BEHAVIOURAL, PHYSIOLOGICAL, AND ECOLOGICAL ASPECTS OF THE AMPHIBIOUS LIFE OF THE PEARL BLENNY *ENTOMACRODUS NIGRICANS* Gill

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Abstract: *Entomacrodus nigricans* Gill is a herbivorous blennioid fish that occurs in high densities on wave-swept, upper intertidal regions of San Andrés Island, Colombia, and at various locations along the Caribbean coast of Panamá. The habitat of this fish requires it to endure alternating periods of intense water turbulence and total emersion, and the pearl blenny depends upon its amphibious capabilities both to maintain position and move in this environment. Orientation studies show that this species is a capable jumper and terrestrial navigator, able to move in the direction of the sea even when water is not in a direct line of sight. The eyes of this fish appear modified for aerial vision. The pearl blenny does not make long, amphibious sojourns and is much less tolerant of air exposure than are more terrestrial species such as mudskippers and rockskippers. When exposed to air by a retreating wave, the pearl blenny continues to ventilate, using water around its body, and then finally gulps air and seals its mouth and opercula. The combined effects of both temperature and humidity determine the air-exposure tolerance of the pearl blenny. Mean survival time of fish exposed to air was 7.5 min in direct sunlight, 168 min in shade, and 228 min at night. Fish exposed to water-vapor saturated air at 25 °C have a mean O_2 consumption rate of $306 \ ml \cdot kg \cdot h^{-1}$, which is not significantly different from rates measured for fish in water. Pearl blennies cannot survive extended exposure to humidities $<80\%$. Amphibious behaviour allows the pearl blenny to exploit supralittoral resources and probably resulted from competition amongst intertidal fishes for space and other resources.

Key words: fish air breathing; amphibious fish behaviour; intertidal fish; Blenniidae; *Entomacrodus nigricans*

INTRODUCTION

This paper reports on the major behavioural and physiological adaptations for and ecological aspects of the amphibious life of the pearl blenny, *Entomacrodus nigricans* Gill. A number of intertidal fish species have independently evolved amphibious

behaviour as a means of avoiding predation and reducing competition while also gaining access to supralittoral resources (Zander, 1967, 1972b, 1983; Graham, 1976; Gibson, 1982; Bridges et al., 1984). These species exhibit a range of amphibious capabilities. Some mudskippers (*Periophthalmus*), for example, spend as much as 90% of their lives out of water (Gordon et al., 1978). By contrast, several species of blennies (*Andamia*, Rao and Hora, 1938; *Blennius, Alticus*, and *Coryphoblennius*, Zander, 1967, 1972b, 1983) and some gobies (*Gobionellus*, Todd, 1976) make brief terrestrial sojourns into the supralittoral zone or are only exposed to air for a matter of seconds during the interval between breaking waves.

Comparative studies show that the highly amphibious fish species have greater capacities for aerial respiration, desiccation and air-exposure resistance, and have also progressed toward solutions of physiological problems related to ion regulation and nitrogen excretion in air (Graham, 1976; Gordon et al., 1978; Iwata et al., 1981). Specializations for terrestrial behaviour and locomotion and for aerial sensory perception are also more prominent in species that are highly amphibious (Graham, 1970, 1971, 1973; Zander, 1972a, 1974; Todd, 1976; Davenport & Woolmington, 1981). Although our knowledge of terrestrial adaptations is fairly extensive in some fishes, we have little insight into the types of adaptations that may have played a role in the early evolution of amphibious behaviour amongst intertidal fishes. A species that makes very brief terrestrial excursions may be, compared with highly amphibious fishes, relatively unspecialized for amphibious life. However, it might be expected to possess morphological, physiological, and behavioural adaptations that distinguish it from fishes that never leave water. Both Todd (1976) and Graham (1976) suggested that behavioural rather than physiological adaptations for terrestrial life may be more prominent in briefly amphibious species. To examine this hypothesis, we carried out a study of the amphibious life of the pearl blenny *Entomacrodus nigricans*, a species that makes very brief terrestrial excursions and often occupies wave-swept areas where it is alternately exposed to air and deluged by water. We examined the distribution and abundance of the pearl blenny in the littoral and supralittoral zones. Its capacity for terrestrial orientation and its tolerance of air exposure were determined. We also studied its air-gulping behaviour and measured its rate of aerial oxygen consumption. The pearl blenny occurs in the western Atlantic Ocean from Brazil to Bermuda, throughout the Caribbean Sea and in the southern parts of the Gulf of Mexico (Springer, 1967). It is restricted to rocky shores and tide pools and seldom occurs deeper than 2 m.

MATERIALS AND METHODS

Field and laboratory investigations of *E. nigricans* were carried out at San Andrés Island, Colombia (Fig. 1) and in Panamá. At San Andrés we studied the community structure of fishes in the upper intertidal zone, including the distribution and abundance of the pearl blenny, its size range, activity patterns, and feeding habits. Pearl blennies collected in surveys were used in tests of jumping, orientation, and navigation abilities,
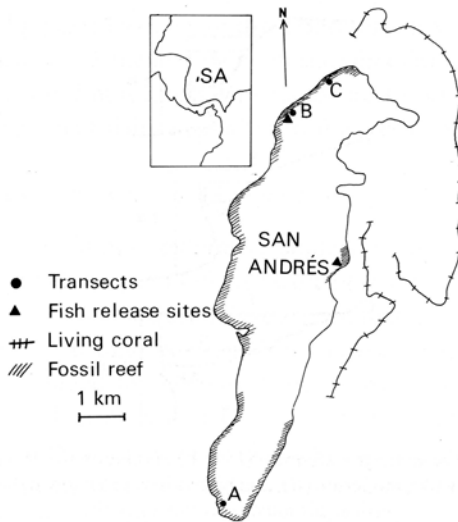
Fig. 1. Fish study sites and general features of San Andrés Island, Colombia: inset shows island location in the Caribbean Sea.

of survival times in air, and for analyses of stomach contents. Measurement of aquatic and aerial oxygen consumption rates ($\dot{V}O_2$) and determination of ventilatory responses of fish abruptly shifted from water to air were made using fish collected in Panamá.

FIELD SURVEYS

The coastline of San Andrés Island consists largely of fossilized, uplifted coral reef (Fig. 1) that has been eroded by wave action and contains many pools and perpendicular surge channels. Along most of the island's coast, *E. nigricans* and other fishes inhabit the area extending from the algal ridge (located at mean lower low water) on the low side to the upper limit of the pools regularly flooded by wave action (Fig. 2). To study the effect of wave action on fish distribution, abundance and diversity, we selected three study habitats (Fig. 1) characterized by low, moderate, and high wave energies. Transects (25×1 m) positioned at the water's edge and parallel to the shore line were surveyed at each study site, and the number of pearl blennies and other fish species was determined. As is the case at most Caribbean Islands, the diurnal tidal range at San Andrés is <0.5 m, and we thus did not have to reposition our survey transects because of tidal change. Fish were censused by netting as many as possible and by visually estimating numbers of escapees. The transect position and total length (TL) of each collected fish were noted. In addition, each habitat was searched shoreward from the algal ridge to determine the upper limit of pearl blenny distribution. About 20 periods of observation were made on blenny behaviour in the three habitats. These were made over 3 days in periods lasting 1–2 h and most (80%) were in daylight (0800–1700). Observers used 7×35 mm binoculars which were supplemented at night by headlamps.
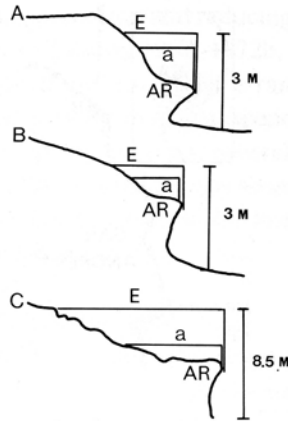
Fig. 2. Distribution range of *Entomacrodus nigricans* (Line E) in relation to the algal ridge (AR) and benthic algal growth (Line a) in the low (A), moderate (B), and high (C) wave energy habitats on San Andrés Island: vertical distances (m) not to scale.

Except when we moved rapidly or approached to within 1 m of a fish, these techniques did not seem to affect fish behaviour.

TERRESTRIAL ORIENTATION EXPERIMENTS

The terrestrial jumping ability of fish of different TL was tested on both moist and dry surfaces. Collected fish were transported in covered buckets to a flat concrete deck, and, as individuals were released in the center of this area, the length of their first jump was measured. The jumps of 12 fish on the dry deck were compared to those of 19 fish which were released just after several buckets of seawater had been splashed over the deck surface. The importance of environmental cues that might facilitate orientation by providing information about the direction of the sea was investigated by scoring the direction of movement of fish released on land. Fish were transferred to flat, supralittoral locations adjacent to their area of capture. (The two-lane highway that extends around the perimeter of San Andrés proved ideal for these tests.) Individual fish were released onto a wet surface and immediately subjected to one of three potentially confusing circumstances: (a) constant water splashing (spray) from the direction opposite to true ocean direction; (b) simulated wave surge (flow) from the side opposite to ocean direction; and (c) release onto a flat, wet surface that was slightly inclined in the direction away from the ocean. These and the jumping tests were conducted in daylight. Sun compass orientation was tested by transporting two groups of fish ($n = 9,10$) in darkly covered buckets to the opposite side of the island (Fig. 1) from where they were collected, and by determining their direction of movement and their relative position at 1 to 3 min following release. In these tests, all fish in the group were released together and in close proximity (30–50 cm) to one another onto the wet surface of the highway.

In the course of holding pearl blennies in the laboratory, it was noted that fish which jumped to the floor always seemed to move in the direction of window light. To test the role of light in terrestrial movement, the responses to polarized and incandescent light were compared for eight fish released onto the wet floor of a darkened room.

EXPOSURE RESISTANCE AND AERIAL RESPIRATION

Twenty-one fish were used in comparative studies of air-exposure tolerance. Three groups of four fish each (TL range, 5–10 cm) were placed in a dry bucket and exposed to three different conditions – direct mid-day sunlight, mid-day shade, and night exposure – and the survival time of each fish was recorded. The effects of relative humidity (RH) were examined by comparing the survival time of five fish exposed to humid air on a moist substratum to RH $\geqslant 95\%$ (30 °C) and four fish exposed to 80–90% RH (30 °C). In these tests, RH was controlled by aerating a beaker of water in the covered test aquarium. RH was monitored with a hygrometer. Respirometry and studies of aerial and aquatic ventilation rates were conducted at the Smithsonian Tropical Research Institute Marine Laboratory in Panamá. Habitats similar to San Andrés occur along the Caribbean Coast of Panamá at Galeta Island, Maria Chiquita, and Pico Feo in the San Blas Archipelago, where fish for these studies were collected. Aerial oxygen consumption rate ($\dot{V}O_2$) was determined using a volumetric respirometer. A Clark oxygen electrode installed in a closed system respirometer was used to measure aquatic $\dot{V}O_2$. Methods for both of these techniques are described in Graham (1973). The effects of sequences of rapid submersion and emersion on opercular ventilation patterns were observed for fish placed in a plastic Petri dish that was tilted slightly and fitted with a small diameter (2 mm ID) tube in its floor, through which the water level could be rapidly raised and lowered (by a 50-ml syringe), thus either emersing or submersing the fish.

RESULTS AND DISCUSSION

FISH DISTRIBUTION AND ABUNDANCE

Entomacrodus nigricans was the dominant species in each of the three habitats, comprising $> 70\%$ of the fish population (Table I). Its density was significantly higher ($P < 0.01$, $\chi^2 = 29.85$, df = 2) in the high energy habitat. Other species observed along the transects were: *Bathygobius soporator* (Cuvier and Valenciennes), the second-most abundant fish, *Tomicodon fasciatus* (Peters), *Blennius cristatus* Linnaeus, *Muraena miliaris* (Kaup), and *Labrisomus nuchipinnis* (Quoy and Gaimard). Total fish density along the water line was also significantly higher in the high-energy habitat ($P < 0.01$, $\chi^2 = 29.85$, df = 2). From the algal ridge to the upper limit of pearl blenny distribution (Fig. 2) pool substratum (background) color became lighter as algal density decreased and mean tidepool depth was less. All of the ≈ 100 blennies collected in the higher parts

TABLE I

Upper littoral zone fish abundance and density estimates for 25 m transects in low (A), moderate (B), and high (C) wave-energy habitats on San Andrés Island: abundance values are $\bar{x}$ number and, in parentheses, the % of total fish.

	Transect		
	A	B	C
Abundance			
Entomacrodus nigricans	13.5 (71)	21.0 (81)	43.5 (70)
Bathygobius soporator	2.5 (13)	1.0 (4)	16.5 (27)
Other fish species	3.0 (16)	4.0 (15)	2.0 (3)
Total fish present	19.0	26.0	62.0
Ratio: *Entomacrodus/Bathygobius*	5.4	21.0	2.6
Density (no. $\cdot$ m^{-2})			
E. nigricans	0.54	0.84	1.74
All fish	0.76	1.04	2.48

of the habitat (2.5 m above the algal ridge) were lighter in color, presumably as a result of crypsis, and smaller (4 cm TL, 0.3–2.0 g) than the ≈ 50 fish (7 cm TL, 6–10 g) found just above the algal ridge. Many pools contained more than one fish, but we rarely saw more than one of medium size (5–7 cm TL, ≈ 3–5 g). Large fish (7 cm TL, ≈ 25 were observed) occurred alone and usually in pools deeper than 20 cm that were located within 1 m of the algal ridge (Fig. 2). These pools had a very dark background color owing to dense clusters of algae.

FEEDING AND ACTIVITY PATTERNS

The pearl blenny is a herbivore and, except in the higher regions of its habitat, food does not appear to be a limiting resource. Algae were present in the stomachs and intestines of fish ($n \simeq 9$) collected during the day (1000), but stomachs of fish ($n \simeq 11$) taken at night (2200) were nearly empty, indicating that this species is a daytime feeder. Regardless of collection site, the stomachs of most fish contained uniserate algae similar in structure to the filamentous brown types common on the algal ridge and lower pool area. (Four genera of alga were identified by Dr. C. Birkeland in material scraped from these areas: *Turbineria, Padina, Dictyopterus*, and *Laurencia*.) Although small fish were observed to graze on blue-green algae in higher pools, these were not detected in their guts.

Pearl blennies are diurnally active. During 4 h of night observation (2100–2200 and 0430–0530) on two separate days, fish remained motionless 98% of the time; they moved occasionally during the remaining time but were not observed to feed. Fish observed at night, in one spot, could often be found later at the same site, suggesting that they were inactive at night and that our lights did not disturb them. During 16 h

of daylight observation, small- and medium-sized fish spent about the same percentage of time feeding: small 27% ($n = 74$), medium 15% ($n = 81$). Nursall (1981) reported that *Ophioblennius*, another Caribbean intertidal blenny, also did not spend large amounts of time feeding. Time spent motionless or in short movements within or between pools accounted for 62% of the time that small *Entomacrodus* were observed (5.2 h) and 84% of the observation time (5.4 h) on medium-sized fish. Small fish engaged in interspecific aggression $\approx 12\%$ of the observation time, medium-sized fish for $\approx 1\%$. This usually involved rapid swimming by one individual towards another without contact, after which both retreated to crevices. Aggression was also seen in small fish when they encountered large conspecifics in lower area pools. Large fish ($n = 82$) were not observed to feed during 5.4 h of observation and were always less active than smaller fish, with movement accounting for only 1% of the observation time. They did not defend territories nor did they exhibit antagonistic displays to smaller conspecifics.

Small fish frequently made directed movements between upper and lower pools. Our observations suggest that small pearl blennies move to lower areas to avoid extreme conditions and to obtain preferred food. This study documented the presence of more diverse algal stands on lower areas, and it is generally the case that high littoral pools become heated by the sun during daylight hours (Gibson, 1982). Thus we attribute the more aggressive behaviour of small fish to both a possibly greater level of conspecific resource competition in the upper reaches of the habitat, as well as the temporary need to occupy space within the domains of larger fish. Although large fish did not appear territorial, we speculate that the presence of larger fish and the smaller blenny's lack of cryptic coloration ultimately required return to higher areas. In spite of an energetic cost associated with movement, the upper range of the pearl blenny habitat may serve both as a safe nursery ground for immature fish and an adequate transitional habitat for younger members of the species waiting for the opportunity to take up residence in lower areas. A similar size-vertical distribution pattern was described for the amphibious Chilean clingfish (*Sicyases*) by Ebeling *et al.* (1970).

EMERSION, JUMPING, AND ORIENTATION TO THE SEA

Pearl blennies were seldom observed to spend > 10 s out of water. When a fish was exposed by a receding wave, it would either hold its position and wait for the next surge of water or, if this did not occur quickly, it would jump toward the surf or into a pool. Fish were observed to ride with waves to new locations but not purposely to climb out of water, as has been seen in mudskippers (*Periophthalmus*) and rockskippers (*Mnierpes*, Graham, 1970, 1973). The pearl blenny is specialized for amphibious locomotion and for orientating while out of water. When approached from land or from along the water line, the fish escapes by jumping, occasionally as far as 1 m, in the direction of sea. Maximum first-jump distance off a wet surface increased significantly with fish TL (Fig. 3). On dry surfaces fish tended to become stuck, and no significant relationship between TL and distance was found.
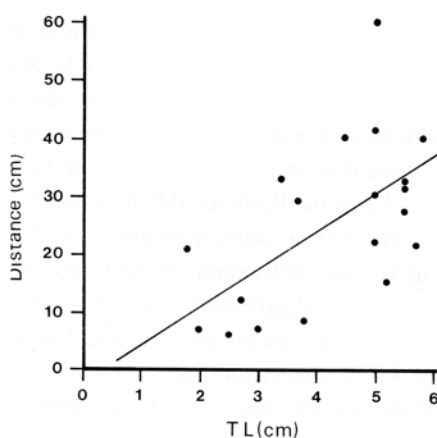
Fig. 3. Relationship between body length and jumping distance for *Entomacrodus nigricans* on wet pavement: equation for line, Y (cm) = − 2.59 + 6.43 TL (cm), $r = 0.59$, $P < 0.05$, $n = 19$).

In its habitat *Entomacrodus nigricans* probably remains orientated to sea direction through water flow and topographic (slope, landmark) cues. While this fish would be expected to have good aquatic vision, the cornea of its eye also appears to have become slightly flattened (Fig. 4) which, by allowing for the uniform refraction of parallel light beams impinging on this surface, probably also improves its aerial vision (Graham, 1971; Zander, 1974). Thus, whether in or out of water, a pearl blenny could rely on vision to orientate. Our observations indicated that amphibious *Entomacrodus* always move towards water, and our experiments demonstrated that this fish can move toward the sea even without familiar landmarks and when water is not in its direct line of sight. Fish ($n = 29$) transferred to supralittoral areas directly inland of capture site (50–100 m from water) consistently made, upon release, directed jumps toward the ocean. None of the experimental treatments (water flow and spray, simulated wave action, slope) which might have signaled a closer water source in a different direction interfered with this strong directional response. Fish released on nearly the opposite side of San Andrés Island from where they were caught also showed the appropriate directional response to the adjacent ocean (Table II). By 2 min after release, nearly all fish in both transplanted groups had jumped in the direction of water ($\chi^2 = 21.1$, $P < 0.001$, df = 18), indicating that a sun compass response is not involved in this orientation. In addition, all eight fish released in a darkened room had moved toward both polarized and incandescent light sources within 3 min, regardless of their direction relative to the sea. Simultaneous testing with both lights at opposite ends of the room, however, resulted in random movements. Several factors are probably involved in the directional escape and orientation responses of *E. nigricans* in its natural environment, since these were observed to occur at night as well as in tests with fish released inside a darkened room.
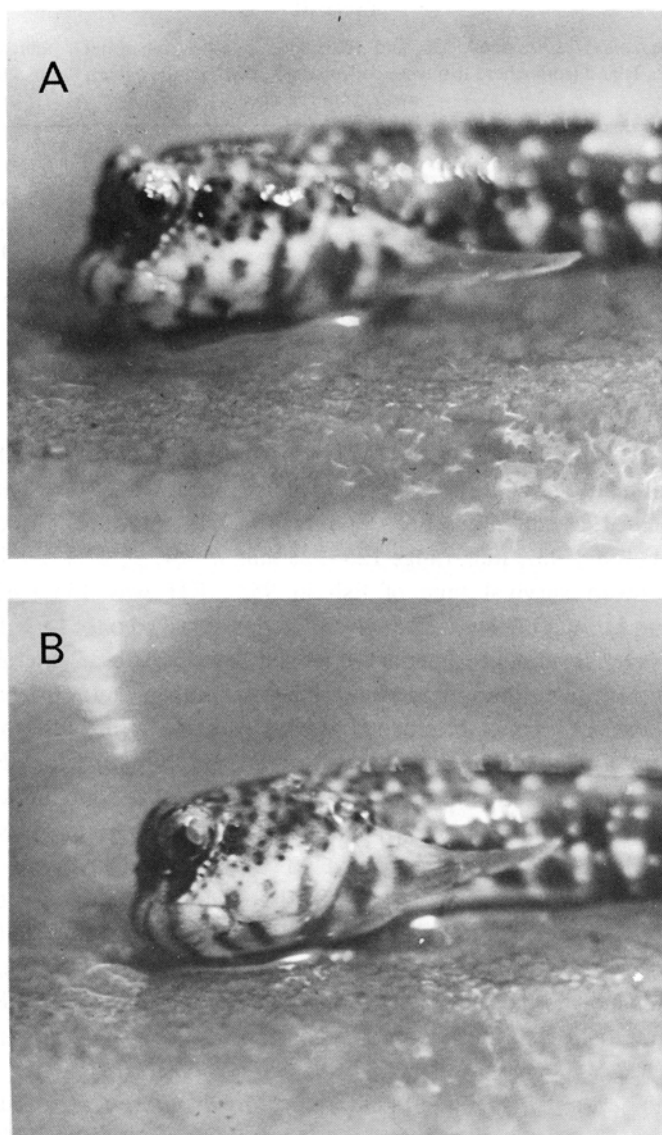
Fig. 4. A, a 4.5-cm *Entomacrodus nigricans* ventilating its gills with residual water around its body following exposure to air. B, an air gulp showing the bulged opercular chamber; faceted corneal surface is evident (see text).

PHYSIOLOGICAL ADAPTATIONS FOR AIR EXPOSURE

The survival time of pearl blennies exposed to air is affected by both air (T_a) and substratum temperature (T_s), solar radiation, and RH. Four fish exposed to air in direct sunlight had a mean survival time of 7.5 ± 0.43 min ($\overline{x}$, SE, range 6–8 min), during which

TABLE II

Position of *Entomacrodus nigricans* 60, 120, and 180 s after release from a fixed point on the opposite side of San Andrés Island from where fish were collected: +, towards the ocean; 0, no change in position; −, away from the ocean.

Relative position (s)	Group release site					
	NW (*n* = 10)			SE (*n* = 9)		
	+	0	−	+	0	−
60	2	8	0	7	2	0
120	8	2	0	9	0	0
180	9	1	1	9	0	0

time T_s increased from 31.8 to 37 °C. (Medium and large fish were used in all tests.) Fish exposed at night (T_a 26.6–27.7 °C) survived significantly (Mann–Whitney U-test) longer ($\bar{x} = 228 \pm 19.1$ min, range 102–336 min, $n = 4$) than those exposed in the shade during daylight (168 ± 43.3 min, range 126–228 min, $n = 4$; T_a 27.0–29.5 °C). At a T_a of 30 °C, the mean survival time of fish in 95% RH was 135 ± 41 min (range 90–180 min, $n = 5$), but at a lower RH (80–90%) fish survived only 45 ± 11 min (range 11–68 min, $n = 4$). Tolerance of exposure by amphibious fishes generally correlates with natural emergence times, and the principal limiting factor for most species appears to be desiccation of respiratory surfaces (Graham, 1973; Gordon *et al.*, 1978). It is therefore not surprising that compared to other amphibious fishes *E. nigricans* is significantly less resistant to air exposure. Under similar test conditions (shade, high RH), rockskippers and mudskippers which typically spend longer periods out of water survived nearly 360 and 540 min, respectively (Graham, 1973).

Pearl blennies are capable of an aerial $\dot{V}O_2$ that is comparable to their aquatic rate (Graham, 1976). The mean of 16 aerial $\dot{V}O_2$ estimates for three small fish (0.36–0.79 g) was 306 ml·kg·h^{-1} (SE = 45.0) at 25 °C and 95% RH. At 80–90% RH, stable respiration could not be measured and fish quickly succumbed. But if RH was kept above 90% these fish were able to maintain a stable $\dot{V}O_2$ throughout a 120-min test period.

Observations on three fish (Fig. 5) held in a chamber where water could be rapidly added or removed revealed how 2 min of air exposure first affected opercular ventilation frequency and then led to air gulping. In water, these fish continuously ventilated their gills at a mean rate of 193·min^{-1} (Fig. 5). Following drainage of water from the chamber, the fish's opercular ventilation rate continued at a reduced frequency (105·min^{-1}) as the small amount of residual water from around their bodies was aspirated. When this water supply was exhausted, an air gulp was taken; mean time to the first air gulp was 48.7 ± 8.0 s (range 38–65 s, $n = 12$) after inital air exposure. Air gulps were usually held for 30–60 s; then, after a 3–5 s period of high-amplitude opercular air ventilations, another air gulp was taken. Flooding the experimental
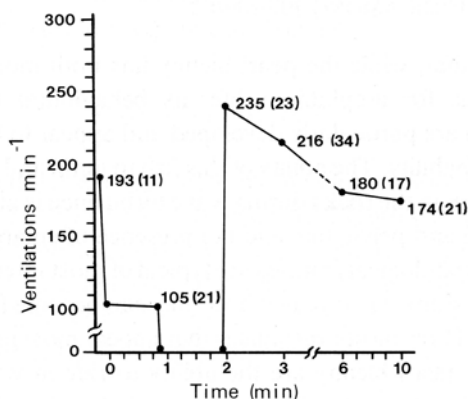
Fig. 5. Mean ventilation rate of *Entomacrodus nigricans* before, during, and after a 2-min exposure to air: initial ventilation rate in water is $193 \cdot min^{-1}$; at time = 0, water is drained from the chamber, the fish is exposed to air, and ventilation is reduced to just over 100; at near time = 50 s exposure the fish gulps air and stops ventilating; at 2 min the chamber is flooded, the fish ejects the gulped air and resumes ventilating water at a relatively faster rate; values are mean (2 SE), determined from observations on three small fish (n = 6); T_a = 23–25 °C, fish weight 0.4–1.1 g.

chamber with sea water resulted in a brief period of a more rapid aquatic ventilation frequency ($235 \cdot min^{-1}$, Fig. 5) which dropped to pre-air-exposure levels within 4 min. The mean ratio of pre- and post-air-exposure ventilation frequency (1.27) was similar for the three fish and was not changed by exposure times ranging from 50 s to 2 min.

Our observations suggest that the pearl blenny can normally continue to respire aquatically even after the upper parts of its body are exposed to air by a retreating wave. If a fish is situated in a small crevice, its supply of water for ventilation may be sufficient to last for several minutes. Moreover, its ventral mouth permits *Entomacrodus* to ventilate much of the residual water remaining, due to surface tension between its body and the adjacent substratum. When this water is used, the fish responds by gulping air and sealing its gill chambers. Air-gulping has also been observed in *Andamia* (Rao & Hora, 1938) and *Periophthalmus* (Stebbins & Kalk, 1961) and probably functions to prevent gill desiccation while also trapping a supply of moist air for gas exchange via the gills and vascular epithelium (Graham, 1976). For *Entomacrodus nigricans*, an air gulp appears to supply oxygen needs from the time water is no longer available until a wave again inundates the fish. The air gulps of this fish are held for short times compared to most air-breathing fishes and, according to field observations, it seems likely that if this fish is not covered by a wave within the time span of several air gulps it would re-enter water. We have observed a large number of capillaries on the ventral and lateral surfaces of *Entomacrodus*, and these may also function for aerial respiration (see Zander, 1972a; Graham, 1976). An increased ventilatory frequency following a return to water (Fig. 5) has been observed for several species (Rao & Hora, 1938; Graham, 1970) and may function to separate gill lamellae and to flush CO_2 from the blood, which cannot always be done effectively by fish exposed to air (Graham, 1976; Daxboeck & Heming, 1982).

AMPHIBIOUS BEHAVIOUR AMONG BLENNIES

Our study shows that, while the pearl blenny has both morphological and physio-logical specializations for amphibious life, its behavioural mechanisms related to terrestrial orientation are particularly developed and appear to be primarily responsible for its amphibious capability. The ability of this fish to jump and climb while out of water and to hold its position in the rocks during wave turbulence is attributable to a low body profile, large pectoral and pelvic fins and the presence of enlarged and incised anal fin rays. While these morphological features are typical of most intertidal blennies, Zander's (1972b) comparative study has revealed how they can become further elaborated for an amphibious lifestyle. Three motor responses that appear most important in the amphibi-ous behaviour of the pearl blenny are the ability to ride in waves to locations in the habitat, the orientation to water from land, and the air-gulping, opercular-sealing response that follows water subsidence. The contribution made to the aerial visual activity of this fish by its flattened corneas is important to all aspects of its terrestrial orientation. By contrast, the air-gulping response of this fish and its resistance to long-term air exposure are not well developed, relative to other amphibious species, and do not permit long-term air exposure. We conclude that the morphological and physiological specializations of pearl blennies work in concert with behavioral mecha-nisms to allow movements on land, brief exposure to humid air and the periodic return to lower regions of the habitat, especially for feeding.

The amphibious activities and behaviour of *E. nigricans* in the Caribbean are similar to those of *E. chiostictus* from Malpelo Island (J.B. Graham, pers. obs.) and to *E. marmoratus* in Hawaii (D.W. Strasburg, pers. comm.). Twenty-two species of *Entomacrodus* occur worldwide in tropical and subtropical littoral communities (Sprin-ger, 1967), and future studies will probably demonstrate amphibious behaviour in other members of this genus. Within the family Blenniidae, some level of amphibious behaviour is known to occur in ≈ 10 tropical species contained in six genera (Graham, 1976). The majority of species in these genera remain to be studied, but we suspect that many of them will prove capable of at least brief terrestrial excursions. Competition among blennies has frequently resulted in the evolution of amphibious species, particu-larly in high wave energy tropical habitats (Zander, 1972a,b, 1974). The presence of morphological preadaptations coupled with the acquisition of adaptations for brief exposure, orientation, and locomotion would enable a blenny to establish itself in the extreme upper intertidal zone, where it could flourish and achieve a large population density as does *Entomacrodus* at San Andrés and Malpelo Islands (McCosker & Rosenblatt, 1975). By becoming specialized for this habitat and amphibious life, a species escapes competition from many other littoral organisms and due to the rough topography and surf conditions is, as well, relatively free of avian and terrestrial predators (Graham, 1976; Gibson, 1982). Since most blennies are herbivores, a high littoral habitat does not seriously compromise food access. Continuous surf action ensures the growth of large quantities of algae within areas occupied by *Entomacrodus*

on San Andrés, and our observations show that, as in other blennies (Nursall, 1981; Gibson, 1982), minimal times are required for feeding.

REFERENCES

BRIDGES, C.R., A.C. TAYLOR & S.J. MORRIS, 1984. Ecophysiological adaptations in *Blennius pholis* (L.) blood to intertidal rock pool environments. *J. Exp. Mar. Biol. Ecol.*, Vol. 77, pp. 151–167.

DAVENPORT, J. & A.D. WOOLMINGTON, 1981. Behavioural responses of some rocky shore fish exposed to adverse environmental conditions. *Mar. Behav. Physiol.*, Vol. 8, pp. 1–12.

DAXBOECK, C. & T.A. HEMING, 1982. Bimodal respiration in intertidal fish *Xiphister atropurpureus* (Kittlitz). *Mar. Behav. Physiol.*, Vol. 9, pp. 23–33.

EBELING, A.W., P. BERNAL & A. ZULETA, 1970. Emersion of the amphibious Chilean clingfish, *Sicyases sanguineus. Biol. Bull. (Woods Hole, Mass.*), Vol. 139, pp. 115–137.

GIBSON, R.N., 1982. Recent studies on the biology of intertidal fishes. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 20, pp. 363–414.

GORDON, M.S., W.W. -S.NG & A.Y. -w.YIP, 1978. Aspects of physiology of terrestrial life in amphibious fishes. III. The Chinese mudskipper *Periophthalmus cantonensis. J. Exp. Biol.*, Vol. 72, pp. 57–75.

GRAHAM, J.B., 1970. Preliminary studies on the biology of the amphibious clinid *Mnierpes macrocephalus. Mar. Biol.*, Vol. 5, pp. 136–140.

GRAHAM, J.B., 1971. Aerial vision in amphibious fishes. *Fauna. Rancho Mirage, California*, Vol. 3, pp. 14–23.

GRAHAM, J.B., 1973. Terrestrial life of the amphibious fish *Mnierpes macrocephalus. Mar. Biol.*, Vol. 23, pp. 83–91.

GRAHAM, J.B., 1976. Respiratory adaptations of marine air-breathing fishes. In, *Respiration of amphibious vertebrates*, edited by G.M. Hughes, Academic Press, London, pp. 165–187.

IWATA, K., I. KAKUTA, M. IKEDA, S. KIMOTO & N. WADA, 1981. Nitrogen metabolism in the mudskipper, *Periophthalmus cantonensis*: a role of free amino acids in detoxication of ammonia produced during its terrestrial life. *Comp. Biochem. Physiol.*, Vol. 68A, pp. 589–596.

McCOSKER, J. & R.H. ROSENBLATT, 1975. Fishes collected at Malpelo Island. *Smithson. Contrib. Zool.*, Vol. 176, pp. 91–93.

NURSALL, J.R., 1981. The activity budget and use of territory by a tropical blenniid fish. *Zool. J. Linn. Soc.*, Vol. 72, pp. 69–92.

RAO, H.S. & S.L. HORA, 1938. On the ecology, bionomics, and systematics of blenniid fishes of the genus *Andamia* Blyth. *Rec. Indian Mus.*, Vol. 40, pp. 377–401.

SPRINGER, V.G., 1967. Revision of the circumtropical shorefish genus *Entomacrodus* (Blenniidae: Salariinae). *Proc. U.S. Nat. Mus.*, Vol. 122, pp. 1–150.

STEBBINS, R.C. & M. KALK, 1961. Observations on the natural history of the mudskipper *Periophthalmus sobrinus. Copeia*, 1961, pp. 18–27.

TODD, E.S., 1976. Terrestrial grazing by the eastern tropical Pacific goby *Gobionellus sagittula. Copeia*, 1976, pp. 374–377.

ZANDER, C.D., 1967. Beiträge zur Ökologie und Biologie litoral bewohnender Salariidae und Gobiidae (Pisces) aus dem Roten Meer. "*Meteor*" *Forsch.-Ergebn.*, Vol. 2, pp. 69–84.

ZANDER, C. D., 1972a. Beziehungen zwischen Korperbau und Lebensweise bei Blenniidae (Pisces) aus dem Roten Meer. I. Aussere Morphologie. *Mar. Biol.*, Vol. 13, pp. 238–246.

ZANDER, C. D., 1972b. Beziehungen zwischen Korperbau und Lebensweise bei Blenniidae (Pisces) des Roten Meeres. II. Bau der Flossen und ihrer Muskulatur. *Z. Morphol. Tiere*, Vol. 71, pp. 299–327.

ZANDER, C. D., 1974. Beziehungen zwischen Korperbau und Lebensweise bei Blenniidae (Pisces) aus dem Roten Meer. III. Morphologie des Auges. *Mar. Biol.*, Vol. 28, pp. 61–71.

ZANDER, C. D., 1983. Terrestrial sojourns of two Mediterranean blenniid fish (Pisces, Blennioidei, Blenniidae). *Senckenbergiana Marit.*, Vol. 15, pp. 19–26.