Vol. 118: 59–68, 1995 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published March 9

# Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement

**Mark I. McCormick, Brett W. Molony**

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

ABSTRACT: The effects of water temperature during the pelagic life-history phase on body characteristics at metamorphosis and settlement were examined for the tropical goatfish *Upeneus tragula* (Mullidae). Water temperatures were recorded daily at 2 stations on the northern Great Barrier Reef from April 1989 to May 1990. Temperature data were used to calculate an estimate of temperature history for individual newly metamorphosed goatfishes from 10 samples, collected at 5 stations across the northern Great Barrier Reef lagoon. Accounting for mean water temperature experienced during the larval phase reduced the within-sample variability in growth rates by 30%. There were significant negative relationships with mean water temperature for both standard length and age of fish at metamorphosis within and among samples. Adjusting for temperature history by analysis of covariance markedly changed the patterns of size at settlement among sampling stations. Use of a summation of daily water temperatures over the larval period of each fish as an estimate of physiological age (in degree-days) also changed the patterns of significance among sampling stations compared to patterns found using age (d) alone. These results suggested the importance of temperature in determining larval patterns of growth. An experiment examined the influence of water temperature on size, age, body composition and muscle development at settlement. Larval *U. tragula* were collected and placed randomly in 3 tanks at each of 2 temperatures, 25 and 30°C. Fishes were fed ad libitum and removed from tanks upon metamorphosis and settlement. Fishes in the 30°C water settled on average 2.8 d earlier than those in the 25°C tanks. The length, weight, muscle development and biochemical composition of fishes did not differ between temperature regimes. Together, the field and laboratory results suggest that relatively small changes in water temperature have the potential to greatly influence the patterns of variability seen in the age and size at metamorphosis in many tropical reef fishes. Developmental rate to metamorphosis appears to be more affected by water temperature than fish length.

KEY WORDS: Temperature · Reef fish · Metamorphosis · Larval duration · Developmental rate

## INTRODUCTION

Water temperature is the environmental variable most frequently linked to the recruitment variability of temperate marine fishes (Sissenwine 1984). Most effort has concentrated on the effects of water temperature on viability and development of the embryo and yolk-sac stages, where most pre-recruitment mortality occurs (e.g. Houde 1974, Ware 1975, Tanasichuk & Ware 1987, Buckley et al. 1990, Fukuhara 1990, Pepin 1990, 1991, Kamler 1992). The end of the larval phase, metamorphosis, has attracted far less attention despite its often close association with the ecologically important transition from a pelagic to demersal existence. Studies of the influence of temperature on this life-stage have comprised almost exclusively laboratory studies on Pleuronectiformes. Unfortunately, studies of tropical fishes have lagged well behind their temperate counterparts in examining the influence of environmental variables on larval rate processes. To date, little information is available for tropical fishes, especially reef-associated fishes, which make up a major part of tropical fisheries.

The emphasis of temperate studies has typically concerned the influence of temperature on cohort survivorship, and the importance of the *average* size and

age of fishes in the target population (e.g Rijnsdorp et al. 1992) Only recently has attention focused on the variability around these population parameters (e.g. Chambers & Leggett 1992, McCormick 1994). Few studies have addressed how temperature influences the rate processes that drive the variability in size, age or body condition of fishes at metamorphosis. The link between growth and development can be a dynamic one (Chambers & Leggett 1987, McCormick & Molony 1992, 1993, McCormick 1994) and is affected by temperature in a diverse range of taxa. Information on the extent to which environmental factors contribute to the variability in body characteristics at metamorphosis is important since these characteristics may determine the fishes' subsequent mortality and growth schedules. For demersal fish where a change in habitat is often associated with metamorphosis, this variability in growth and development may be of paramount importance (Chambers & Leggett 1992). Planktonic processes that influence the developmental rates of larvae will subsequently influence the temporal patterns of recruitment to demersal populations.

For the tropical goatfish *Upeneus tragula*, there is considerable variation at metamorphosis in all features commonly used as indices of quality and condition (McCormick 1993, 1994, McCormick & Molony 1993). Moreover, growth and developmental rates to metamorphosis vary significantly over a wide range of temporal and spatial scales (McCormick 1994). This is not unusual for demersal reef fishes. For instance, Wellington & Victor (1992) found regional variation in the age and growth rates to settlement (and metamorphosis) of a species of wrasse (*Thalassoma lucasanum*) and 2 species of damselfish (*Stegastes flavilatus* and *Microspathodon dorsalis*) in the tropical eastern Pacific. The growth rates through to metamorphosis were found to differ by 1.5 times among 4 sampling sites spread over 3500 km. A knowledge of the influence of temperature on growth rates up to and including metamorphosis may aid the interpretation of the high variation in body attributes seen in the field.

The present study uses daily water temperature records to construct temperature histories for 10 samples of newly settled *Upeneus tragula* (family Mullidae), from 5 sampling stations across the northern Great Barrier Reef, Australia. These histories are used to examine the extent to which temperature influenced the patterns of age and size at settlement among stations over time. An experiment investigates how water temperature during the larval phase influences the body development (muscular and biochemical), age and size at metamorphosis and settlement. This is one of the first studies to use field collections of newly metamorphosed individuals to examine the importance of temperature history. The study shows that temperature histories should be accounted for to enable unconfounded intra- and inter-specific comparisons of larval duration and growth rates.

## METHODS AND MATERIALS

**Field study.** Samples were collected in conjunction with a study that examined the spatio-temporal distribution patterns of mullids on the northern Great Barrier Reef (McCormick & Milicich 1993). Sampling design and methodology used in this study will therefore only be briefly mentioned. Five stations across the northern Great Barrier Reef lagoon were sampled between November 1989 and January 1990. Station locations were: 9 km NW of the Turtle Island Group; 4 km S of Nymph Island; 5 km N of Eagle Island; Lizard Island backreef; midway between Lizard Island and Carter Reef (abbreviated to MLC; Fig. 2 in McCormick & Milicich 1993). At each station, ten 1 × 1 m plastic aggregation rafts were deployed. Rafts were left for 4 h and the small fish which aggregated were collected with a 14 × 2 m plankton-mesh purse seine (0.5 mm mesh). Once collected, a subsample (50 to 1000) of larval-stage *Upeneus tragula* was transferred to holding tanks of aerated seawater with a fine-mesh dip net, and transported live to the Lizard Island Research Station. Overnight some of these metamorphosed and settled to the bottom of the holding tanks. These newly settled fishes were used in the present study. The number of metamorphs per collection date ranged from 6 to 27.

Upon settlement, fishes were killed by cold shock, measured and their otoliths removed. Fishes were aged from validated daily increments on their sagittal otoliths following the methodology of McCormick (1994).

Water temperature data were collected over a 12 to 13 mo period between April 1989 and April 1990 at 2 locations on the northern Great Barrier Reef: an inshore station at the Turtle Island Group (14° 43' S, 145° 12' E) and a mid-shelf station at Lizard Island (14° 41' S, 145° 27' E). Data were collected by the staff of the Lizard Island Research Station, using calibrated dataloggers (HUGRUN Seamon UTR-B) at depths of 10 to 12 m.

**Temperature experiment.** The experiment was conducted at the Lizard Island Research Station between 8 and 27 January 1991. Experimental fishes were collected at the Eagle sampling station. Fishes were attracted to a series of aggregation rafts that were moored for 2 h and then sampled using a plankton-mesh purse seine. Once captured they were transported to the laboratory in blackened 70 l containers of aerated seawater. After 12 h, larval *Upeneus tragula*

between 20 to 23 mm standard length, SL (over halfway through their larval life), were randomly assigned to 1 of 2 temperature treatments: 25 or 30°C. As the results will show, these temperatures represent the temperature range over the main recruitment period (October to March). Three tanks were set up for each treatment. A refrigeration coil in a header tank reduced the water temperature of the flow-through seawater from an average of 28°C to a constant 25°C. Water heaters kept the other tanks at 30°C. Fish were fed ad libitum 36 to 48 h old *Artemia* sp. nauplii (Ocean Star strain).

Twenty fish were placed in each of three 20 l tanks per treatment. At 06:30 h each day, prior to feeding, tanks were examined for newly settled individuals. These individuals were removed and processed. Ten of these fishes were prepared for biochemical and 10 for histological comparisons. Mortality over the course of the experiment was negligible. Processing methods were similar to those used in McCormick & Molony (1992).

Prior to preservation a variety of morphological measurements were made: wet weight, standard length and body depth at the base of the pectoral fin and anal fin. Since fish were randomly assigned to the temperature treatments, the tanks were assumed to contain fishes with a similar age distribution. This assumption has a high probability of being valid because there is generally little variability in the age at metamorphosis within a sample of *Upeneus tragula* (McCormick 1994). The average time for the fishes to settle in each tank was recorded and compared between treatments since this was indicative of the effect of the treatments on age at settlement.

Muscle development was measured as an indicator of how water temperature affected somatic development. Muscle development was measured as the size distribution of 50 muscle fibres from histological sections of 5 fish from each of 2 tanks per temperature treatment. Fishes were preserved in formalin:acetic acid:calcium chloride for histological examination of striated muscle development. A cross section of muscle was removed at the start of the anterior dorsal fin, sectioned at 6 µm, and then stained with trichrome. Maximum muscle fibre diameters were then determined for 50 fibres within the second dorsal-most myotome (*musculus carinatus dorsalis*). Size distribution of muscle fibres from the experiment were compared to a field sample of fish that settled in the collection bins the night after capture.

Body constituents, measured as total lipids, carbohydrates, proteins and water content (mg $g^{-1}$ wet wt) were obtained for 7 to 10 fish from each treatment tank. Total protein was estimated colorimetrically (Bradford 1976), total carbohydrate was determined by perchloric acid extraction (Mann & Gallagher 1985), while chloroform/methanol extraction (Mann & Gallagher 1985) was used to determine lipid content. Duplicates were run for each fish and an average used for statistical analysis of differences between treatments.

**Analysis.** The relationship between larval growth rate and water temperature was investigated for each metamorph collected during the cross-shelf sampling programme. An approximation of larval growth rate was obtained by dividing the difference between the size at metamorphosis and hatching (estimated to be 2 mm SL; McCormick 1994) by the age at metamorphosis. For each fish, the mean daily water temperature experienced through its larval phase was determined. Mean water temperature per day was calculated for the 2 stations where temperature was recorded. Otolith increments were used to back-calculate spawning dates for each fish, thereby enabling the calculation of a mean temperature history for each metamorph. Temperature data from the inshore Turtle station were used for fish samples collected from the Turtle and Nymph stations, whilst temperature records from the Lizard Island station were used for samples collected from the Eagle, Lizard and MLC stations. Regression analysis was used to examine the relationship between growth rates of fish within a sample and water temperature. Homogeneity of the slopes of these relationships among samples was examined, and differences among sample means adjusted for water temperature (i.e. the covariate) were tested for using analysis of covariance (ANCOVA).

The influence of water temperature on age and size at metamorphosis were also examined separately. The homogeneity of the slopes of the relationship between mean water temperature (calculated for each fish) and age was investigated among samples. The summation of temperature over the larval period for each newly settled fish yielded a proxy for physiological age, expressed as 'degree-days' (°d, Ricker 1979). This parameter summarises all available information on the temperature history of each fish. The mean physiological age (°d) of each sample of fishes was calculated and compared to standard age (d) to examine the influence of temperature history on the interpretation of age-related trends among samples. Analysis of variance (ANOVA) was used to test for differences among samples. Tukey's HSD tests were used to identify the differences among sample means found by ANOVA.

The influence of temperature history on standard length of fishes within and among samples was examined by ANCOVA. Mean water temperature, calculated for each metamorph, was used as a covariate to remove some of the variability in the standard length of fishes attributable to temperature history and

thereby examine the influence of temperature on the trends observed among sample. Planned comparisons were used on least-squares estimates of the mean standard length (i.e. means adjusted for the temperature history covariate) to identify whether adjusted means differed among samples.

Tests for differences between temperature treatments were analysed with ANOVA, with tanks as replicates (n = 3). Tank mean values for body morphometrics and biochemical composition of fishes were used in analyses due to the lack of independence of individual fishes within particular tanks.

## RESULTS

The 2 stations across the northern Great Barrier Reef lagoon showed similar trends in temperatures over a year (Fig. 1). The minimum temperature at 10 to 12 m depth for 1989 to 1990 was 22.4°C at the inshore Turtle Island station, and 23.0°C at the midshelf Lizard Island station, both of which occurred in late July 1989. The maximum temperatures were 30.6°C during early February at the Turtle Island station and 30.0°C in early March at the Lizard Island station. The temperature range of the daily means over the main reef fish recruitment period (October to March) was 25 to 30°C, while water temperatures ranged from 26.6 to 28.9°C during the cross-shelf sampling programme (12 November 1989 to 16 January 1990).

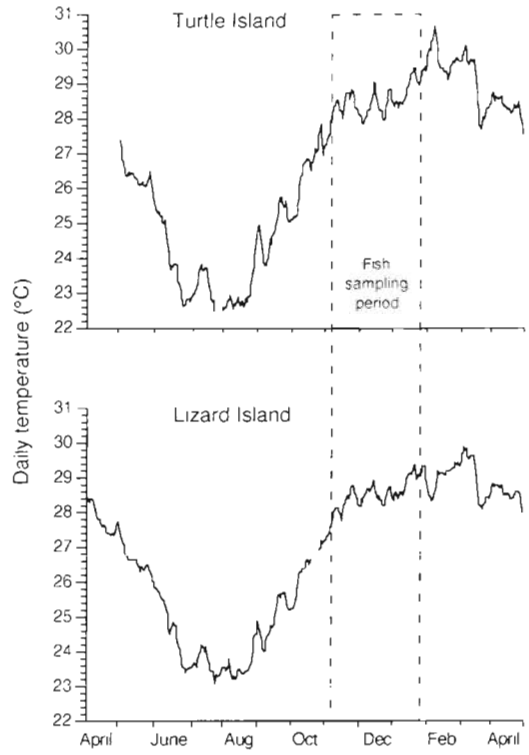


Fig. 1. Water temperatures at an inshore (Turtle Island Group) and mid-shelf station (Lizard Island) on the northern Great Barrier Reef (10 to 12 m depth). The period over which fishes were sampled is indicated

Larval growth rate increased with the mean water temperature experienced during larval life for all 10 samples collected from the cross-shelf sampling programme. The slopes of the relationship did not significantly differ among samples ($F_{9,161}$ = 1.45, p = 0.171; Fig. 2) and had a common slope of 0.45 mm $d^{-1}$ $°C^{-1}$. Overall, there was a 30% reduction in the within-sample variability in growth rates by accounting for mean water temperature experienced by the larvae. Within samples, the slopes of the relationship ranged from 0.25 to 1.06 mm $d^{-1}$ $°C^{-1}$ with variability in mean water temperature explaining between 3 and 83% of the variability in larval growth rate (Table 1).

There was a negative relationship between standard length of the newly metamorphosed fishes and mean water temperature experienced during the larval stage when all fishes were pooled (slope = −1.5 mm SL $°C^{-1}$, $r^2$ = 0.14, p = 0.0001, n = 181). The within-sample relationship of standard length and temperature did not

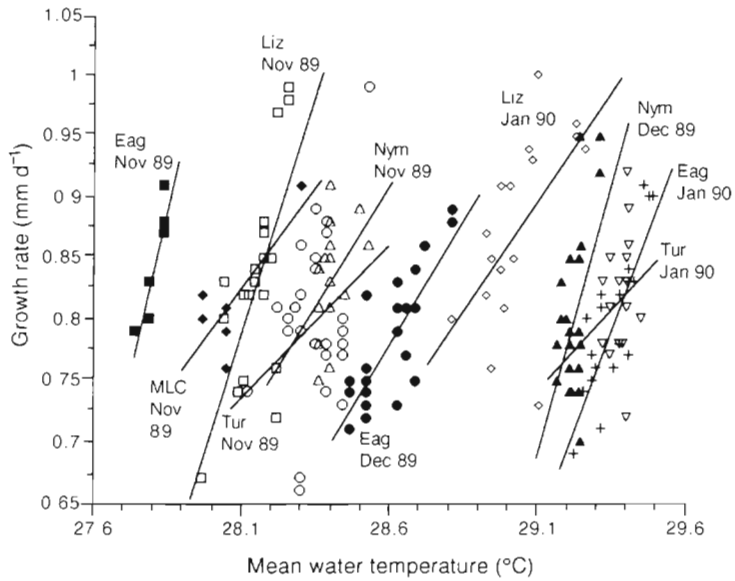


Fig. 2. *Upeneus tragula*. Relationship between growth rates averaged over the larval phase and mean water temperature experienced by each fish during larval development for 10 samples of newly metamorphosed fish. Regression lines for each sample are given and labels follow the sample identifications given in Table 1

Table 1. *Upeneus tragula*. Descriptive statistics for the relationship between growth rates averaged over the larval phase and mean water temperature experienced by each fish for 10 samples of fishes collected from 5 locations

| Sample | Sample size | Regression slope | $r^2$ | p |
|---|---|---|---|---|
| Eagle Island, Nov 1989 | 6 | 1.06 | 0.83 | 0.01 |
| Lizard Island, Nov 1989 | 23 | 0.78 | 0.44 | 0.0005 |
| MLC[a], Nov 1989 | 6 | 0.33 | 0.63 | 0.05 |
| Nymph Island, Nov 1989 | 18 | 0.40 | 0.19 | 0.08 |
| Turtle Group, Nov 1989 | 27 | 0.25 | 0.1 | 0.12 |
| Eagle Island, Dec 1989 | 22 | 0.41 | 0.64 | 0.0001 |
| Nymph Island, Dec 1989 | 23 | 0.89 | 0.24 | 0.02 |
| Eagle Island, Jan 1990 | 20 | 0.66 | 0.67 | 0.0001 |
| Lizard Island, Jan 1990 | 17 | 0.36 | 0.34 | 0.01 |
| Turtle Group, Jan 1990 | 17 | 0.26 | 0.03 | 0.48 |

[a]Midway between Lizard Island and Carter Reef

differ among the 10 field samples of fish ($F_{9,161} = 1.18$, $p = 0.313$) having a common slope of $-4.1$ mm SL °C$^{-1}$. These field samples suggest that fishes that experienced higher water temperatures during their larval phase metamorphosed at a smaller standard length compared to fishes that developed in cooler water temperatures.

When the standard length of fishes was adjusted for the mean water temperature experienced by each fish using ANCOVA, the rankings of the mean standard lengths among field samples of fishes changed markedly (Fig. 3). Our estimate of temperature history had a significant effect on standard length for any given field sample of metamorphosed fish ($F_{1,170} = 6.74$, $p = 0.01$). Adjusting for temperature history accentuated the magnitude of the among-sample differences in proportion to the difference of the samples in their average temperature histories (i.e. the covariate). Adjusted standard lengths at settlement were higher in samples collected in January than either of the other 2 months (Fig. 3). However, the use of the estimate of temperature history as a covariate in an ANCOVA only reduced the within-sample variability in standard length by 3%.

Overall, there was a negative relationship between larval duration and mean water temperature (slope = $-1.76$ d °C$^{-1}$, $r^2 = 0.19$, $p = 0.0001$, $n = 181$). However, the slope of this relationship within samples was considerably more abrupt and differed among the 10 field samples of fish ($F_{9,161} = 78.75$, $p = 0.0001$), ranging from $-16.1$ to $-45.1$ d °C$^{-1}$. The acuteness of these slopes is due to the relatively low variability of the ages of fish within a sample, and the estimate of temperature history used in analysis being a mean value. When expressed as a mean, a 0.1°C difference in water temperatures averaged over the whole larval period represents a large difference in water temperatures experienced by an individual within a sample. Accounting for the mean water temperature experienced by each metamorph (by using it as a covariate in an ANCOVA) explained an additional 50% of the variability in ages of fish at metamorphosis, over and above the 45% already explained by identifying the sample number alone. This suggests that water temperature may be a major influence on the age at which *Upeneus tragula* undergoes metamorphosis.

When age was expressed as degree-days the ranking of samples changed subtly, as did the pattern of similarity among samples (Fig. 4). The November 1989 Eagle sample had a markedly lower age when expressed as degree-days. This may be due to the low sample size (n = 6) yielding a poor representation of the average response of fishes to the temperature regime experienced by that sample. In general, expressing age as physiological age made little change to the rankings of the mean ages at metamorphosis among samples. This supports the high correlation between age and mean water temperature within samples found above.

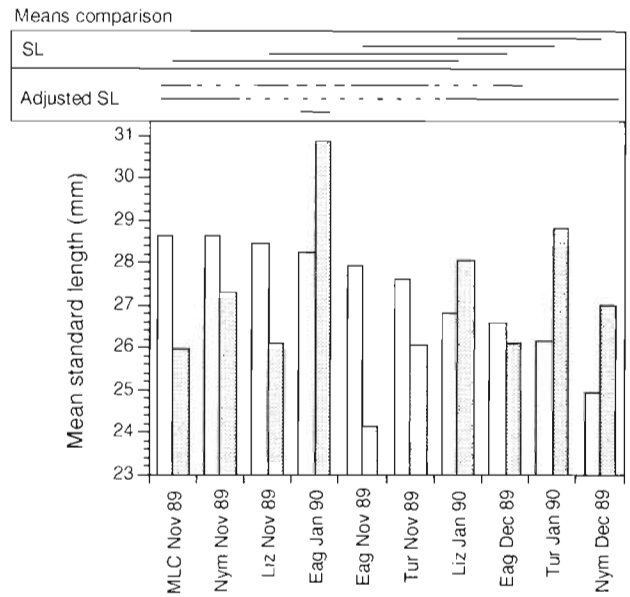


Fig. 3. *Upeneus tragula*. Comparison of the mean standard lengths (SLs) at metamorphosis for 10 samples of fish and their SLs adjusted for the influence of temperature history (i.e. mean water temperature experienced by each fish during the larval phase; shaded bars). Samples were collected from 5 sampling stations across the northern Great Barrier Reef. Mean SLs (not adjusted) were compared among samples with Tukey's (HSD) tests. Comparisons of adjusted sample means among samples were constructed for planned comparisons of least-squares means (SAS 1989)

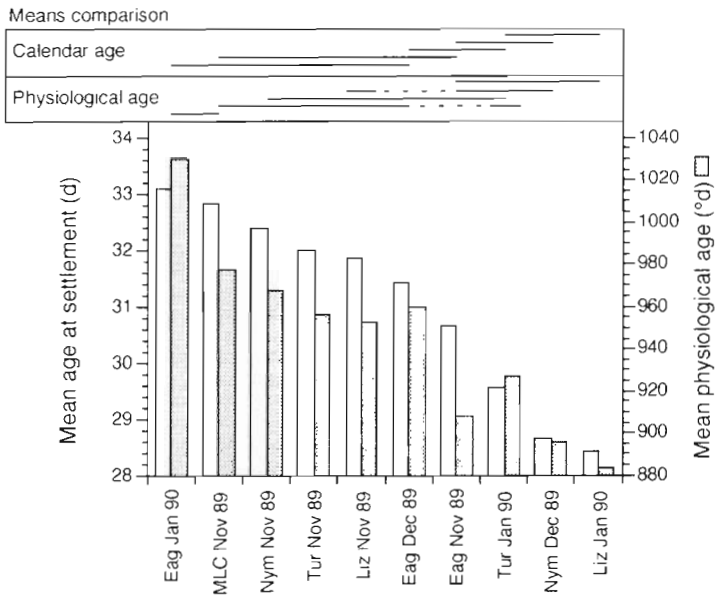


Fig. 4. *Upeneus tragula*. Comparison of the age (d) at settlement for 10 samples of newly metamorphosed fish, together with physiological age as estimated by degree-days (°d, shaded bars). The results of Tukey's (HSD) tests are shown for each among-sample comparison

The temperature experiment revealed no significant difference between the 2 temperature treatments in any of the 3 body dimensions measured (i.e. SL, body depths at the pectoral fin and anal fin) (Table 2). The body depth and body weight measurements mirrored trends in the standard length, with all mean values for body measurements being slightly higher for fishes in the 25°C treatment (Table 2).

The average number of days for a fish to metamorphose and settle to the bottom of the tank differed significantly between treatments (Table 2). Fishes within the 30°C tanks settled on average 2.8 d earlier than those in the 25°C tanks (mean 9.18 vs 11.97 d respectively; Table 2). When the number of days that fishes were within tanks was converted to degree-days there was only a small (7%) difference between the 25°C and 30°C treatments (277.2 vs 299.0 °d). This difference was not statistically significant between treatments ($F_{1,4}$ = 1.96, p = 0.234).

Muscle development was not influenced by temperature. A contingency table analysis found that there was no significant difference in the maximum muscle-fibre diameter distributions among the 2 temperature treatments and a field sample ($\chi^2_{12\ df}$ = 1.128, p > 0.9; Fig. 5).

The temperature treatments had no detectable effect on the biochemical composition of the fishes. There was no significant difference between the 2 temperature treatments for any of the body constituents measured (Table 2).

## DISCUSSION

Water temperature during the larval stage was shown in this study to potentially explain 30% of the variability in the growth rates of *Upeneus tragula* averaged over the larval phase. Furthermore, accounting for estimated temperature history during the larval stage changed the relative differences among sampling stations with respect to both standard length and age of the fishes at metamorphosis and settlement. This was despite the fact that the average daily temperatures only ranged 2.3°C over the sampling period. Experimentally, a 5°C increase in water temperature decreased the time to metamorphosis by 2.8 d for *Upeneus tragula* reared from midway through their pelagic life phase. This temperature increase did not affect muscle development or biochemical composition of the fishes. However, mean length and body depth were smaller, and mean wet weight lower at the higher rearing temperature, although this was not statistically significant. These field and laboratory findings stress the potential importance of water temperature in driving some of the variability in age and size at metamorphosis for this species of tropical reef fish.

Unfortunately, comparative data are few. There are no reliable field data on the effect of temperature on the timing of metamorphosis and settlement in Oste-

Table 2. *Upeneus tragula*. Comparison of body morphology, biochemical composition and time taken to settlement for fishes maintained in aquaria under 2 temperature regimes. Means are given with standard errors in parentheses (n = 3 tanks). Significance tests for differences between treatment means are also given

| Attribute | 25°C | 30°C | $F_{1,4}$ | p |
|---|---|---|---|---|
| Standard length (mm) | 27.46 (0.31) | 26.25 (0.24) | 1.36 | 0.308 |
| Pectoral body depth (mm) | 6.46 (0.17) | 6.26 (0.07) | 1.29 | 0.319 |
| Anal body depth (mm) | 5.52 (0.19) | 5.37 (0.09) | 0.50 | 0.518 |
| Weight (g) | 0.38 (0.025) | 0.362 (0.019) | 0.49 | 0.524 |
| Time to settlement (d) | 11.97 (0.16) | 9.18 (0.56) | 23.38 | 0.008 |
| Total lipids (mg $g^{-1}$) | 68.25 (5.60) | 76.70 (9.06) | 1.37 | 0.307 |
| Total carbohydrates (mg $g^{-1}$) | 14.48 (2.09) | 12.62 (1.62) | 1.26 | 0.325 |
| Total proteins (mg $g^{-1}$) | 67.10 (3.71) | 63.38 (1.79) | 0.67 | 0.459 |
| Water content (mg $g^{-1}$) | 732.53 (6.31) | 726.37 (4.91) | 0.59 | 0.484 |

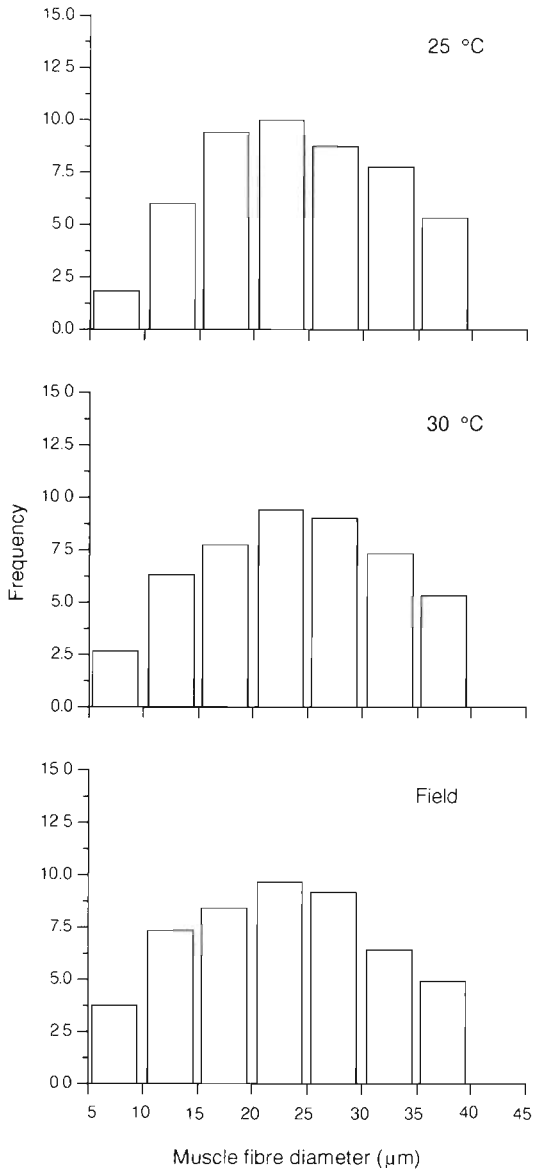


Fig. 5. *Upeneus tragula*. Maximum muscle fibre diameter size frequencies for newly metamorphosed fishes from 2 temperature treatments and a field sample

ichthyes (Youson 1988), and laboratory studies are limited to the flatfishes. Studies on 8 temperate flatfishes (*Pseudopleuronectes americanus*, Laurence 1975; *Solea solea*, Fonds 1979; *Platichthys stellatus*, Policansky 1982, 1983; *Rhombosolea tapirina* and *Ammotretis rostratus*, Crawford 1984; *Paralichthys olivaceus*, Seikai et al. 1986; *Paralichthys californicus*, Gadomski & Caddell 1991; *Paralichthys dentatus*, Keefe & Able 1993) show a marked reduction in larval duration with increasing temperature, similar to that found for a tropical goatfish in the present study. This inverse relationship between temperature and larval duration was responsible for a large portion of the variability in age at metamorphosis found among field samples of *Upeneus tragula* in the present study.

When age at metamorphosis was expressed as degree-days there was no difference among temperature treatments for either the present study or in 7 of the 8 flatfish studies (see Chambers & Leggett 1992, for the 6 earliest flatfish studies; exception is Gadomski & Caddell 1991, where degree-days to settlement are markedly higher in the 16°C cf. 20°C treatment). This expression of physiological age greatly reduces the between-population differences in the ages at metamorphosis and highlights interspecific ones. However, these were laboratory studies where all other factors except temperature were maintained constant. Degree-days were used in the present study to highlight the importance of temperature in driving some of the patterns of growth and development in a field dataset. The changes in ranking of the stations and the accentuation of differences in age and size by the incorporation of degree-days also suggests the importance of other factors that where previously masked by the influence of temperature.

Interpretations of the temperature-adjusted parameters can be problematic. In an uncontrolled environment, such as any field situation, interactions may exist between temperature and body rate processes, and removing the simple effects of temperature will not remove any synergistic effects that may exist. Cui & Wootton (1988) examined the effects of temperature and ration on the body composition of the freshwater minnow *Phoxinus phoxinus*. Temperature interacted with ration level to produce effects that were unpredictable from the simple action of either temperature or food alone. The use of a degree-days term to factor out differences in temperature history so that the underlying pattern can be examined should be approached with caution.

In general, laboratory studies have shown that the effect of temperature on size at metamorphosis appears slight and species specific. Similarly to the present field data and laboratory experiment, studies of *Solea solea* (Fonds 1979), *Ammotretis rostratus* (Crawford 1984) and *Paralichthys olivaceus* (Seikai *et al.* 1986) found average size at metamorphosis varied inversely with temperature. In contrast, temperature was directly related to size in *Platichthys stellatus* (Policansky 1982) and *Rhombosolea tapirina* (Crawford 1984). Laurence (1975) did not provide size information but found that the dry weight of *Pseudopleuronectes americanus* was lower at 5°C than at 8°C. Only Policansky (1982) formally tested whether size at metamorphosis differed between rearing temperatures, finding a slight but significant difference. Unfortunately, the conclusions of these 5 studies must be treated cautiously because they were pseudorepli-

cated, using only 1 tank per temperature treatment. This is a serious problem since Chambers & Leggett (1987) found high variability in the size at settlement among 18 tanks of winter flounder from the same spawning, held under similar laboratory conditions. Until further evidence is available we can only speculate whether the difference in the relationship between size and temperature found among these studies is taxon specific, an age-related response, or simply an experimental artefact.

The use of wild-caught larvae rather than fishes reared from eggs of known parentage reduced the sensitivity of the present experiment to changes due to temperature by incorporating genetic and age variability. This will lead to more conservative tests. However, the use of field-captured fishes rather than reared larvae has 2 distinct advantages. Wild-caught fishes have less tank and rearing artefacts, which Chambers & Leggett (1987) have shown can be high. Secondly, a variable genetic pool and age distribution is characteristic of the field population. Thus, conducting an experiment incorporating this variability increases the pertinence of the results to the field situation.

This study suggests that progeny spawned early in the extended reproductive season and developing in cooler water are likely to have slower growth rates, but may metamorphose and settle at an older age and a larger size, than those spawned into warmer waters later in the season. This prediction is supported by latitudinal and regional differences in size or age at settlement suggested in other studies (Randall 1961, Thorrold & Milicich 1990). The analysis of the field data presented here suggests that temperature history does explain some of the variability in the age and size at which *Upeneus tragula* is competent to settle. Both age and standard length were negatively related to water temperature but these relationships were much stronger within samples than among samples. Despite these relationships, data collected during the following austral summer conflicts with these predictions. McCormick (1994) examined the variation in the size of *Upeneus tragula* at settlement over 8 samples from a single station off Lizard Island during November and December 1991 (4 samples $mo^{-1}$). Fishes that settled early in the season were found to be significantly smaller than fishes that settled later (November: 26.9 mm SL; December: 28.1). Furthermore, the mean age at settlement did not differ between months (32.2 and 31.4 d respectively). This discrepancy between trends with temperature among fish within samples and among samples may be due to an interaction between water temperature and the availability of the planktonic food items on which the pelagic stages feed. This interaction may be expected to have less influence on the differences among individual fish within a sample than it does among samples of fishes collected over a 2 mo period.

Our temperature experiment suggested that temperature history over the late pelagic stage does not influence the biochemical composition of *Upeneus tragula* at settlement (as measured by total lipids, proteins and carbohydrates). This is of interest given the high variability in proximate composition among samples found for *U. tragula* (McCormick & Molony 1993). Studies to date show that temperature influences condition through its action on metabolic rates. More energy is devoted to maintenance of body structures at high temperatures (within the fishes' natural temperature range) than at lower temperatures. Body protein levels are conserved over a range of temperatures in all but the most extreme ration levels (Brett et al. 1969, Elliott 1975) whilst the quantities of storage lipids vary by a species-specific function of food availability and temperature (Brett et al. 1969, Allen & Wootton 1982, Vondracek et al. 1988). Clearly, experiments that manipulate both temperature and food availability are required to attain a detailed understanding of how temperature influences food utilisation and the rates of growth and development in *U. tragula*.

To enable unconfounded comparisons of larval duration among species of reef fishes or between geographic regions, as has been done for pomacanthids (Thresher & Brothers 1985), labrids (Victor 1986b) and pomacentrids (Wellington & Victor 1989), temperatures experienced by larvae should be reported, even if these are approximated. Adjusting for variable water temperatures may aid in determining whether the differences found in larval duration are true species differences or simply a product of different temperature histories experienced between collection dates or across a spatial temperature gradient. The age, size and body composition of a newly metamorphosed fish represents the product of all planktonic influences experienced, such as temperature, feeding history and parentage (lineage and nutritional status). The easiest way of overcoming differences in pelagic life histories experienced by larvae when attempting species comparisons is by collecting samples over a wide range of environmental (and thereby developmental) conditions. This will be particularly important for fishes with long larval durations and high associated variability (e.g. Victor 1986b).

Many flatfishes and reef-associated wrasses have high variability associated with their larval durations (Victor 1986a, b, Chambers & Leggett 1987, 1992, Cowen 1991). Active delays in settlement, as found for many invertebrates (Pechenik 1990, Pechenik et al. 1993), have been suggested as the mechanism underlying this variability in wrasses (Victor 1986a, 1987, Cowen 1991). On the other hand, researchers on flat-

fishes favour explanations that involve developmental flexibility under changing environmental conditions (Gadomski & Caddell 1991, Keefe & Able 1993). Active delays have seldom been posited as a major factor influencing larval durations of non reef-associated fishes. It is difficult to determine the relative influence of delayed metamorphosis and an extension of larval duration due to the action of environmental factors on developmental rates. One has to wonder whether this polarity of proposed mechanisms simply reflects methodological and historical bias. Experimental studies on reared fishes dominate the temperate fisheries literature whilst field collections form the basis of the tropical literature. The present experimental study of a tropical goatfish shows that relatively small fluctuations in water temperature can influence the patterns of size and age at settlement. It is only by rearing reef fishes under a range of experimental conditions (e.g. temperature, ration and salinity) that we will gain an understanding for the extent that environmentally driven changes in growth and developmental rates influence the variability seen in size and age at settlement. At that time we will be better able to judge the relative contribution of environmentally induced extensions to larval periods and actively delayed metamorphosis.

*Acknowledgements.* Many thanks to the people who kindly gave their time and energy to the project, in particular: B. Kerrigan, J. McIlwain, V. Hall, L. Axe. This manuscript benefited from discussions with J. Leis and M. Milicich and comments from 3 anonymous reviewers. This research was funded by the Australian Museum, through a Lizard Island Doctoral Research Fellowship (M.I.M.) and by an Australian Research Council minor research grant. Logistic support was provided by the Department of Marine Biology at J.C.U. This paper is a contribution from the Lizard Island Research Station, a facility of the Australian Museum.

## LITERATURE CITED

Allen, J. R. M., Wootton, R. J. (1982). The effect of ration and temperature on the growth of the three-spined stickleback, *Gasterosteus aculeatus* L. J. Fish. Biol. 20: 409–422

Bradford, M. M. (1976). A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein-dye binding. Analyt. Biochem. 72: 248–254

Brett, J. R., Shelbourn, J. E., Shoop, C. T (1969). Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Bd Can. 26: 2363–2394

Buckley, L. J., Smigielski, A. S., Halavik, T. A., Laurence, G. G. (1990). Effects of water temperature on size and biochemical composition of winter flounder *Pseudopleuronectes americanus* at hatching and feeding. Fish. Bull. U.S. 88: 419–428

Chambers, R. C., Leggett, W. C (1987). Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. Can. J Fish. Aquat. Sci. 44: 1936–1947

Chambers, R. C., Leggett, W. C. (1992). Possible causes and consequences of variation in age and size at metamorphosis in flatfishes (Pleuronectiformes): an analysis at the individual, population and species levels. Neth. J. Sea Res. 29: 7–24

Cowen, R. K. (1991). Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. Mar Ecol. Prog. Ser. 69: 9–15

Crawford, C. M. (1984). Preliminary results of experiments on the rearing of Tasmanian flounder, *Rhombosolea tapirina* and *Ammotretis rostratus*. Aquaculture 42: 75–81

Cui, Y., Wootton, R. J. (1988). Effects of ration, temperature and body size on the body composition, energy content and condition of the mimmow, *Phoxinus phoxinus* (L.). J. Fish. Biol. 32: 749–764

Elliott, J. M. (1975). Body composition of brown trout (*Salmo salar* L.) in relation to temperature and ration size. J. Anim. Ecol. 45: 273–289

Fonds, M. (1979). Laboratory observations on the influence of temperature and salinity on development of the eggs and growth of the larvae of *Solea solea* (Pisces). Mar Ecol. Prog. Ser 1: 91–99

Fukuhara, O. (1990). Effects of temperature on yolk utilization, initial growth, and behaviour of unfed marine fish-larvae. Mar. Biol. 106: 169–174

Gadomski, D. M., Caddell, S. M. (1991). Effects of temperature on early-life-history stages of California halibut *Paralichthys californicus*. Fish. Bull. U.S. 89: 567–576

Houde, E. D. (1974). Effects of temperature and delayed feeding on growth and survival of larvae of three species of subtropical marine fishes. Mar. Biol. 26: 271–285

Kamler, E. (1992). Early life history of fish: an energetics approach. Chapman & Hall, London, p. 267

Keefe, M., Able, K. W. (1993). Patterns of metamorphosis in summer flounder, *Paralichthys dentatus*. J. Fish Biol. 42: 713–728

Laurence, G. C. (1975). Laboratory growth and metabolism of the winter flounder *Pseudopleuronectes americanus* from hatching through metamorphosis at three temperatures. Mar. Biol. 32: 223–229

Mann, K., Gallagher, B. M. (1985). Physiological and biochemical energetics of larvae of *Teredo navalis* L. and *Bankia gouldi* (Bartsch) (Bivalvia: Teredinidae). J. exp. mar. Biol. Ecol. 85: 211–228

McCormick, M. I. (1993). Development and changes at settlement in the barbel structure of the reef fish, *Upeneus tragula* (Mullidae). Environ. Biol. Fish. 37: 269–282

McCormick, M. I. (1994). Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the Great Barrier Reef lagoon. Mar. Ecol. Prog. Ser 103: 1–15

McCormick, M. I., Milicich, M. J. (1993). Late-pelagic stage goatfishes: distribution patterns and inferences on schooling behaviour. J. exp. mar. Biol. Ecol. 174: 15–42

McCormick, M. I., Molony, B. W. (1992). Effects of feeding history on the growth characteristics of a reef fish at settlement. Mar. Biol. 114: 165–173

McCormick, M. I., Molony, B. W. (1993). Quality of the reef fish *Upeneus tragula* (Mullidae) at settlement: is size a good indicator of condition? Mar Ecol. Prog. Ser. 98: 45–54

Pechenik, J. A. (1990). Delayed metamorphosis by larvae of benthic marine invertebrates: does it occur? is there a price to pay? Ophelia 32: 63–94

Pechenik, J. A., Rittschof, D., Schmidt, A. R. (1993). Influence

of delayed metamorphosis on survival and growth of juvenile barnacles *Balanus amphitrite*. Mar. Biol. 115: 287–294
Pepin, P. (1990). Biological correlates of recruitment variability in North Sea fish stocks. J. Cons. int. Explor. Mer 47: 89–98
Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48: 503–518
Policansky, D. (1982). Influence of age, size and temperature on metamorphosis in the starry flounder, *Platichthys stellatus*. Can. J. Fish. Aquat. Sci. 39: 514–517
Policansky, D. (1983). Size, age and demography of metamorphosis and sexual maturation in fishes. Amer. Zool. 23: 57–63
Randall, J. E. (1961). A contribution to the biology of the convict surgeonfish of the Hawaiian islands, *Acanthurus sandvicensis*. Pacif. Sci. 15: 215–272
Ricker, W. E. (1979) Growth rates and models. In: Hoar, W. S., Randall, D. J. (eds.) Fish physiology, 8. Academic Press, Orlando, p. 677–743
Rijnsdorp, A. D., Van Beek, F. A., Flatman, S., Millner, R. M., Riley, J. D., Giret, M., De Clerck, R. (1992). Recruitment of sole stocks, *Solea solea* (L.), in the northeast Atlantic. Neth. J. Sea Res. 29: 173–192
SAS (1989). SAS/STAT user's guide, Version 6, 4th edn, Vol. 2. SAS Institute, Inc., Cary, NC
Seikai, T., Tanangonan, J. B., Tanaka, M. (1986). Temperature influence on larval growth and metamorphosis of the Japanese flounder *Paralichthys olivaceus* in the laboratory. Bull. Jap. Soc. Sci. Fish. 52: 977–982
Sissenwine, M. P. (1984). Why do fish populations vary? In: May, R. M. (ed.) Exploitation of marine communities. Springer-Verlag, New York, p. 59–94
Tanasichuk, R. W., Ware, D. M. (1987). Influence of interannual variation in winter temperature on fecundity and egg size in Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 45: 1485–1495
Thorrold, S. R., Milicich, M. J. (1990). Comparison of larval duration and pre- and post-settlement growth in two species of damselfish, *Chromis atripectoralis* and *Pomacentrus coelestis* (Pisces: Pomacentridae), from the Great Barrier Reef. Mar. Biol. 105: 375–384
Thresher, R. E., Brothers, E. B. (1985). Reproductive ecology and biogeography of Indo-west Pacific angelfishes (Pisces: Pomacanthidae). Evolution 39: 878–887
Victor, B. C. (1986a). Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). Can. J. Fish. Aquat. Sci. 43: 1208–1213
Victor, B. C. (1986b). Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasse (family Labridae). Mar. Biol. 90: 317–326
Victor, B. C. (1987). Growth, dispersal, and identification of planktonic labrid and pomacentrid reef-fish larvae in the eastern Pacific Ocean. Mar. Biol. 95: 145–152
Vondracek, B., Wurtsbaugh, W. A., Cech, J. J. (1988). Growth and reproduction of the mosquitofish, *Gambusia affinis*, in relation to temperature and ration level: consequences for life history. Environ. Biol. Fish. 21: 45–57
Ware, D. M. (1975). Relation between egg size, growth and mortality of larval fish. J. Fish. Res. Bd Can. 32: 2503–2512
Wellington, G. M., Victor, B. C. (1989). Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Mar. Biol. 101: 557–567
Wellington, G. M., Victor, B. C. (1992). Regional differences in duration of the planktonic larval stages of reef fishes in the eastern Pacific Ocean. Mar. Biol. 113: 491–498
Youson, J. H. (1988). First metamorphosis In: Hoar, W. S., Randall, D. J. (eds.) Fish physiology, 11(B). Academic Press, New York, p. 135–196

*This article was presented by D. M. Alongi (Senior Editorial Advisor), Townsville, Australia*

*Manuscript first received: February 22, 1994*
*Revised version accepted: October 21, 1994*