discussion

Population size structure has received little attention in studies of mechanisms that structure reef fish assemblages (Robertson 1998). Here we examine the size distribution of *G. caudovittatus* along the depth gradient with relation to other zooplanktivore species and possible predators. Several studies have suggested that young fish inhabit the same or shallower depths as adults [see Introduction and also Green (1996) and a review by Jones (1988)]. In this study we show an opposite trend for one species, *G. caudovittatus*, in which juveniles occupied deeper waters than the adults. This oddity raises interesting questions regarding juvenile–adult depth partitioning in zooplanktivorous fish. Size-dependent differences in bathymetric distribution can be influenced by different habitat needs, intra-specific competition

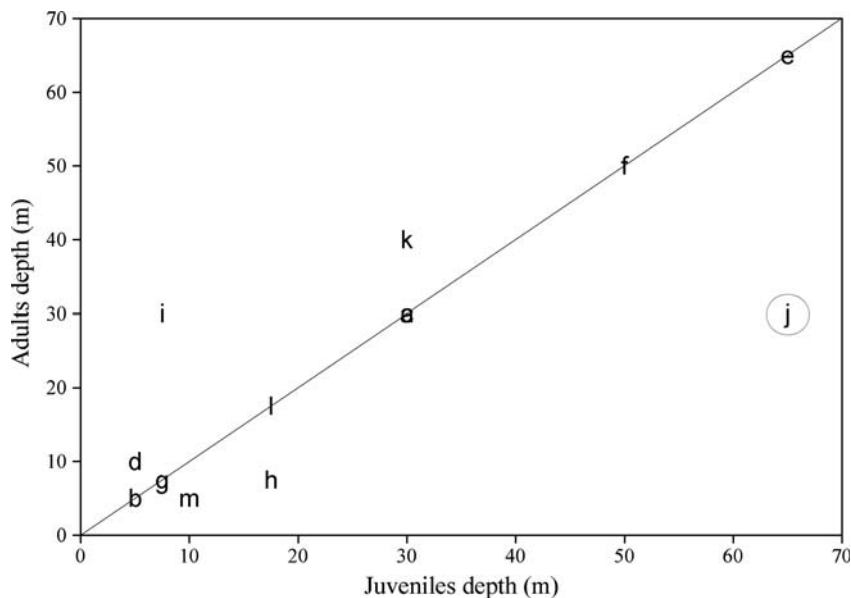


Fig. 1 The maximum depth of occurrence for the adults and juveniles of 13 species of diurnal zooplanktivores. The diagonal is the line of equality. Letters represent the different species: a – *Amblyglyphidodon flavilatus*; b – *Chromis dimidiata*; c – *C. pembrae*; d – *C. viridis*; e –

Cirrhilabrus blatteus; f – *C. rubriventralis*; g – *Dascyllus aruanus*; h – *D. marginatus*; i – *D. trimaculatus*; j – *Genicanthus caudovittatus*; k – *Paracheilinus octotaenia*; l – *Pomacentrus trichourus*; m – *Pseudanthias squamipinnis*

Fig. 2 Size class distribution of *G. caudovittatus*. Error bars not included, see text for details

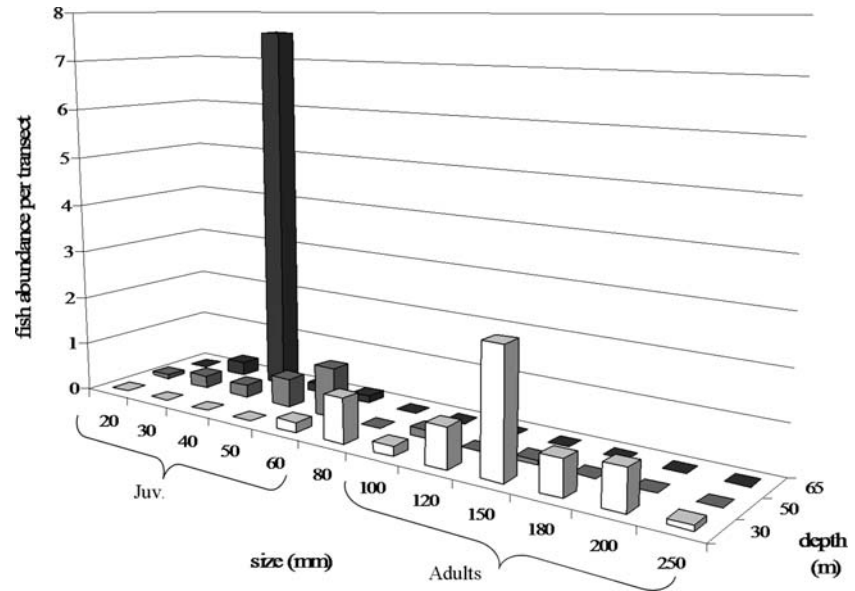
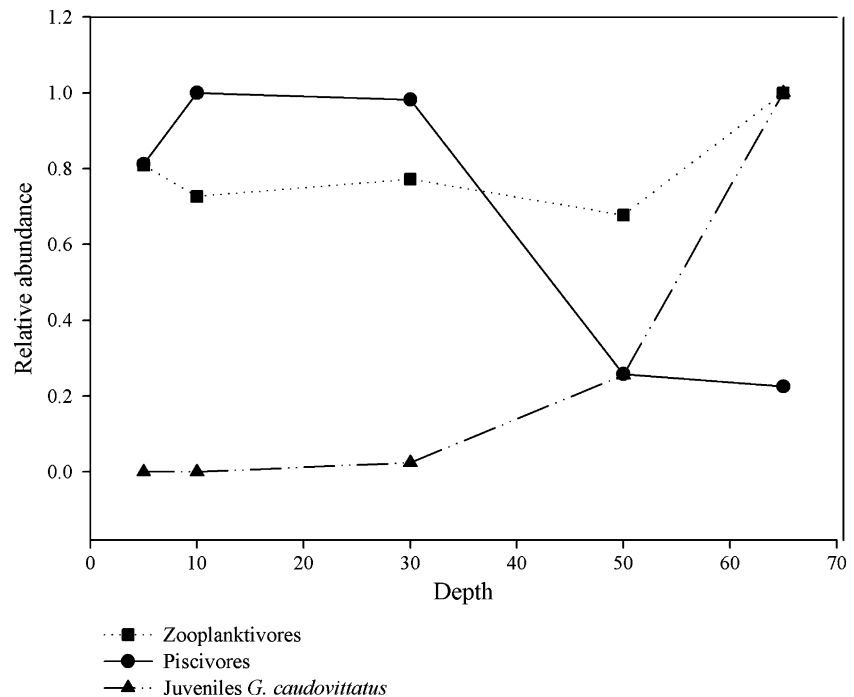


Fig. 3 Relative average abundance (relative to maximum abundance in each group) of juveniles *G. caudovittatus*, and other diurnal zooplanktivores and piscivores (of all sizes)



(including territoriality by the adults), interspecific competition with other zooplanktivores, predation and/or hydrodynamic processes which determine larval bathymetric distribution. Although this study did not directly test any of these possibilities, we speculate as to the cause of the observed size variation with depth. We here

raise several hypotheses as to why the young individuals of the zebra angelfish appear in deeper waters than adults, which should be further examined.

Because adults and young *G. caudovittatus* differ greatly in size, it is very likely that they have different diets and shelter needs which

reduce intra-specific competition (Jones 1988; Fishelson and Sharon 1997; McCormick 1998; Robertson 1998). Furthermore, if juveniles of this species do not compete with the adults over territory or mates, which is likely, habitat segregation by sexual maturity may not seem a necessity. The abundance of zooplanktivorous fishes, seems to peak at the same depth of juveniles *G. caudovittatus*, or at least does not change with depth. As a consequence inter-specific competition would probably not lead the juveniles to go deeper. Piscivorous fishes, on the other hand, were found to be significantly less abundant in the deeper habitats suggesting that deep reefs may be offering juvenile *G. caudovittatus* a refuge from predation. Whether predation indeed drives *G. caudovittatus* juveniles deeper, and the reasons why juveniles of this species, as oppose to all others, are able to use the deep reef should be further studied.

This study demonstrates that the deep reefs may serve as nursery grounds for *G. caudovittatus*. So far nursery grounds were mainly reported in areas distant from the reef such as shallow waters, gravel regions and sea-grass (Beck et al. 2001; Gullstrom et al. 2002; Dorenbosch et al. 2004; Mumby et al. 2004). The finding of a deep nursery ground further stress the importance of deep coral reef research for understanding the ecological patterns and processes defining the reef community structure. These findings also suggest that when conservation decisions and plans are made, the deep reef should be included for enabling sustainable persistence of some reef fishes.

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References

- Allen GR, Steene RC, Allen M (1998) A guide to Angel fishes and Butterfly fishes. Odyssey Publishing, Perth, WA
- Bean K, Jones GP, Caley MJ (2002) Relationships among distribution, abundance and microhabitat specialisation in a guild of coral reef triggerfish (family Balistidae). *Mar Ecol Prog Ser* 233:263–272
- Beck MW, Heck KLJ, Able KW et al (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51:633–641
- Bell JD, Craik GJS, Pollard DA et al (1985) Estimating length frequency distributions of large reef fish underwater. *Coral Reefs* 4:41–44
- Bortone SA, Hastings RW, Oglesby JL (1986) Quantification of reef fish assemblages: A comparison of several in situ methods. *Northeast Gulf Sci* 8:1–22
- Brokovich E (2001) The community structure and biodiversity of reef fishes at the northern Gulf of Aqaba (Red Sea) with relation to their habitat. M.Sc. Thesis (in Hebrew, with English abstract), Tel Aviv University, Tel-Aviv
- Debelius H (1993) Indian Ocean tropical fish guide. Aquaprint Verlags GmbH, Frankfurt
- Debelius H (1998) Red Sea reef guide. IKAN, Frankfurt
- Dorenbosch M, van Riel MC, Nagelkerken I et al (2004) The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. *Estuar Coastal Shelf Sci* 60:37–48
- Fishelson L, Sharon O (1997) Spatial and foraging behaviour, diet and morphogenesis of post-larvae and juveniles of *Pempheris vanicolensis* in the Gulf of Aqaba, Red Sea. *J Fish Biol* 51:251–265
- Froese R, Pauly D (eds) (2006). Fishbase. World Wide Web electronic publication. www.fishbase.org
- Green AL (1996) Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (Family Labridae). *Mar Ecol Prog Ser* 133:1–11
- Gullstrom M, de la Torre Castro M, Bandeira SO et al (2002) Seagrass ecosystems in the western Indian ocean. *AMBIO* 31:588–596
- Jones GP (1988) Ecology of rocky reef fish of north-eastern New Zealand: a review. *NZ J Mar Freshwat Res* 22:445–462
- Khalaf MA, Disi AM (1997) Fishes of the Gulf of Aqaba. The Marine Science Station, Aqaba
- Khalaf MA, Kochzius M (2002) Community structure and biogeography of shore fishes in the Gulf of Aqaba, Red Sea. *Helgol Mar Res* 55:252–284
- Koczaja C, McCall L, Fitch E et al (2005) Size-specific habitat segregation and intraspecific interactions in banded sculpin (*Cottus caroliniae*). *Southeastern Nat* 4:207–218
- Lesser MP (2004) Experimental biology of coral reef ecosystems. *J Exp Mar Biol Ecol* 300:217
- Letourneur Y, Ruitton S, Sartoretto S (2003) Environmental and benthic habitat factors structuring the spatial distribution of a summer infralittoral fish assemblage in the north-western Mediterranean Sea. *J Mar Biol Assoc UK* 83:193–204
- McCormick MI (1998) Ontogeny of diet shifts by a microcarnivorous fish, *Cheilodactylus spectabilis*: relationship between feeding mechanics, microhabitat selection and growth. *Mar Biol* 132:9

- Methven DA, Schneider DC, Rose GA (2003) Spatial pattern and patchiness during ontogeny: post-settled *Gadus morhua* from coastal Newfoundland. *ICES J Mar Sci* 60:38–51
- Mumby PJ, Edwards AJ, Ernesto Arias-Gonzalez J et al (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427:533
- Randall JE (1975) A revision of the Indo-Pacific Angelfish genus *Genicanthus*, with description of three new species. *Bull Mar Sci* 25:393–421
- Randall JE (1983) Red Sea reef fishes. IMMEL, London
- Randall JE (1995) Coastal fishes of Oman. Crawford House, Bathurst
- Rilov G, Benayahu Y (1998) Vertical artificial structures as an alternative habitat for coral reef fishes in disturbed environments. *Mar Environ Res* 45:431–451
- Rilov G, Benayahu Y (2000) Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. *Mar Biol* 136:931–942
- Robertson DR (1998) Implications of body size for interspecific interactions and assemblage organization among coral-reef fishes. *Austral Ecol* 23:252–257
- Rosland R, Giske J (1994) A dynamic optimization model of the diel vertical-distribution of a pelagic planktivorous fish. *Prog Oceanogr* 34:1–43
- Rossier O, Kulbicki M (2000) A comparison of fish assemblages from two types of algal beds and coral reefs in the south-west lagoon of New Caledonia. *Cybium* 24:3–26
- Sassa C, Kawaguchi K, Hirota Y et al (2004) Distribution patterns of larval myctophid fish assemblages in the subtropical–tropical waters of the western North Pacific. *Fish Oceanogr* 13:267–282
- Williams DM, Hatcher AI (1983) Structure of fish communities on outer slopes of inshore, mid-shelf and outer-shelf of the Great Barrier Reef. *Mar Ecol Prog Ser* 10:239–250
- Zeller D, Pauly D (2001) Visualisation of standardized life-history patterns. *Fish Fisheries* 2:344–355