# Dartfish use teredinid tunnels in fallen mangrove wood as a low-tide refuge

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ABSTRACT: The considerable quantities of dead wood in the intertidal zone of mature mangrove forests are tunnelled by bivalves of the family Teredinidae. When the surface of heavily tunnelled wood is broken open, cryptofauna are able to use tunnels as refuges. In this study, the exploitation of this niche during low tide by the dartfish *Parioglossus interruptus* was investigated. The majority of tunnels offer a close fit falling within the range of typical dartfish diameters. The fish found within wood tended to be smaller than fish found swimming between mangrove roots at high tide. Dartfish were found in tunnelled wood even where it was emersed for over 11 h d$^{-1}$, but favoured wood in the lower intertidal. Within the wood, daytime thermal maxima were reduced by 6.5°C compared with adjacent tidepools. Wind-tunnel observations indicated that this lowering could be due to evaporative cooling. However, dartfish were found to be notably tolerant of high temperatures, with a critical thermal maximum that exceeded temperatures reached in tunnelled wood and pools. Nonetheless, such tolerance may impose a metabolic cost that would be reduced by occupying tunnels. Teredinid tunnels are also likely to give dartfish protection from desiccation and predation. During high-tide, free-swimming dartfish were observed to favour areas of *Rhizophora* roots over open creeks. In aquaria, fish swam actively during the day, but took refuge in teredinid tunnels at night. Sampling of wood at low tide and direct observations at high tide indicate that a substantial proportion of the dartfish population takes refuge in wood during low tide. Thus, teredinid-tunnelled wood is a key low-tide refuge especially for younger fish, which would otherwise be exposed to predators. This study provides an example of a mechanism whereby mangrove forests support intertidal biodiversity.

KEY WORDS: Teredinidae · Cryptofauna · Niche-creation · Mangrove wood · Thermal tolerance

## INTRODUCTION

Mangrove forest productivity is often higher than that of forests inland and, at higher levels of productivity, mangroves allocate more production to woody tissues, which can represent >95% of above-ground biomass (Ross et al. 2001, Komiyama et al. 2008). Woody tissues in live trees are subject to tunnelling by insect or isopod borers (Feller & Mathis 1997, Feller 2002, Sousa et al. 2003), but most wood falls to the forest floor and accumulates as a major compo-

nent of total forest biomass (Donato et al. 2011). Accumulated woody detritus enhances biodiversity in inland forests (Harmon 1986) and freshwater ecosystems (Ogren & King 2008), but less is known about its effect in mangrove ecosystems, though biodiversity support is identified as one of the services provided by these ecosystems (Kathiresan & Bingham 2001, Nagelkerken et al. 2008).

Dead mangrove wood is subject to slow degradation by marine fungi, but also to much more rapid break-down due to wood-boring bivalves of the fam-

ily Teredinidae (Kohlmeyer et al. 1995, Cragg 2007, Filho et al. 2008). Teredinid tunnelling can cause >90% of the weight loss from trunks of the mangrove *Rhizophora* during the early stages of degradation, generating a major flux of carbon (Robertson & Daniel 1989, Robertson 1991). Initially, the log surface is hardly affected, as tunnel entrance holes are <1 mm in diameter. Eventually tunnels riddle and weaken the wood, and where the surface is broken open, cryptic organisms can gain access to tunnels (Cragg & Hendy 2010).

One such organism is the interrupted dartfish *Parioglossus interruptus* Suzuki & Senou, 1994, which is common within teredinid-tunnelled wood at low tide; at high tide, it has often been found swimming in shallow water between the prop roots of *Rhizophora* trees in the Tukang Besi Archipelago, Indonesia (Cragg & Hendy 2010). Interrupted dartfish are also known from Iriomote Island, Japan (Suzuki & Senou 1994), and New Guinea (Rennis & Hoese 1985). Dartfishes (Ptereleotridae) are benthopelagic gobioids inhabiting warm-temperate to tropical tidal estuaries and mangrove swamps within the western Pacific and the Indian Ocean (McDowall 2001). These fish occupy structurally complex habitats such as seagrass beds or mangrove roots that provide access to the zooplankton upon which they feed (Keith et al. 2004), but also protection from predators (Verweij et al. 2006). Within mangrove forests, falling tides expose the substratum, and the only remaining water is in permanent creeks and ponds, so the cover provided by emergent mangrove roots is lost. However, by occupying tunnelled wood, fish may be protected from predators at low tide. Thus, moving into the wood may be viewed as cryptic behaviour, which is typically seen as being motivated by predator avoidance (Ruxton et al. 2004).

Rapid changes of salinity and temperature are common within mangrove forests (Tomascik et al. 1997), and forests of the Tukang Besi Archipelago experience large diel fluctuations in water temperature, oxygen level and salinity (Taylor et al. 2005, Cragg & Hendy 2010). These environmental fluctuations may be buffered within the teredinid tunnel niche, so dartfish within tunnelled wood may be protected from high temperatures and desiccation.

In the present study we characterised the amphibious, cryptic behaviour of the interrupted dartfish and evaluated the significance of this behaviour for the autecology of the fish. In addition, we assessed the ecosystem service of biodiversity maintenance of vacant teredinid tunnels. We hypothesised that dartfish:

(1) Reduce their risk of predation by taking refuge in teredinid-tunnelled wood at low tide;

(2) Are protected by the tunnels from thermal stress and desiccation.

## MATERIALS AND METHODS

### Field studies

Samples were collected from all large woody debris (LWD) (defined as wood pieces >20 mm diameter) encountered along 8 transects in the *Rhizophora stylosa*–dominated mangrove forest at Langira, Kaledupa Island (05° 27.53′ S, 123° 46.33′ E) in the Tukang Besi Archipelago, Sulawesi, Indonesia. The transects were 4 m in width and extended perpendicularly from the strandline out to the seaward fringe for a mean distance of 380 m. A total of 196 pieces of LWD were collected from the transects. These were split lengthwise and photographed (to provide a measure of the proportion of wood removed by teredinid tunnelling), then broken open to remove all fauna occupying teredinid tunnels. All interrupted dartfish *Parioglossus interruptus* found within the LWD were removed, counted and measured (±0.1 mm; standard length from the anterior tip to the caudal peduncle). These measurements were compared with the lengths of dartfish (not in tunnels) caught at high tide via the seine-haul fishing technique. A seine net that had hole diameters smaller than diameters of juvenile dartfish was positioned around *Rhizophora* prop roots that had whole populations of dartfish swimming among them. This method was very effective, as whole populations of dartfish were captured.

The internal diameters of 1455 randomly chosen teredinid tunnels in LWD were measured using calipers. Measurements of dartfish diameters (standard diameter recorded at the posterior end of the gill operculum) and tunnels were also compared. Measurements of length and diameters were made from images of the sampled fish using the digital analysis package ImageTool Version 3.00 (The University of Texas Health Science Centre at San Antonio).

Stations measuring 3 sets of temperatures matched temperatures inside tunnelled wood and in adjacent shallow tidepools (±0.5°C, hourly intervals) over a period of 1 mo. The temperature loggers, 6 Thermochron iButtons®, were placed in the mid- and low-intertidal areas of the forest, at 1.5 to 1.0 m and at <1.0 m above mean sea level. The buttons were replaced twice during the measurement period.

To determine the heights above sea level along the transects, the level of high tide was marked on mangrove trees using high visibility string. At low tide, the distance from the substrate to the mark on the tree was measured and then subtracted from the height of high tide as given in the Indonesian tide tables. Emersion times for the LWD were estimated by relating their tidal height to data in regional tide tables. To determine the volume of dead wood available to the dartfish, all fallen LWD (n = 109) was measured within nineteen 20 × 20 m plots randomly placed along the transects.

The number of dartfish swimming in tidal creeks within the *Rhizophora* forest and in the water among *Rhizophora* prop roots adjacent to open water were counted by snorkel visual census at high tide daytime and night. During the day, counts were made in belt transects measuring 25 × 4 m, placed at random along creeks in the low-, mid- and high-intertidal areas of the mangrove. At night, transects (n = 4) were established in the same areas and tidal zones. Nine transects were surveyed at each tidal level. Visual census was not extended beyond the fringing areas, as densely packed roots prevented access.

### Laboratory studies

A 60 × 20 cm Perspex wind tunnel with an air-flow-induced wind speed of 3 m s$^{-1}$ was used to measure evaporative cooling within teredinid tunnelled LWD samples (n = 45) each approximately 64 cm$^3$ in volume. Samples were placed on a mesh-box to ensure that all sides received equal air-flow. Using a calibrated thermocouple thermometer (Oakton WD-35427-00 Temp 10 Type J), temperatures were recorded over 30 min within the wind tunnel. The thermometer had 2 temperature probes: one probe was placed upon the wood surface and the other approximately 3 cm below the surface.

The upper thermal tolerance of dartfish was determined using groups of 20 dartfish both with and without the presence of teredinid tunnels in 3 aquaria. The dartfish were acclimated for 7 to 10 d at 27 or 35°C. The low and high acclimation temperatures approximate the mean open water temperature and the tidepool maximum at the site where experimental fish were collected (Taylor et al. 2005, Eme & Bennett 2009a). The aquaria were placed within a 95 l bath, the water in each aquarium was aerated by a linear air pump, and ~30% of the water was changed daily. Heat in the bath was provided by a 300 W glass AZOO® heater (AZOO, Taikong), and water in the bath was circulated using 2 AZOO® pumps. Dartfish were fed Sera® Vegetarian Diet flake food once per day, but were not fed 24 h prior to the critical thermal maximum (CTM) trials. Fish acclimated to 35°C were brought to this constant acclimation temperature by increasing water temperature 1.9 ± 0.9°C d$^{-1}$ for 4 d, and were then held at this constant temperature for 7 d. Fish acclimated to 27°C were also held at this temperature for 7 d.

Following 7 d of acclimation, each fish was exposed to a CTM trial with a constant temperature increase of 0.3°C min$^{-1}$ until loss of equilibrium (LOE) was observed. For each CTM trial, randomly selected fish were placed into 250 ml Nalgene® beakers filled with clean seawater at the appropriate constant acclimation temperature. Beakers were suspended within a 20 l, insulated, recirculating water bath and provided with moderate aeration to prevent thermal stratification. A mercury thermometer (certified Fisherbrand® NIST) was used to monitor temperature in each beaker. Water temperature in the CTM water bath was raised using 600 to 800 W of aquarium heater wattage until the final LOE was reached. LOE was defined as the inability to maintain dorso-ventral orientation for at least 1 min (Beitinger et al. 2000). For observations of teredinid tunnel use under laboratory conditions, fish were placed into beakers with a piece of calcareous lining from a teredinid tunnel measuring 3 to 5 cm in length and kept at the acclimation temperature for at least 6 h prior to the trial. The dartfish CTM work was tested with and without teredinid tunnel linings to determine if the tunnel environment enhanced their CTM, as the dartfish may have been less stressed when in the tunnel linings.

Ten dartfish were placed into each of 4 aquaria, and each aquarium contained 9 teredinid tunnels. Observations of whether the fish were in the tunnel linings or free in the water were recorded every 10 min during daytime (08:00 to 15:00 h) and nighttime (21:00 to 02:00 h). After 4 d, the dartfish in each aquarium were replaced with new groups of 10 fish, which were given 24 h to acclimate. This change took place 3 times. All fish were released at their site of capture following experiments.

For all field and laboratory studies, statistical significance was determined based on α = 0.05. Statistical analyses were performed using MINITAB (MINITAB, Version 13.20).

### RESULTS

The forest study sites were dominated by *Rhizophora stylosa*, with densely packed prop roots
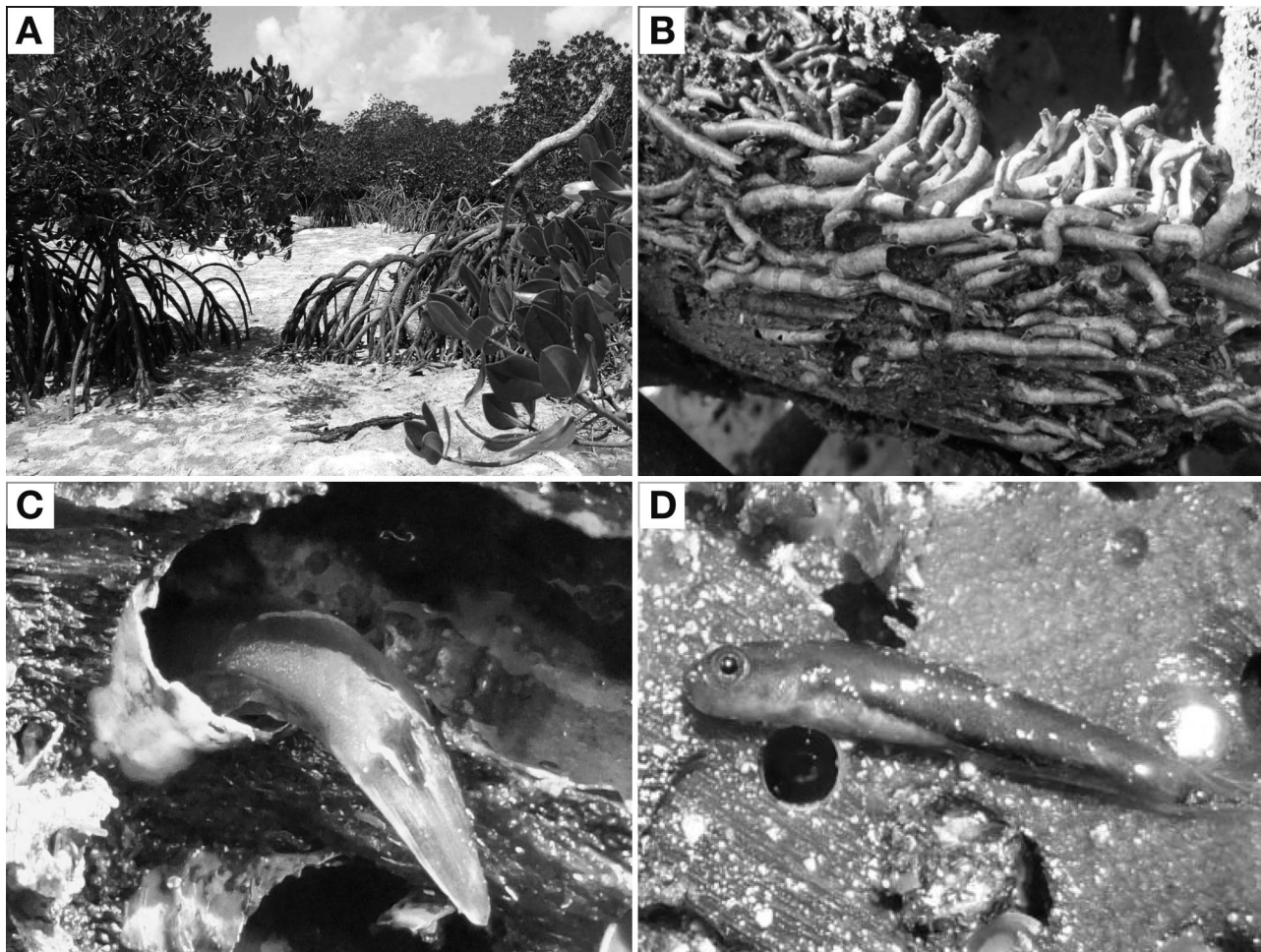
Fig. 1. Langira mangrove forest, Kaledupa Island, Tukang Besi Archipelago, Sulawesi: (A) the mid-intertidal zone of the forest, where at high tide, dartfish *Parioglossus interruptus* congregate between the immersed prop-roots; (B) heavily tunnelled mangrove wood, with calcareous linings of tunnels exposed by disintegration of the wood; (C) a dartfish within a closely fitting teredinid tunnel; and (D) a fully exposed dartfish lying on a cross-cut log with teredinid tunnels

(Fig. 1A). Fallen wood in these sites was heavily tunnelled by teredinids (Fig. 1B). Interrupted dartfish *Parioglossus interruptus* were commonly found within tunnels (Fig. 1C,D).

Dartfish had diameters that fell within the range of the most numerous tunnel diameters (Figs. 1 & 2A). Dartfish collected from shallow water between mangrove roots at high tide were significantly longer than those collected from within wood at low tide: 2.6 ± 0.02 cm (mean ± SE, n = 271) and 2.1 ± 0.03 cm (n = 188), respectively (Fig. 2B: 2-sample *t*-test; dartfish at high tide vs. dartfish in wood, $t = 14.48$, p ≤ 0.001).

Mean temperatures measured within emersed wood were lower than in tidepools adjacent to the wood (Fig. 3A,B: 2-way ANOVA, with wood/pool, emersion/immersion and night/day as factors, $F_{1,1272} = 61.68$, p < 0.001). This difference was more marked in the mid-intertidal zone (Fig. 3A). The temperature differential between tunnels in wood and adjacent tidepools was most marked when tidepool temperatures peaked (10:00 to 16:00 h; Fig. 3C,D), which occurred at low tide during daytime in the mid-intertidal (Tukey's pairwise comparisons).

When tunnelled wood was subject to airflow, temperatures were slightly reduced (approximately 1°C) at the surface, but by ≥2°C in the tunnels (Fig. 3E). The rate of cooling was 6.7 times greater inside decaying wood than at the surface, because more water was retained per unit surface area in the tunnels compared to the wood surface. The mean rate of cooling on the wood surface was $0.03 ± 0.01$°C min$^{-1}$, and the rate of cooling within the wood was $0.2 ± 0.01$°C min$^{-1}$ (mean ± SE, n = 45 in both cases).

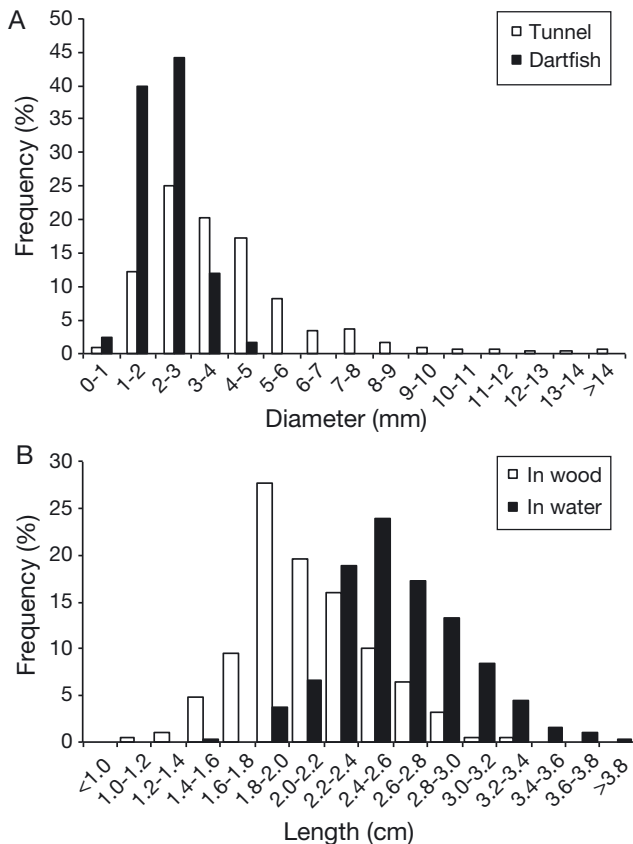The CTM of dartfish acclimated to 27°C, measured without teredinid tunnel cover, was 41.1 ± 0.3°C

Fig. 2. *Parioglossus interruptus.* (A) Size distributions of dartfish diameters (n = 168, black bars) compared against teredinid tunnel diameters (n = 1455, black bars); (B) size distributions of dartfish removed from woody detritus (n = 188, white bars) at low tide and dartfish captured during high tide between prop-roots (n = 271, black bars)

(n = 20). The CTM of dartfish acclimated to 35°C, measured without tunnel cover, was significantly higher: 42.9 ± 0.1°C (ANOVA, with acclimation temperature and tunnel position as factors; $F_{1,53} = 183.47$, $p \leq 0.001$). This is an acclimation response of an increase of 1.8°C, or 0.23°C of tolerance for every 1°C increase in acclimation temperature. There was no difference between fish CTM with and without tunnel cover, within either acclimation treatment (Fig. 4: ANOVA, $F_{1,53} = 0.72$, $p = 0.401$).

There was no significant difference in the volume of dead wood available to dartfish at different tidal heights (1-way ANOVA, $F_{2,16} = 1.11$, $p = 0.354$). Analysis of LWD samples revealed that wood with a higher percentage surface area of teredinid tunnelling had a greater frequency of dartfish occupying the vacant tunnels (Fig. 5; chi-squared $p \leq 0.001$).

The degree of tidal emersion also affected the degree of LWD occupancy of dartfish (Fig. 6). With increasing emersion time (h), the amount of wood occupied by dartfish was markedly reduced. The greatest proportion of wood occupied by dartfish was collected in areas of the mangrove with <5 h of emersion (chi-squared $p \leq 0.001$).

Dartfish abundance during daytime high tide within the Langira forest was significantly higher between *Rhizophora* roots than in open channels (11 433.3 ± 1690.7 compared with 222.2 ± 156.5 fish ha$^{-1}$ of total forest, mean ± SE, paired *t*-test: open channels vs. roots, $t = -5.57$, $p < 0.001$). Within the forest, approximately 50% of the area was covered by roots and 50% consisted of open creeks. No dartfish were found between roots or in open channels during high tides at night-time (22:00 to 03:00 h), and no dartfish were observed in creeks at low tide during daytime (07:00 to 16:00 h). The number of dartfish estimated to be in LWD during low tide in the Langira forest was 4304.5 ± 805.7 fish ha$^{-1}$ of total forest.

Observations of fish in aquaria containing pieces of teredinid tunnel linings revealed a significant difference of use in the tunnels between day and night. The majority of night-time observations of fish location were of fish within the linings (88.2%), while the majority of daytime observations were of fish free in the water (84.4%) (percentages relate to 4200 observations each for daytime and night-time conditions, chi-squared, $p < 0.001$).

## DISCUSSION

The observed daytime abundance of swimming dartfish *Parioglossus interruptus* at high tide, but absence during night-time high tides, indicates a pattern of activity consistent with diurnal zooplanktivory, which is the mode of feeding ascribed to the genus *Parioglossus* (Keith et al. 2004). This diurnal activity pattern was also evident in the laboratory, where inactive fish were found to take refuge in teredinid tunnels at night. Unfortunately, night-time sampling of dartfish within wood was not done, but a substantial proportion of the dartfish population was found to take refuge in tunnelled wood during daytime low tides. The shift from foraging to hiding could be triggered by a change in water depth, as is the case for the 4-eyed fish *Anableps*, which also forages between mangrove roots at high tide (Brenner & Krumme 2007). Such a trigger could account for the higher intensity of crypsis in wood near the seaward margin of the forest. Taken together these observations indicate day-time foraging during periods of tidal immersion and use of the tunnelled wood refuge at low tide and at night.
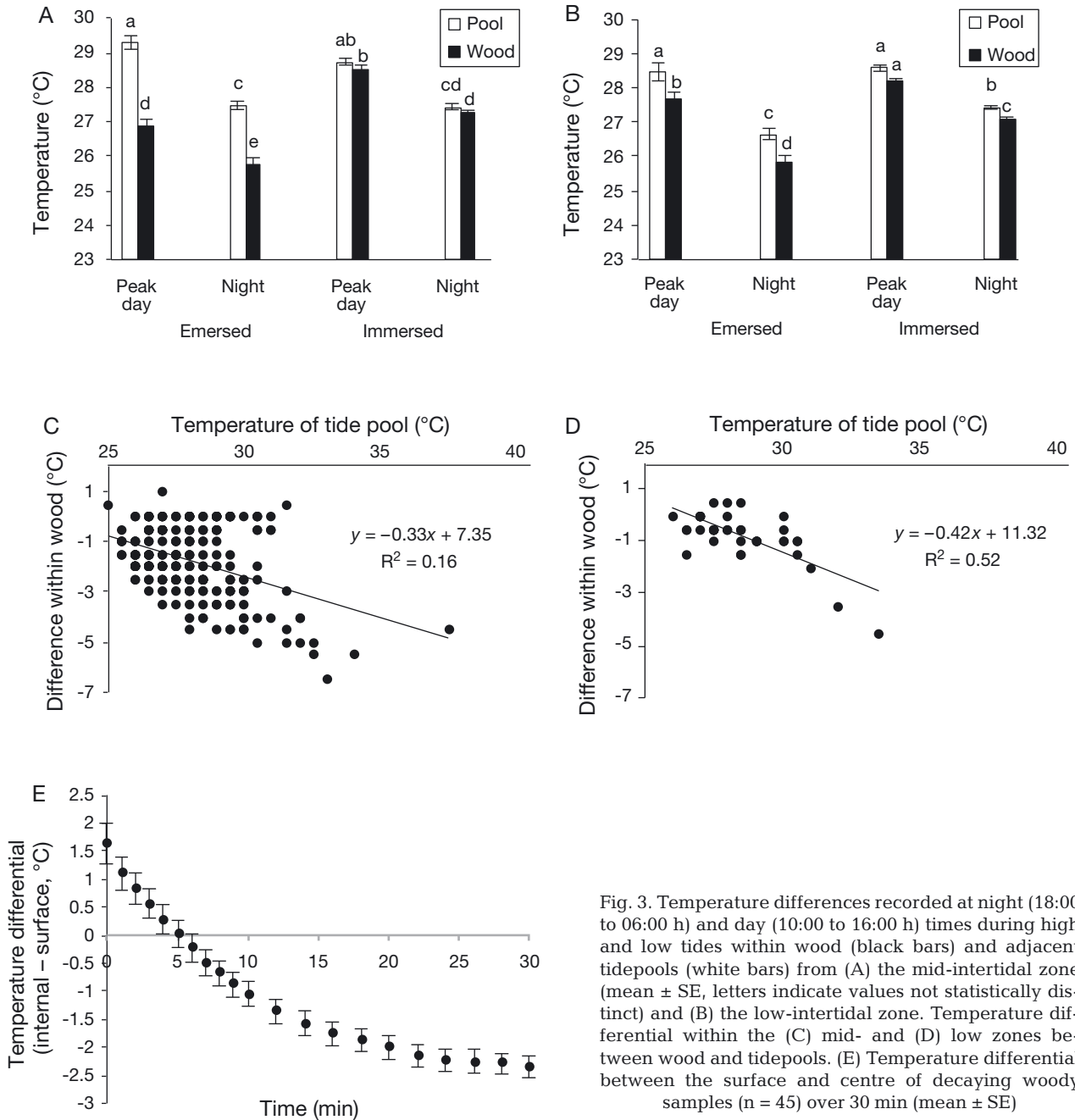
Fig. 3. Temperature differences recorded at night (18:00 to 06:00 h) and day (10:00 to 16:00 h) times during high and low tides within wood (black bars) and adjacent tidepools (white bars) from (A) the mid-intertidal zone (mean ± SE, letters indicate values not statistically distinct) and (B) the low-intertidal zone. Temperature differential within the (C) mid- and (D) low zones between wood and tidepools. (E) Temperature differential between the surface and centre of decaying woody samples (n = 45) over 30 min (mean ± SE)

This use of teredinid tunnels by dartfish is an unusual and virtually unknown behaviour among fishes, although juvenile moray eels have also been reported to occasionally occupy tunnelled wood, as do a range of marine invertebrates and terrestrial arthropods (Cragg & Hendy 2010). In tropical Atlantic mangroves, the mangrove rivulus *Kryptolebias marmoratus* exploits galleries created by terrestrial insects in decaying mangrove logs (Taylor et al. 2008)—a similar niche, but distinctly higher in the intertidal than the teredinid-tunnelled wood exam-

ined in this study. Indeed, mangrove rivulus are amphibious, even to the point of foraging on land, and may also emerge under damp leaf litter, in crab tunnels and beneath plastic debris (Davis et al. 1995, Taylor et al. 2008). Dartfish, however, appeared to be specifically bound to the teredinid-tunnel niche, and the alternative niches used by rivulus were not common in the intertidal range occupied by dartfish at the sites examined in this study. The niche provided by tunnelled wood could provide protection for dartfish from thermal stress, desiccation and predation.
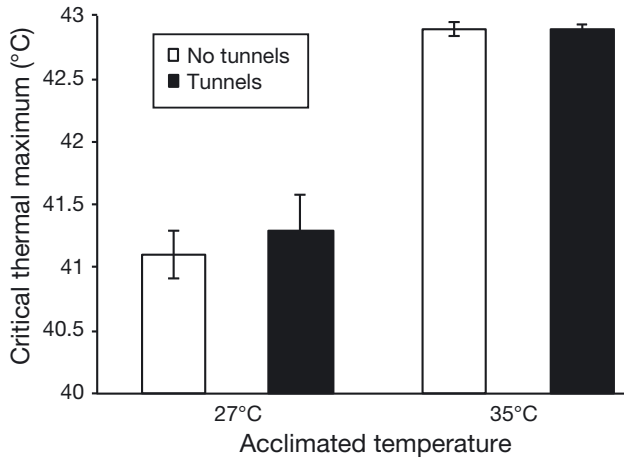
Fig. 4. *Parioglossus interruptus.* Critical thermal maxima of dartfish (n = 60). Fish acclimated to 27 and 35°C showed no difference in temperature tolerance with (black bars) or without (white bars) tunnels. Significant differences in temperature tolerance between fish acclimated to 27 and 35°C were found (mean ± SE)
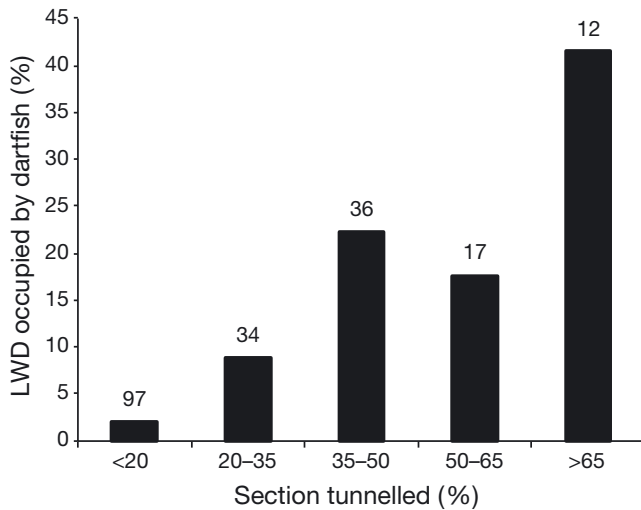


Fig. 6. *Parioglossus interruptus.* Variation of occupancy of large woody debris (LWD) by dartfish with length of tidal emersion over a 24 h period. Numbers above the bars indicate the number of pieces of wood analysed



Fig. 5. *Parioglossus interruptus.* Variation in occupancy of large woody debris (LWD) samples by dartfish with the level of teredinid tunnelling, as measured by the percentage of wood longitudinal section occupied by tunnels. Numbers above the bars indicate the number of LWD samples analysed

Dartfish show similar thermal tolerance values to many shallow water fishes in the Tukang Besi Archipelago, particularly tidepool-resident goby species (Eme & Bennett 2009b). Approximately 60% of the 65 species captured from shallow, near-shore regions such as mangroves, tidepools and seagrass beds around one of these islands are able to acclimate to temperatures of 35°C or more (Bennett 2010). Dartfish show approximately twice the acclimation response of tidepool-resident gobies (0.23°C of upper
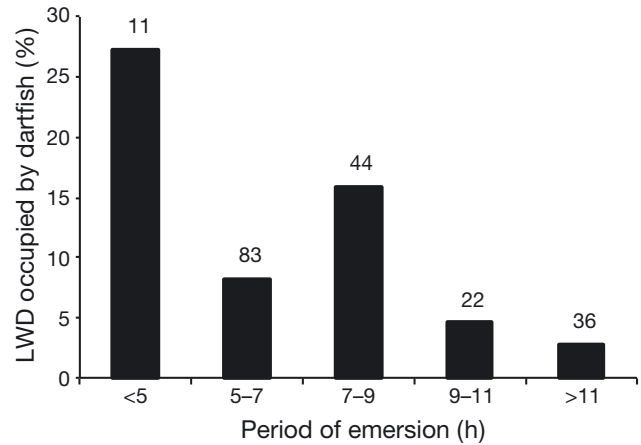
thermal tolerance per degree increase in acclimation, compared with 1.3°C) and also have CTM that are higher than those of reef fish species (Eme & Bennett 2009b). Thus, dartfish thermal biology is that of a robust, shallow-water fish that has an upper thermal tolerance sufficient to deal with temperatures >40°C. Though exposed logs and the adjacent tidepools may be affected by rapid fluctuations in temperature on a scale of minutes to hours (Taylor et al. 2005, Bennett 2010), temperatures measured in our study in tidepools near LWD are unlikely to be limiting. Nonetheless, dartfish would have a lower metabolic rate inside the cooler tunnels, which would reduce the metabolic cost of the cryptic period. The tunnel environment is likely to retain water and thus will also reduce the risk of desiccation. Cryptic niches are typically exploited by animals to avoid predation (Ruxton et al. 2004). Within teredinid-attacked wood, dartfish fit teredinid tunnels quite closely so that they will encounter predators no larger than themselves and only predators capable of locomotion and feeding within the tunnel environment. By occupying teredinid tunnels, dartfish avoid being stranded on mud flats or being carried by the ebbing tide into open water where there is no protection from predators such as piscivorous birds and larger fish. Free-swimming dartfish favour areas with mangrove roots over open water, possibly another predator-avoidance strategy for small and juvenile fish (Laegdsgaard & Johnson 2001, Verweij et al. 2006, MacDonald et al. 2009).

If the dartfish found in LWD at low tide belong to the same population of fish as that sampled between the roots and in open channels at high tide, the esti-

mates in this study suggest that almost 40% of dartfish from the Langira mangrove seek teredinid-attacked LWD at low tide during the day. The fish in tunnelled wood are smaller than those caught from between roots at high tide and also smaller than the reported adult maximum of 3 cm (Allen et al. 2003). Vulnerable juveniles appear more likely to seek refuge in wood than fully grown adults, and thus teredinid-tunnelled wood is likely to be a key refuge for juveniles of this species.

While the ecosystem service derived from dead wood in the form of carbon flux has been well-documented (Robertson 1991, Kathiresan & Bingham 2001), the role of this resource in supporting biodiversity is less well understood. This study gives an example of how biodiversity supports ecosystem services for one species, but a wide range of other species exploit this niche (Cragg & Hendy 2010). In any planning for management of mangrove ecosystems, particularly where timber harvesting is involved, care should be taken to ensure that sufficient dead wood is retained within the ecosystem to protect such ecosystem services.

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