

Short lifespan and high mortality in the western Pacific coral reef goby *Trimma nasa*

Richard Winterbottom*, Laura Southcott

Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada
Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada

ABSTRACT: An age-at-length relationship was generated for the tiny Indo-Pacific coral reef goby *Trimma nasa* using presumed daily increment counts of sagittal otoliths from 110 specimens captured in Palau in May 2007. From these data, the estimated maximum age was approximately 87 d, and the average length of the pelagic larval duration was 33.9 ± 3.7 d (SD), nearly 39% of the maximum lifespan. Linear and power regression lines fit the data equally well ($r^2 = 0.8458$ and 0.8464 , respectively). Mixed model analysis of age, length and sex data produced a better fit, with significant effects of age ($p < 0.0001$), sex ($p = 0.0134$) and age \times sex interaction ($p = 0.0059$) on standard length. Males were significantly smaller than females and juveniles when corrected for age ($p < 0.05$). The male age-at-length relationship was also significantly different from those of females ($p = 0.0218$) and juveniles ($p = 0.0066$). Daily mortality rate as calculated by Hoenig's equation was 4.7%. These findings are in keeping with an increasing body of data demonstrating that small reef fish lead short lives with linear growth and high mortality, with important consequences for their contribution to the biomass and, hence, energy production of coral reefs.

KEY WORDS: Life history · Gobiidae · *Trimma nasa* · Otoliths · Pelagic larval duration · Cryptobenthic fishes

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Studies of coral reef fish assemblages have often missed or ignored many of the small and/or cryptic species that numerically dominate this habitat (Ackerman & Bellwood 2000). Until recently, this has resulted in their virtual exclusion from investigations of reef ecology. Newly developed evidence, however, suggests that their contribution to reef trophodynamics is far from negligible. Although the so-called cryptobenthic fishes make up the majority of reef fishes, their small size means that they have very low standing biomass (Ackerman & Bellwood 2000, Depczynski et al. 2007). Despite this, they account for a large portion of overall biomass production and overwhelmingly dominate the length production of reef fishes, i.e. the 'overall' growth in body length of all fish (as determined in cm m^{-2}) per unit time (Depczynski et al. 2007).

Several features of the life history of these small fishes are responsible for this significant contribution to overall productivity. Body size is negatively correlated with several life history features, including mortality, and positively correlated with such traits as lifespan and time of maturation (Blueweiss et al. 1978, Calder 1984, Roff 1992). Recently, Depczynski & Bellwood (2006) characterized the entire life cycle of 3 members of the cryptobenthic fish fauna of the Great Barrier Reef: the pygmy gobies *Eviota sigillata*, *E. melasma* and *E. queenslandica*. These incredibly short-lived fish (*E. sigillata* is the shortest-living vertebrate known, with a maximum recorded age of 59 d) exhibited rapid, linear growth, produced several generations over their exceedingly brief lifespans, and experienced high daily mortality (Depczynski & Bellwood 2006). Species of the Gobiidae make up a large portion of the cryptobenthic community (Depczynski & Bellwood 2003, Depczynski et al. 2007),

*Email: rickw@rom.on.ca

and several other species in this family have short lifespans and similarly high mortalities (e.g. *Istigobius decoratus*, Kritzer 2002; *Valenciennea strigata*, Reavis 1997). These factors combine to produce a rapid turnover of the cryptobenthic community, resulting in its disproportionately large contribution to overall production.

The genus *Trimma* is a speciose group of small (mostly <30 mm standard length), colourful, Indo-Pacific coral reef gobies. Some 58 valid species have been described to date, with a further 30 to 40 remaining undescribed. In Palau, the nasal pygmygoby *Trimma nasa* is similar in size to *Eviota sigillata*, and is one of several western Pacific species in the genus that hover in large, loose schools adjacent to the steep or vertical walls of the outer reef. Members of these schools usually adopt a 'head-up' posture and probably pick zooplankton in the water column (Saeki et al. 2005, Winterbottom 2005). As such they are best described as epibenthic, though epi- and cryptobenthic are part of a continuum of reef fish behaviour (Miller 1979). These tiny fish are good candidates for life history analysis because if they show the rapid growth and turnover of other small gobies, their consumption of (probably allochthonous) plankton and presumable role as a food source for larger reef fishes may put them at an important trophic intersection.

This study investigated the age-length relationship, approximate lifespan, timing of settlement and mortality of *Trimma nasa* using information obtained from otoliths. These data will provide a foundation for future work on population structure and biomass production in this and other small but abundant reef fish species.

MATERIALS AND METHODS

Fish collection. Fish were collected on 10 May 2007 at the Mutremdiu wall, Uchelbeluu Reef (Short Drop Off), in Palau at a depth of 15 m using the anaesthetic quinaldine and a hand-net. Captured fish were immediately placed in 80% ethanol. Within 3 wk of capture, all 110 specimens were sexed based on external genital morphology and their standard lengths were measured to the nearest 0.1 mm. Genital morphology is a good indicator of sex in these types of gobies, but does not necessarily indicate sexual maturity (K. Cole pers. comm.); thus, while we assumed fish with undifferentiated genitalia were sexually immature, not all differentiated individuals had necessarily reached maturity.

Otolith preparation. Sagittal otoliths were extracted from all specimens, cleaned, dipped in 70% ethanol

and stored dry in plastic culture plates. Each sagitta was mounted, sulcus side down, on a microscope slide with the thermoplastic glue Crystalbond 509™ with the anterior end (but not the core) hanging over the edge. The anterior end was ground on 9 and 3 µm lapping film until level with the edge of the slide, and progress was monitored under a dissecting microscope. The glue was then reheated so the otolith could be repositioned with the ground surface face down. The posterior end was ground to provide a thin section showing the entire sequence of increments from the primordium to the outer edge.

Age determination. Sections were viewed at 400× magnification on a computer monitor by means of a Spot Flex model 15.2 camera attached to a Leitz Dialux 22 compound microscope using Spot Diagnostic Instruments software (v4.5.9.5). Increments were counted from the core outward along the longest axis (Fig. 1). These increments were assumed to be deposited daily, as recent studies have confirmed daily increment deposition in 9 species of reef-associated goby (Hernaman et al. 2000, Shafer 2000, Depczynski & Bellwood 2006) as well as several tropical estuarine (Hernaman et al. 2000) and temperate marine (e.g. Iglesias et al. 1997) gobies. In addition, the first increment was assumed to be deposited at hatching. The hatch check, as the first increment is often called, may coincide with hatching, mouth opening or absorption of the yolk sac (Neilson 1992). In several species of *Trimma* and in the

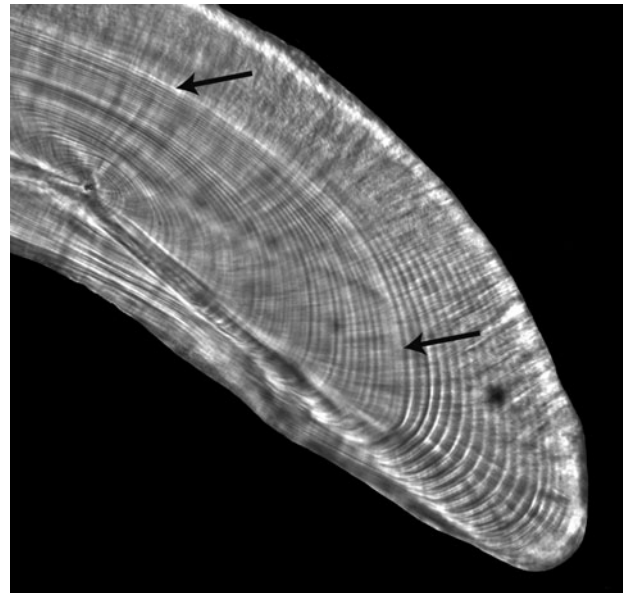


Fig. 1. *Trimma nasa*. Otolith from 12.2 mm (standard length) male with approximately 60 rings and settlement mark at 42 d (Royal Ontario Museum 82500_T1D6). Not all pre-settlement increments are visible in this focal plane. Arrows indicate the settlement mark

related *Priolepis nocturna*, these events all occur within 24 h (Sunobe 1995, Wittenrich et al. 2007). The location of the settlement mark, an abnormal increment corresponding to the transition from larval to settled life, was also noted when possible. Each otolith was counted twice; if counts differed by >10% of the mean, the otolith was re-counted and the average of the 2 closest counts was used, provided that they agreed within 10%.

Data analysis. Linear and power regression lines were fitted to the age-at-length data. A mixed model of the effects of age, sex, and age \times sex interaction on standard length was performed using SAS statistical software to investigate sex-specific growth. Hoenig's (1983) equation was used to estimate the total daily mortality rate from the maximum age of the fish examined as follows:

$$\ln Z = 1.46 \times 1.01 \ln T_{\max}$$

where Z = instantaneous mortality rate and T_{\max} = maximum age.

RESULTS

The mean increment number versus standard length data were fitted with linear and power regression lines (Fig. 2), with resulting coefficients of determination of $r^2 = 0.8458$ and 0.8464 , respectively. The maximum age was 87.5 d. In the mixed model, the effects of age, sex and age \times sex interaction were all significant (Table 1). Tukey's HSD post hoc test revealed that males were significantly smaller than females and juveniles ($p < 0.05$; Fig. 3). The male age versus length relationship was significantly different from those of females and juveniles ($p = 0.0218$ and 0.0066 , respectively; Fig. 4).

In 60% of otoliths examined, a change in increment morphology that was interpreted as a settlement mark was observed (Fig. 1). It consisted of an abrupt decrease in increment width accompanied by a change in increment contrast and focal plane. Based on the position of this settlement mark, the mean pelagic larval duration (PLD) was found to be 33.9 ± 3.7 d (Fig. 2); this constitutes 38.7% of the maximum recorded lifespan

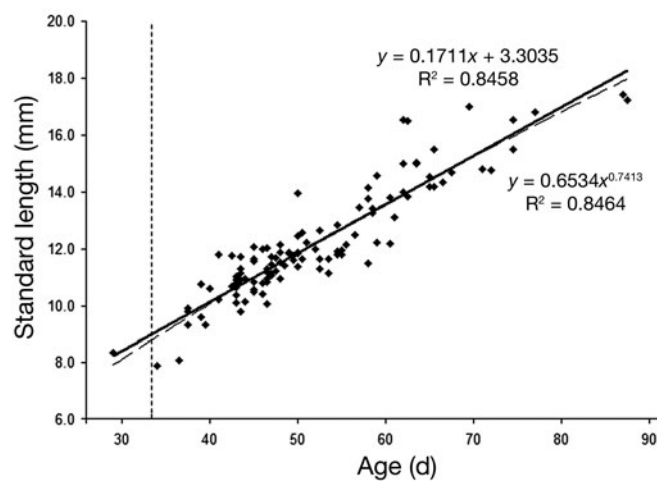


Fig. 2. *Trimma nasa*. Age versus standard length showing linear (solid) and power (dashed) regression lines. Vertical dashed line indicates mean age at which settlement occurs (33.9 ± 3.7 d SD)

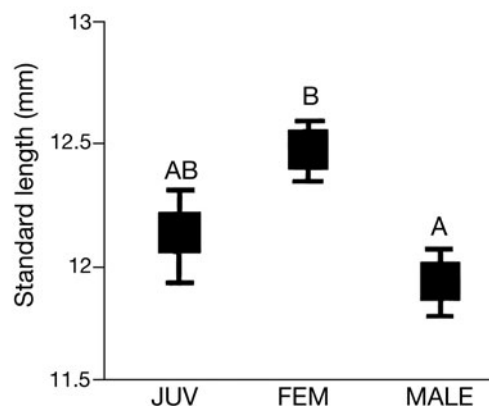


Fig. 3. *Trimma nasa*. Male, female and juvenile standard lengths (least squares mean \pm SE). Values not sharing letters in common are significantly different at the $p = 0.05$ level. $n = 29$ males, 46 females and 38 juveniles

and corresponds to 53.6 d of post-settlement life. Daily total mortality (Z) obtained from Hoenig's equation was 4.7%.

DISCUSSION

Linear and power regression lines fit the age-at-length data equally well; therefore, more sampling at the extremes of the size spectrum could determine the growth trajectory more accurately. We conducted an ANOVA to look for effects of sex as well as of age; both factors, plus an age \times sex interaction term, had significant effects on length. Interestingly, males were smaller than females when corrected for age. Males

Table 1. *Trimma nasa*. Results of mixed model of age, sex and age \times sex interaction on standard length

Effect	df	F	p
Age	1,104	292.34	<0.0001
Sex	2,104	4.26	0.0166
Age \times Sex	2,104	5.39	0.0059

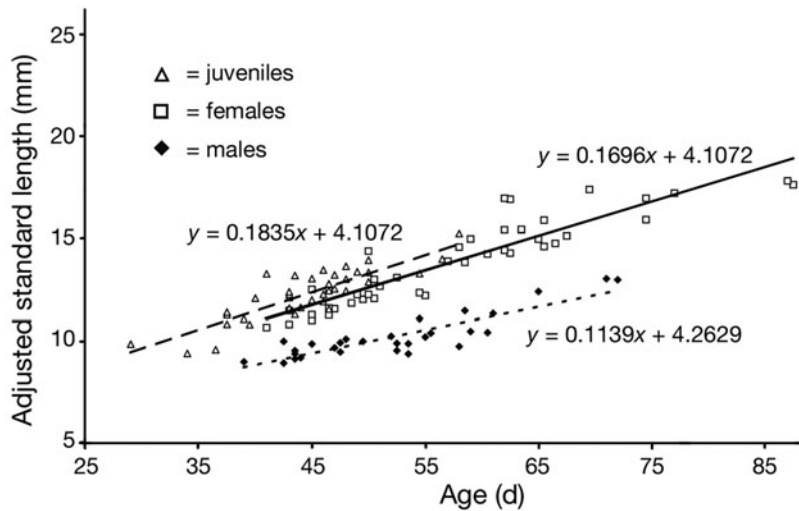


Fig. 4. *Trimma nasa*. Growth of males (◆, short-dashed line), females (□, solid line), and juveniles (△, long-dashed line) based on results of mixed model. Male growth differs significantly from female ($p = 0.0218$) and from juvenile ($p = 0.0066$) growth

also had significantly slower growth than females and undifferentiated juveniles, which suggests that their growth is not strictly linear but instead fits a 'broken stick' or 'breakpoint' model in which growth slows after maturity (Toms & Lesperance 2003); however, accurate determinations of sexual maturity status based on gonad histology will be necessary to refine our description of the growth trajectory.

Sex-based differences in growth patterns are known in other gobies and often can be explained by the mating system. For example, Hernaman & Munday (2005) reported larger, faster-growing males compared with females in 3 polygynous gobies, and no difference between male and female growth in 2 monogamous species. In addition, Reavis (1997) reported no overall size difference between males and females in the monogamous goby *Valenciennea strigata*, although pairs tended to be assorted by size.

Trimma nasa's mating system is not currently known; however, its congener, *T. okinawae*, is a harem, serial sex-changer (Sunobe & Nakazono 1990). *T. nasa* females are larger and faster-growing than males, but the sex ratio is only slightly female-biased (1 male : 1.6 females). At present, there is no obvious evidence that *T. nasa* is hermaphroditic; no individuals with intermediate gonad morphology have been found. The lack of a strongly biased sex ratio and the presence of larger females suggest that polygyny is unlikely, but there is little clear evidence for any particular mating system. Further study may be worthwhile to see whether small body size and short lifespan in fish place constraints on the mating system.

Female growth, unlike male growth, is not significantly different from that of undifferentiated juveniles.

Females maintain their pre-reproductive growth rates throughout their lives, seemingly disregarding the usual trade-off between somatic growth and reproduction. This, and their faster growth compared with males, is probably due to selection for larger female size and, thus, greater fecundity (see e.g. Depczynski & Bellwood 2006), but the presence of this selective pressure has not yet been tested.

The settlement mark appeared as a transition from narrower to wider increments, accompanied by a change in increment contrast and focal plane. This transition can be classified as a Type IV settlement mark (Wilson & McCormick 1999). Although we have not verified that this mark corresponds to settlement, Sponaugle & Cowen (1994) and Shafer (2000) reported that a similar mark was associated with settle-

ment in 3 other gobies: *Coryphopterus glaucofraenum* and *Gnatholepis thompsoni* in the Caribbean, and *Bathygobius coalitus* in Hawaii.

The 33.9 d larval life fits within the typical 3 to 6 wk duration reported by Brothers et al. (1983) for 12 reef fish families including the Gobiidae. However, as a percentage of the total lifespan, the PLD of *Trimma nasa* is remarkably long, i.e. 38.7% of the maximum recorded age. The vast majority of reef fishes for which data exist spend less than 1% of their lives as pelagic larvae (Depczynski & Bellwood 2006). Four small (<30 mm standard length), cryptic reef fish species—3 gobies and 1 tripterygiid—exceed 20%, with *Eviota sigillata* spending 41.8% of its total life in the plankton (Longenecker & Langston 2005, Depczynski & Bellwood 2006). Just as an increasing amount of data indicate that many reef fishes have short lifespans with linear growth, it is likely that further investigation of PLD compared with total lifespan in small reef fishes will uncover many more species for which the PLD represents a large proportion of the total life. There may be a lower limit on PLD length due to a minimum level of development required for settlement onto the reef.

Trimma nasa experiences 4.7% daily mortality, similar to the values reported for *Eviota melasma* and *E. queenslandica* by Depczynski & Bellwood (2006). This value represents natural mortality (M) because *T. nasa* is not exploited by humans, and furthermore, mortality is expected to be primarily due to predation in small (<50 mm total length) species. Theory predicts selection for early maturity and high reproductive effort when mortality is high (Miller 1996). Experimen-

tal work, such as that of Reznick & Endler (1982), has shown that increased predation selects for earlier maturation and faster growth in fish. Extensions of this work to *T. nasa* and other small reef fishes will help us understand the role mortality plays in shaping their life histories.

In addition to the questions about the consequences of small body size for life history that it raises, this study lays a foundation for further ecological work on small gobies. *Trimma nasa* and its relatives potentially play an important trophic role because, if their food source is primarily allochthonous plankton, they may be importing energy to the reef. While these fishes account for only a small part of the standing biomass (Depczynski et al. 2007), their generation times are probably very short, as in *Eviota* (Depczynski & Bellwood 2006), leading to rapid turnover and, thus, higher biomass production. A precise, histological determination of age at female maturity—the factor on which generation time mainly depends—has yet to be done for *T. nasa*, but if we use the estimate that female maturation occurs at about 65% of maximum length in fish generally (Charnov 1993), age at maturity is less than 45 d, hinting at a minimum of 5 generations per year. Such a rapid turnover combined with their potential status as a trophic intermediate and their large numbers on suitable parts of the reef suggest that *T. nasa* may significantly affect reef trophodynamics, out of proportion to their small body size. This has implications for coral reef conservation, arguing for spatial management rather than management on a species-by-species basis.

Trimma nasa has many of the life history characteristics of small reef fish: short lifespan, relatively long pelagic larval duration, rapid post-settlement growth and high mortality. Its sex-based differences in growth, apparently unusual among gobies, may be products of its presently unknown mating system. As one of several gobiid fish at the extreme small end of the vertebrate body length scale, the evolutionary consequences of its size on its life history and mating system are worth investigating. As an epibenthic planktivore, it may be an important trophic intermediate, importing energy from the pelagic plankton to the reef. As part of the diverse assemblage of small fish that numerically dominate the Uchelbeluu Reef ecosystem in Palau, its influence on reef ecology may be disproportionately large.

Acknowledgements. We are especially indebted to P. and L. Colin of the Coral Reef Research Foundation, Palau, who responded rapidly and effectively on very short notice by sending us the specimens on which this study is based, and later reviewed the manuscript. C. Healy generously allowed us almost unlimited access to her compound microscope. Many thanks to M. Depczynski for providing detailed, effec-

tive instructions on the preparation of miniscule goby otoliths and helpful comments on an early draft, to K. C. Cole, University of Hawaii, for input on interpreting goby genital papillae, and to D. R. Bellwood, James Cook University, Townsville, and D. Davis, University of Toronto, who generously provided us with complimentary lapping film. J. Friedman, S. Yakiowski and R. Colautti, University of Toronto, provided invaluable advice on statistical protocols. Thanks are also extended to 2 anonymous reviewers whose comments significantly improved the manuscript. This study was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant 7619 to R.W. and by an NSERC Undergraduate Student Research Award to L.S.

LITERATURE CITED

- Ackerman JL, Bellwood DR (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Mar Ecol Prog Ser* 206:227–237
- Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. *Oecologia* 37:257–272
- Brothers EB, Williams DM, Sale PF (1983) Length of larval life in twelve families of fishes at 'One Tree Lagoon', Great Barrier Reef, Australia. *Mar Biol* 76:319–324
- Calder MJ (1984) Size, function, and life history. Harvard University Press, Cambridge, MA
- Charnov EL (1993) Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford
- Depczynski M, Bellwood DR (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. *Mar Ecol Prog Ser* 256:183–191
- Depczynski M, Bellwood DR (2006) Extremes, plasticity, and invariance in vertebrate life history traits: insights from coral reef fishes. *Ecology* 87:3119–3127
- Depczynski M, Fulton CJ, Marnane MJ, Bellwood DR (2007) Life history patterns shape energy allocation among fishes on coral reefs. *Oecologia* 153:111–120
- Hernaman V, Munday PL (2005) Life-history characteristics of coral reef gobies. I. Growth and life-span. *Mar Ecol Prog Ser* 290:207–221
- Hernaman V, Munday PL, Schläppy ML (2000) Validation of otolith growth-increment periodicity in tropical gobies. *Mar Biol* 137:715–726
- Hoening JM (1983) Empirical use of longevity data to estimate mortality rates. *Fish Bull* 82:898–903
- Iglesias M, Brothers EB, Morales-Nin B (1997) Validation of daily increment deposition in otoliths. Age and growth of *Aphia minuta* (Pisces: Gobiidae) from the northwest Mediterranean. *Mar Biol* 129:279–287
- Kritzer JP (2002) Stock structure, mortality and growth of the decorated goby, *Istigobius decoratus* (Gobiidae), at Lizard Island, Great Barrier Reef. *Environ Biol Fishes* 63: 211–216
- Longenecker K, Langston R (2005) Life history of the Hawaiian blackhead triplefin, *Enneapterygius atriceps* (Blennioidae, Tripterygiidae). *Environ Biol Fishes* 73:243–251
- Miller PJ (1979) Adaptiveness and implications of small size in teleosts. *Symp Zool Soc Lond* 44:263–306
- Miller PJ (1996) The functional ecology of small fish: some opportunities and consequences. *Symp Zool Soc Lond* 69: 175–199
- Neilson JD (1992) Sources of error in otolith microstructure examination. In: Stevenson DK, Campana SE (eds) Otolith microstructure examination and analysis. *Can Spec Publ*

- Fish Aquat Sci, Vol 117, Department of Fisheries and Oceans, Ottawa, p 115–125
- Reavis RH (1997) The natural history of a monogamous coral-reef fish, *Valenciennesa strigata* (Gobiidae): 1. abundance, growth, survival and predation. *Environ Biol Fishes* 49: 239–246
- Reznick D, Endler JA (1982) The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 36:160–177
- Roff DA (1992) The evolution of life histories. Chapman & Hall, New York
- Saeki T, Sakai Y, Hashimoto H, Gushima K (2005) Foraging behaviour and diet composition of *Trimma caudomaculata* and *Trimma caesiura* (Gobiidae) on coral reefs in Okinawa, Japan. *Ichthyol Res* 52:302–305
- Shafer DJ (2000) Evaluation of periodic and aperiodic otolith structure and somatic-otolith scaling for use in retrospective life history analysis of a tropical marine goby, *Bathygobius coalitus*. *Mar Ecol Prog Ser* 199:217–229
- Sponaugle S, Cowen RK (1994) Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae): contrasting early life histories in demersal spawners. *Mar Biol* 120:133–143
- Sunobe T (1995) Embryonic development and larvae of three gobiid fish, *Trimma okinawae*, *Trimma grammistes* and *Trimmatom* sp. *Jpn J Ichthyol* 42:11–16
- Sunobe T, Nakazono A (1990) Polygynous mating system of *Trimma okinawae* (Pisces: Gobiidae) at Kagoshima, Japan with a note on sex change. *Ethology* 84:133–143
- Toms JD, Lesperance ML (2003) Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84:2034–2041
- Wilson DT, McCormick MI (1999) Microstructure of settlement-marks in the otoliths of tropical reef fishes. *Mar Biol* 134:29–41
- Winterbottom R (2005) Two new species of the *Trimma tevegae* species group from the Western Pacific (Percomorpha: Gobiidae). *Aqua J Ichthyol Aquat Biol* 10:29–38
- Wittenrich ML, Turingan RG, Creswell RL (2007) Spawning, early development and first feeding in the gobiid fish *Priolepis nocturna*. *Aquaculture* 270:132–141

Editorial responsibility: Hans-Heinrich Janssen,
Oldendorf/Luhe, Germany

Submitted: September 27, 2007; Accepted: April 3, 2008
Proofs received from author(s): July 31, 2008, 2007