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Ethogram of *Boleophthalmus boddarti* (Pallas) (Teleostei, Gobiidae), a mudskipper found on the mudflats of Kuwait

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ABSTRACT

This ethogram describes the basic behavioral repertoire of the common Indo-Pacific mudskipper *Boleophthalmus boddarti* (Pallas). The population found on the mudflats of Sulaibikhat Bay, Kuwait was studied and is composed of territorial individuals of both sexes which build and defend mud-walled polygonal territories, and smaller, errant or non-territorial individuals. The mudskippers' non-social and maintenance behaviors including feeding, thermoregulatory responses and wall construction behavior is described. The basic formations, fin and head positions during both agonistic and courtship display behavior are also described. The behavior of the errant individuals is similar to that of the territorial fish except that they do not engage in construction or male courtship activity. The activity of *Boleophthalmus boddarti* is highly seasonal, being correlated with the considerable seasonal and daily changes in temperature. Many of the fishes' maintenance behaviors can be explained in terms of adaptation to an amphibious way of life under such conditions. Other behavior patterns found in agonistic and courtship behavior can be interpreted as adaptations to selection pressures exerted on substrate-bound fish. Some of the problems in reproductive biology presented by the unique territorial mosaic social system of *B. boddarti* are mentioned.

INTRODUCTION

The amphibious gobiid fish or mudskippers are important members of the mangrove and mudflat fauna throughout the Indo-Pacific region. These fish live in the upper intertidal zone burrowing into the thick, organically enriched mud found in these environments (McNae 1968). Usually two or more species of mudskipper live sympatrically. Among the periophthalmids, for example, some differences in microhabitat selection depend on the fishes' tolerance to desiccation and/or salinity changes (Berry 1972); whilst others depend on competitive exclusion (Nursall 1981). Often, however, the mudskippers are from different genera and habitat division is based on differences in diet (McNae 1968). The mudskipper's amphibious nature has prompted much research into their physiology (*cf.* Gordon *et al.* 1969; Morii *et al.* 1978). Except for the work of Brillet (1969, 1980) on a carnivorous periophthalmid, however, little is known of their behavior. The present paper aims to provide

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Plate 1. Territories of *Boleophthalmus boddarti* in Sulaibikhat Bay. Most territories are completely walled and only one territorial fish (of either sex) occupies each territory.

information on the hitherto neglected aspects of behavior and ecology of a herbivorous mudskipper, *Boleophthalmus boddarti* (Pallas), and briefly mentions some aspects of the species social organization and reproductive biology.

STUDY SITE

The mudflats of Kuwait are formed from the Tigris and Euphrates river silt which finds its way into the Arabian Gulf through the Shatt Al-Arab (Emery 1956). The gentle tides and anticlockwise flowing currents of the upper Gulf lead to the silt's deposition around Kuwait Bay. The composition of the intertidal sediment is remarkably constant throughout its 200 km^2 area. The one exception is where the mud begins to wedge out as it nears the shore and exposes the underlying sand (Parks 1978). The interface zone is marked by a darkening of the surface and this also indicates the landward extent of the habitats of *B. boddarti* and *Scartelaos viridis*; *Periophthalmus koelreuteri* extends well beyond this interface into the supralittoral zone.

The mudskipper zone is exposed for the greater part of the local semidiurnal tidal cycle, only being covered for an hour or two either side of high water (Jones & Clayton 1983). Consequently, the fish are exposed to the summer and winter extremes of Kuwait's desert climate for long periods and the fish burrow into the mud. Since the mud is two metres deep the relatively simple water-filled burrow systems (*cf. Periophthalmus* spp.: Brillet 1969, Kobayashi *et al.* 1971; *Boleophthalmus* spp.: Mutsaddi & Bal 1969a) can be quite extensive and provide a microhabitat that is appreciably different from that of the surface (Tytler & Vaughan 1983).

Field observations were made on a population of mudskippers inhabiting Sulaibikhat Bay, a restricted area of the Kuwait Bay mudflats (Fig. 1). This site was chosen for convenience and for the presence of the polygonal mudwalled territories of *B. boddarti* (Plate 1) where individuals could easily be identified by the territory they occupied. In other areas of Kuwait Bay *B. boddarti* does not construct such complete territorial boundaries (Clayton 1987).

A brief description of these territories is appropriate here. The territorial system of *Boleophthalmus* is a good example of the territorial mosaic system with contiguous polygonally shaped territories as described by Keenleyside (1979). The territorial areas are confined to a 60–80 m wide band running parallel to the shore. Here the mud is of appropriate consistency for wall construction; closer inshore it is too dry and further out too wet. Islands of dry mud and pools of wet mud are, however, found within the territorial zone and on such areas boundary walls are absent. Typically, these areas are surrounded by territories which are otherwise completely walled. Dry areas are riddled with small crab (e.g. *Cleistostoma dotilliforme*) holes and in the wet areas small (60–140 mm) *Boleophthalmus* congregate. These errant non-territorial individuals wander over wide areas of the mudflat and are repeatedly chased out of territories by the larger resident territorial individuals. *Periophthalmus* and *Scartelaos* are also found in the territorial areas, the former often having their burrow systems within the thickness of the territorial walls made by *B. boddarti*. *Scartelaos* generally share the wet areas with the smaller *Boleophthalmus*.

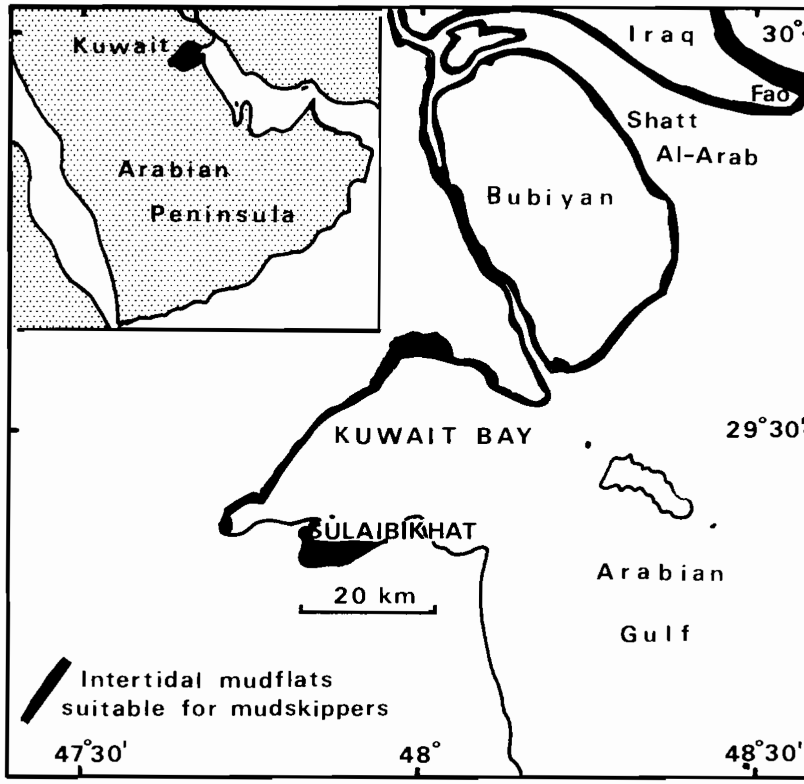

Fig. 1. Map showing the general location of the Sulaibikhat study site in Kuwait at the head of the Arabian Gulf.

MATERIALS AND METHODS

SUBJECTS

In the mudflats of Kuwait the fauna is dominated by three species of mudskipper, *Periophthalmus koelreuteri*, *Boleophthalmus boddarti* and *Scartelaos viridis* (Clayton 1986). *Boleophthalmus boddarti* is the largest of the three species and is herbivorous with a characteristically long gut (McNae 1968). It grazes on the soft mud ingesting diatoms and filamentous algae (Pankow & Hug 1979), but it also ingests nematodes, teleost eggs and crustacean larvae where they are found on the mud surface (Mutsaddi & Bal 1969b).

As in other mudskippers there is little or no sexual dimorphism in *Boleophthalmus boddarti*. There are no size or weight differences (Clayton & Vaughan 1982) and the shape of pectoral fin (Mutsaddi & Bal 1969b) is not a useful diagnostic characteristic especially in the field; the shape of the genital papilla (Mutsaddi & Bal 1969a) is the only useful external sexual characteristic applicable to the fish in Kuwait.

The local population of *Boleophthalmus* can be divided into two classes, territorial and errant fish, the former inhabiting mud-walled territories and the latter ranging widely over the mudflat. Territorial fish are nearly always larger than errant fish (Fig. 2), but both classes are sexually mature (Mutsaddi & Bal 1970). This is similar

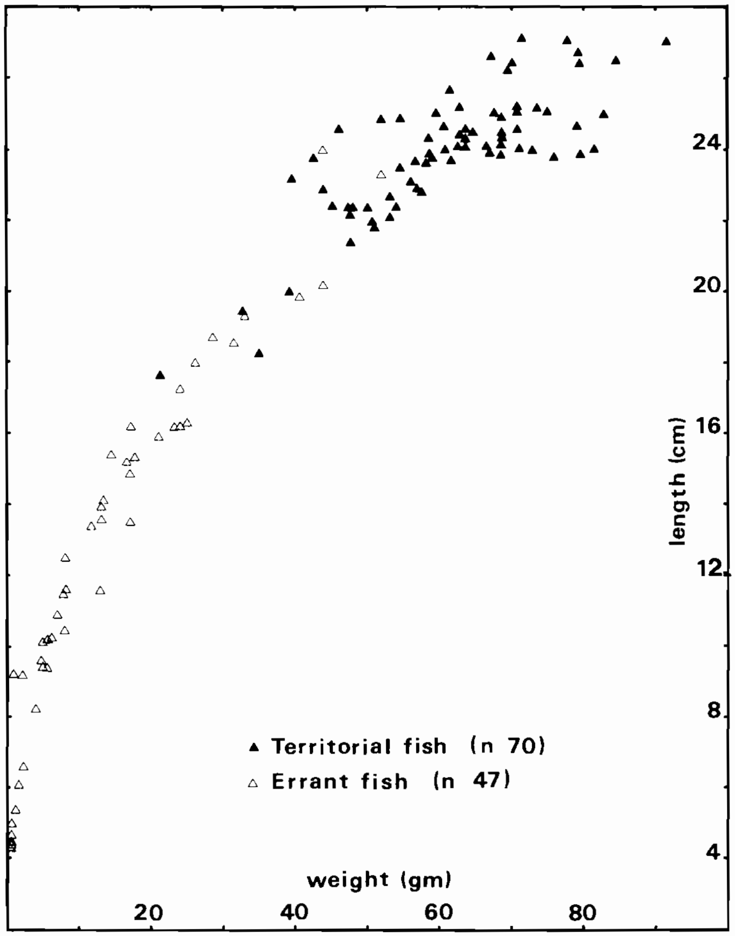

Fig. 2. Length/weight relationship of territorial and errant or non-territorial *B. boddarti*.

to the situation reported for *Periophthalmus sobrinus* (Brillet 1975) and *P. koelreuteri* (Brillet 1970).

PROCEDURES

The fish were observed intermittently from September 1978 to July 1982. Direct observation was carried out from platforms on the soft mud or from the shoreline. Typically, the approach of an observer caused most of the fish to seek the shelter of their burrows but after a few minutes the fish would begin to reappear. The large territorial fish were always the last to resume surface activity. For the duration of the observation period *B. boddarti* which were closer than 3–4 m to the observer would remain in their burrows, surfacing occasionally but immediately diving again. Provided the observer sat quietly the fish further away could be observed undisturbed. Field observations were supplemented by photography and videorecordings (Sony camera DXC 1600P and portable videocassette VO 3800P). Individual recognition

Fig. 3A. Horizontal position of *Boleophthalmus boddarti.*

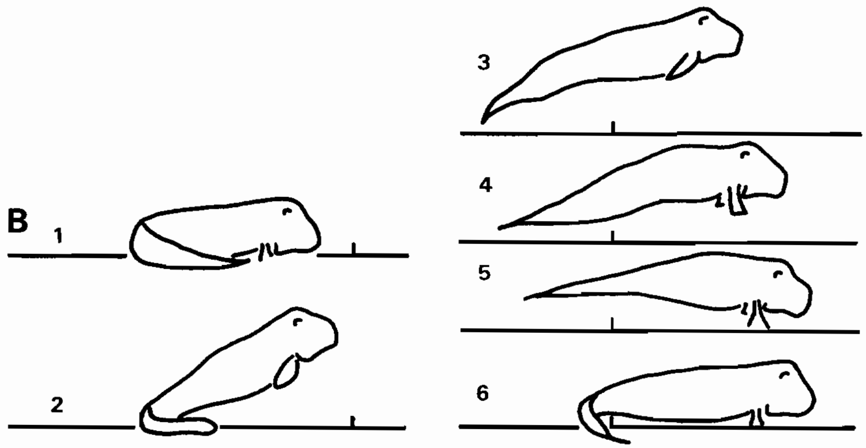

Fig. 3B. Jumping behavior of *Boleophthalmus boddarti.* 1–6, jump sequence, a ground reference point enables the forward progression of the fish to be determined. At the end of the jump (6) the tail is curled in preparation for a second jump.

of fish from one observation period to the next was not possible except in so far as one could presume that a territorial holder remained in the same territory.

Most of the observations reported here were made on the larger territorial fish. The errant individuals display similar behavior except that they do not exhibit wall building. The social encounters described for the territorial fish are also seen in the errant fish and may serve to maintain individual distances.

DESCRIPTIONS OF BEHAVIOR PATTERNS

It is convenient to divide the descriptions into two sections, non-social and maintenance behavior and social behavior. This division does not imply any fundamental dichotomy, however, since some patterns of behavior occur in both non-social and social situations.

NON-SOCIAL AND MAINTENANCE ACTIVITIES

A. *Stationary postures*

Whilst on the mud surface *B. boddarti* is inactive for long periods and adopts one of several characteristic positions during such periods. From these positions the fish is able to move quickly towards intruders or away from possible predators as they become visible above the territorial boundary walls.

(1) *Horizontal posture.* The fish lies partially submerged in the shallow water of the

pool or totally exposed on the mud slope (Fig. 3A). The pectorals are held almost against the flanks and the fish is supported by the pelvics. Whilst in this position in the pool, opercular or maxillary vibration may occur producing concentric ripples of water radiating out from the head. In the deeper parts of the pool total submersion is possible but frequently the fish remains with the dorsally placed eyes and a fraction of the head exposed.

(2) *Vertical posture.* The fish lies in its burrow with just the eyes and anterior dorsal portion of its head protruding from the water.

(3) *Perch.* Using its pelvics for support the fish may mount and remain perched on a wall for some time. The pectorals remain along the flanks. Perching individuals on walls rarely maintain the position for long since they usually avoid approaching neighbors. When the territories are flooded by the tide, walls become vantage points on which fish can stay out of water.

(4) *Basking.* The fish adopts a horizontal position on the exposed mud slope of its territory with its body at right angles to the sun. In the cooler parts of the year many fish show the same orientation as they bask to increase their body temperature (see Tytler & Vaughan 1983).

B. *Locomotion*

Any one or a combination of the following forms of locomotion, occurring in any sequence, are used by the fish to move.

(1) *Crutching.* The pectoral fins are used as crutches (Harris 1960). They are stretched forwards and then the body swings forward on them. At the end of the swing the weight is transferred to the pelvics to allow the pectorals to swing forward again. Crutching is used when the fish crosses walls or other dry, firm mud.

(2) *Rowing.* In contrast to crutching, the body is not lifted off the substrate but is pulled or dragged forwards by the concerted action of the pectorals. The pelvics are not employed during this action. This is the commonest form of movement and usually occurs in the shallow pools of the territories and across open areas of wet mud.

(3) *Reversing.* Tail-first movement is accomplished by a form of rowing in which the power-stroke of the pectorals is in the opposite direction and in which the pectorals are moved alternately instead of together. Reversing usually occurs on the very wet mud adjacent to the burrow entrance. Commonly a fish which has not completely emerged from its burrow will reverse back into it.

(4) *Skating.* The tail is bent forwards and to one side with the caudal rays digging into the mud. The backwards flexion of the tail provides the power that propels the fish forward along the mud's surface. The pelvics and pectorals are only used to stop the forward motion. Skating only occurs on very wet mud when fish need to move a short distance rapidly as when chasing or avoiding other fish.

(5) *Jumping*. The power for the movement is generated in the same way as that for skating and the pelvics provide the thrust to launch the animal into the air. The length of a jump is variable but the fish may travel several body lengths and be several centimetres clear of the mud surface (Fig. 3B, 1–6). Since both the length and direction of the jumps are variable, consecutive jumps are rarely similar. This produces a fast and highly erratic form of movement. Jumping is used on all mud surfaces and, as the fastest form of locomotion, is used predominantly in avoidance situations.

(6) *Swimming*. The fish swims with the normal motions of a typical anguiliform fish but when in shallow (pool or tidal) water its swims at the surface with the greater part of its head out of water. In deep water where the fish is totally submerged swimming is the usual means of locomotion but in shallower water, where the animal could row or crutch, swimming is used to attain greater speed.

C. *Feeding behavior*

The diet of adult *B. boddarti* is essentially a herbivorous one whereas that of the juveniles is more carnivorous (Mutsaddi & Bal 1969b; Pankow & Hug 1979). Both juveniles and adults, however, feed in essentially the same way. They extract their food from the surface layer of mud making no attempt to feed off the pieces of algae brought in and left by the tide. The feeding actions described below are shown by both juveniles and adults. While juveniles limit most of their feeding to the pools adults feed mainly on the exposed mud surfaces.

(1) *Grazing*. Generally a fish advances across exposed mud with rapid lateral to-and-fro movements of its highly mobile head. The feeding site of the fish can easily be identified from the track left behind. A series of fine parallel arc-shaped lines appears on the smoothed surface and there may be a single or many (overlapping) arcs in an area, depending on the duration of the grazing bout. The arcs are caused by the row of fine conical, comb-like teeth in the upper maxillae through which the mud is sifted. The buccal and opercular musculature serve to produce a suction pressure sufficient to draw the mud through the teeth into the buccal cavity where it mixes with water held in the mouth. After a bout of grazing the fish returns to the pool where it mixes the strained mud by further movements of the buccal and opercular cavities. This often sets up vibrations in the water and concentric ripples can be seen emanating from the fish's head during this phase of feeding. More water may be sucked into the mouth at this stage. Rejected mixture is ejected through the small opercular opening as a cloudy, light-coloured stream. The fish then returns to graze on the mud slope. Whilst most feeding is performed on the mud slope of the territory the fish may also graze along the walls or in the shallower margins of the pool. In the former case the grazing bout is often interrupted by a neighbor's approach. In the latter case, the ready availability of water means that feeding is continuous and the fish both grazes and mixes the sifted material as it moves along.

(2) *Scraping*. Where exposed stones or other rubbish are found, the fish feed off the algal matting (usually *Sargassum* sp.). Algae are scraped off with the teeth of the upper jaw by a downward movement of the head.

(3) *Tearing.* If the algal growth is a profuse one, the fish simply bite a piece and tear it off by vigorous side-to-side head-shaking.

D. *Other maintenance activities*

The fish perform several activities to keep themselves moist.

(1) *Lateral roll.* The fish rolls on to its side, the caudal region acting as the pivot. The caudal and two dorsal fins are collapsed during the movement and the pectorals are laid against the flanks. Lateral rolls may be to either side but there is no fixed sequence: sometimes several successive lateral rolls may be to one side, at other times the fish alternate. Most commonly a single lateral roll occurs and more than two or three are rarely performed at once. Lateral rolls usually occur when the fish is stationary but also occur when the fish is rowing as a momentary pause in forward progression.

(2) *Pectoral fin flap.* The pectoral fin is spread widely and applied to the fish's flank posteriorly. It is then swung forward to touch the opercular cavity briefly before returning to the resting position. The action is rarely repeated immediately and the intervals between successive pectoral fin flaps and the side-to-side sequencing of them are highly variable. The fish may preface the movement by rolling slightly to allow the pectoral fin free movement. Pectoral fin flaps occur when the fish is at rest or between bouts of feeding. Factors which influence the frequency and side-to-side sequencing probably include temperature, relative humidity and sun and wind direction.

(3) *Eye retraction.* The eyes can be retracted into their sockets. Both bilateral and unilateral eye retractions occur when the animal is stationary but the latter also occurs at other times. During the lateral roll the eye to the same side as the roll is retracted and during the pectoral fin flap the eye to the same side as the moving fin is retracted.

E. *Construction behavior*

Construction behavior is shown principally by the territorial animals. Wall building is a type of construction behavior which is social in nature since it is a response to the presence of conspecifics (Clayton 1987). It is convenient, however, to include wall building with the other non-social aspects of mud excavation and deposition. Errant individuals rarely excavate a burrow or build walls and no mud deposition by small fish has been observed. The descriptions of the elements of construction behavior are derived from observations of territorial fish engaged in clearing the burrow entrance, collecting mud from the pool, and in wall building. No direct observation of deep burrow excavation has been possible but it is probable that the fish excavate it by carrying mouthsful of mud to the surface. Depending on the water content of the mud the fish may collect it either by scooping or digging.

(1) *Scooping.* Soft mud is picked up by the fish as it rows or crutches slowly forward. The lips of the upper jaw remain immersed in the mud and the lower mandible must

be held slightly open to collect the mud. Scooping occurs mainly in and around the edges of the pool. Since the fish frequently use particular paths between the burrow entrance and the peripheral areas of the territory, scooping may result in the formation of deeper channels in an otherwise shallow pool.

(2) *Digging*. Considerable effort may be involved in removing hard mud and the animal may spend several seconds in digging to pick up a mouthful. The action is similar to that shown in tearing except that powerful forward thrusts are also performed. In water, swimming provides the necessary thrust whilst on the exposed mud surfaces the power is produced by curling the tail to one side and then vigorously straightening the body loop. Sometimes digging is achieved by the fish lunging upwards and forwards and biting out a portion of mud as it lands back on the substrate. The duration of digging is longer and more variable than that of scooping. Digging can occur anywhere in the territory (and presumably the burrow) except on the hard compacted mud of the exposed slopes, the open margins and the wall.

(3) *Transport*. The mud is transported in the mouth and the fish move from the excavation point to the deposition site by crutching. After deposition the fish may perform a lateral flip (see below) and return along its outward route by rowing or crutching. Alternatively, if the distance is short the fish may return to the collection point by reversing. This frequently occurs when the fish is excavating the burrow and depositing mud on a closely adjacent wall. Most mud from the burrow is relatively soft and hence easily collected.

(4) *Deposition*. The mud gobbet is forcibly ejected from the buccal cavity by contraction of the pharyngeal musculature. Wall construction is a seasonal occurrence (autumn and spring) and at other times individual mud gobbets will be deposited anywhere in the territory. The consistency of both the substrate and the mud gobbet will clearly affect the gobbet's durability once deposited. A wet gobbet deposited in the pool will quickly disappear, whereas if it is deposited on the slope or the wall it

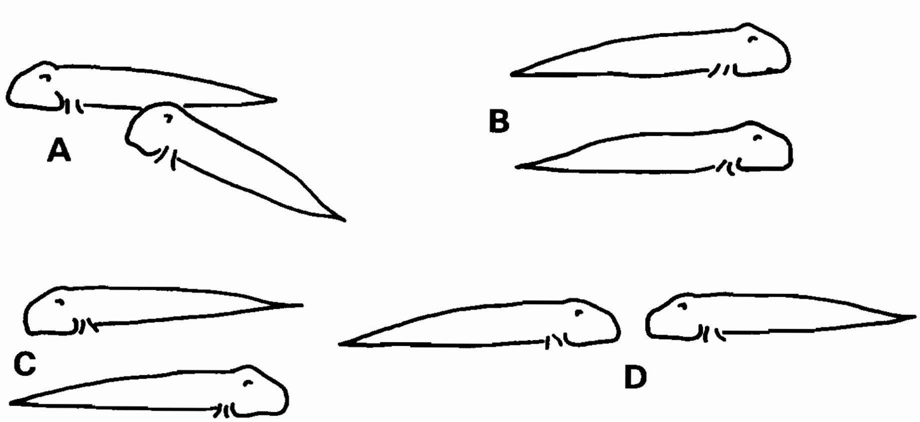

Fig. 4. Basic formations adopted by *B. boddarti* during agonistic encounters. A, T-formation; B, parallel; C, reverse parallel; D, face to face.

will retain some of its shape. During a bout of wall building the fish will concentrate on one area of the wall at a time. Consecutive mud gobbets are placed in the same 4–6 cm stretch rather than being spread out along the wall's length. Small breaches in the wall are simply repaired by depositing mud in the breach but, if the gap is larger, or if a new wall is being constructed, deposition follows a different pattern. Instead of extending the existing walls the first deposition is approximately in the center of the stretch to be re-constructed. The wall is raised to its full height before being extended to meet the other walls. Where two fish are building the same wall, deposition is not synchronized since the fish have to transport mud over different distances. When together at the wall, however, there is no antagonism between the two fish. The majority of wall building activity occurs during the period following exposure of the mudflat by the receding tide, presumably because the mud is most malleable at this time.

SOCIAL BEHAVIOR

A. *Agonistic behavior*

Outside the breeding season the territorial exclusion of conspecifics constitutes the major part of the social behavior of the mudskippers. For errant individuals maintenance of individual distance is of equal importance. The patterns of behavior performed depend on the size, the territorial status of the interacting fish and the location of the encounter. No sex differences in the response of individuals to one another were observed outside the breeding season. Encounters between fish of different sizes were usually decided on the basis of size. Smaller fish give way to larger fish unless the latter is a neighbor intruding into the territory of another fish. Since territorial fish are usually larger, errant individuals will be displaced even outside a territorial holder's own territory.

Before considering the behavioral interactions as a whole, the common elements of display will be described. These include the juxtaposition of the fish during encounters, the range of fin and head positions and body movements.

Basic formations

Four formations are commonly seen in agonistic encounters (Fig. 4) but it should be made clear that the fish may show some deviation from these formations, especially during transition from one to another, but also at other times when a particular display is held for some moments. Depending on the formation adopted, the distance separating the two fish is subject to considerable variation. Sometimes the fish may almost be touching one another whilst on other occasions the distance may be as much as 30 cm, well in excess of one fish length. All but the last formation are equally common.

(1) *T-formation.* One fish, the upright of the 'T' is perpendicular to, and facing the flank of the other (Fig. 4A).

(2) *Parallel formation.* The two fish lie parallel to one another facing in the same direction (Fig. 4B).

(3) *Reverse parallel formation.* The two fish lie parallel to one another but facing in opposite directions (Fig. 4C).

(4) *Face-to-face.* The two fish lie in a straight line directly facing one another (Fig. 4D).

Fin positions

All but the pelvic fins can be expanded or erected and used in display behavior. Agonistic displays mainly involve the unpaired dorsal, caudal and anal fins.

(1) *First dorsal fin (D1) erection.* The most frequently seen display position of the first dorsal fin is its partial erection to form a crescent shape (Fig. 5A). The position of the fin is maintained for several seconds. It is performed most frequently by errant individuals but also by territorial fish on an open margin or in a wet area and occurs when two individuals of a similar size approach to within several fish lengths of one another. The response may be given by either individual and may or may not be reciprocated. For example, a grazing individual commonly performs D1 partial erection without interrupting its feeding. The fish which elicited the display usually alters course to move away from the signalling fish. Sometimes, however, the approaching fish also performs D1 partial erection without altering course.

(2) *Second dorsal fin (D2) erection.* In contrast to D1 erection, D2 erection is usually

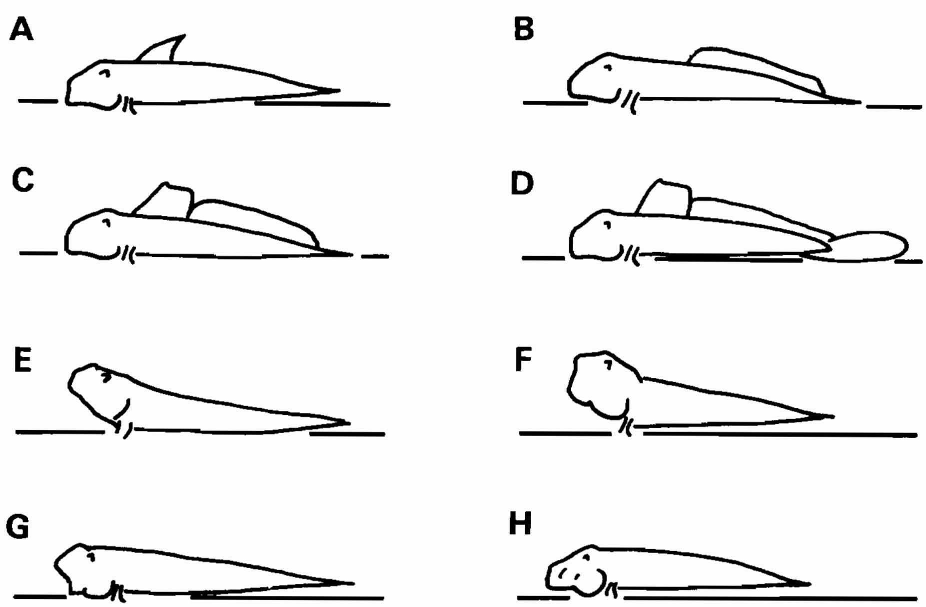

Fig. 5. Elements of agonistic display behavior involving movements of the dorsal fins and the head, mouth and buccal cavity of *B. boddarti*. A, D1 erection; B, D2 erection; C, D1 + 2 erection; D, DC erection; E, head-up; F, gape; G, yawn; H, bulge.

complete (Fig. 5B) but very brief and is performed at the end of a rapid approach or at the beginning of an avoidance response. It is shown by both territorial and errant mudskippers.

(3) *First and second dorsal fin (D1 + 2) erection.* Both of the dorsal fins are raised simultaneously to their full extent (Fig. 5C). The duration of the display depends on the situation. When the fish is moving, as when a territorial fish is approaching an intruder the display is brief. When the fish is stationary, as in a T-formation for example, the display can last for several seconds.

(4) *First dorsal, second dorsal and caudal fin (DC) erection.* The three largest fins are erected simultaneously to their full extent (Fig. 5D). The action is never brief and is held for some moments. DC erection occurs during the longer agonistic encounters and whilst it may be shown by fish in any of the four formations it is more commonly seen in face-to-face and T-formation encounters.

Head movements

Displays can be enhanced by movements of the head, mouth and buccal cavity.

(1) *Head-up.* The stationary fish raises itself on its pelvics so that the head is lifted up (Fig. 5E). The height of the head during head-up is usually greater than during crutching. The action is performed at the approach of other fish and may be all that is necessary to deter further approach, especially in the case of errant individuals entering a territory. If the head-up is ignored by the intruder, orientation towards it and/or fin erection follow the head-up.

(2) *Gape.* The head is lifted up and the mouth is opened to expose the indigo-black lining of the oral cavity (Fig. 5F). Typically the mouth is fully open, but all degrees of opening have been observed. Gaping usually occurs during face-to-face encounters with D1 erection but it also occurs during face-to-face and T-formation encounters when it is paired with DC erection.

(3) *Yawn.* The mouth is fully open during a yawn but the head is not lifted (Fig. 5G). A yawn is always followed by a bulge (see below). Yawning has been observed predominantly in apparently non-social situations where the animal is stationary within the pool. No territorial intruders were present but it is possible that yawning is a social signal used at a distance.

(4) *Bulge.* The mouth is closed and the whole buccopharyngeal and opercular region is inflated (Fig. 5H). Yawning usually, but not always, precedes bulging. In face-to-face agonistic contests one fish may reverse for about a fish length and then bulge. Like yawning, bulging may thus be a social signal but it is possible that it is simply a respiratory response (see discussion).

(5) *Bite.* A fish may attack by biting its opponent somewhere in the flank. Biting is rare and usually occurs during T-formation and, less frequently, in face-to-face encounters. The aggressor is usually the fish in the stem position of the 'T' and the

bite is directed towards the anterior of the opponent's body. In face-to-face encounters the fish arch laterally and the bite is directed toward the opercular region. Dorsal fin erection often accompanies the action.

(6) *Jostle.* During face-to-face encounters the fish may push against one another with wide open mouths (Fig. 6A, 1 & 2). The pointed elongate teeth near the symphyses of the jaws may become locked together. Whilst pushing, the head may be moved from side to side and is always accompanied by, and often preceded by, D1 erection.

(7) *Lateral flip.* The basic action consists of raising of the head and its rapid lateral displacement through the air (Fig. 6B, 1–5). The degree of turning away varies approximately between 40 and 150°. The movement is preceded by the erection of the second dorsal fin and is accompanied by that of the first dorsal fin. Both fins collapse as the fish lands. The lateral flip signifies an end of an encounter but usually is performed by one fish only.

Size of the contestants is clearly the single most important factor determining success; bigger fish always win. Most interactions are of short duration (less than 10 sec) and the shortest involve signalling at a distance. D1 erection or head-up are all that is necessary to cause the recipient of the display to change direction. If the interaction involves both fish in display, it is usually terminated by one fish performing a lateral flip and then moving away. Smaller errant fish usually display D1 erection at a distance and will avoid fish larger than themselves. The largest fish are always established territorial holders and an approach and fin display towards an intruder are usually sufficient to deter further trespass. Most agonistic encounters involving territorial fish are concerned with errant individuals' trespass (Clayton 1987).

B. *Courtship behavior*

There are clear sex differences in the courtship behavior of *B. boddarti*: certain elements of courtship are performed only by males. The female's identity is less easily established since they are recognized by the absence of these behaviors and therefore may be confused with non-displaying males. During the breeding season males do not remain sexually inactive for long and observation over several days is therefore more than adequate to establish the sex of fish. Behavioral establishment of sexual identification has been confirmed by gonadal inspection of captured, known individuals.

Courtship has only been observed in territorial fish and the male's conspicuous behavior attracts territorial neighbors into his territory. The female's role in courtship is largely passive and consequently it is appropriate to consider the behavior of the male first.

(1) *Leap.* The basic element of the leap consists of the male throwing himself vertically into the air by rolling onto his flank and pushing up from the caudal region Fig. 6C, 1–5). At the height of a leap two-thirds of the fish may be clear of the ground. Landing ventrally on his pelvic fins, the fish may retain the same orientation as the beginning of the leap or, by twisting his body, may finish up to 120° away from it. The leap is embellished by the erection of fins and the start of the whole

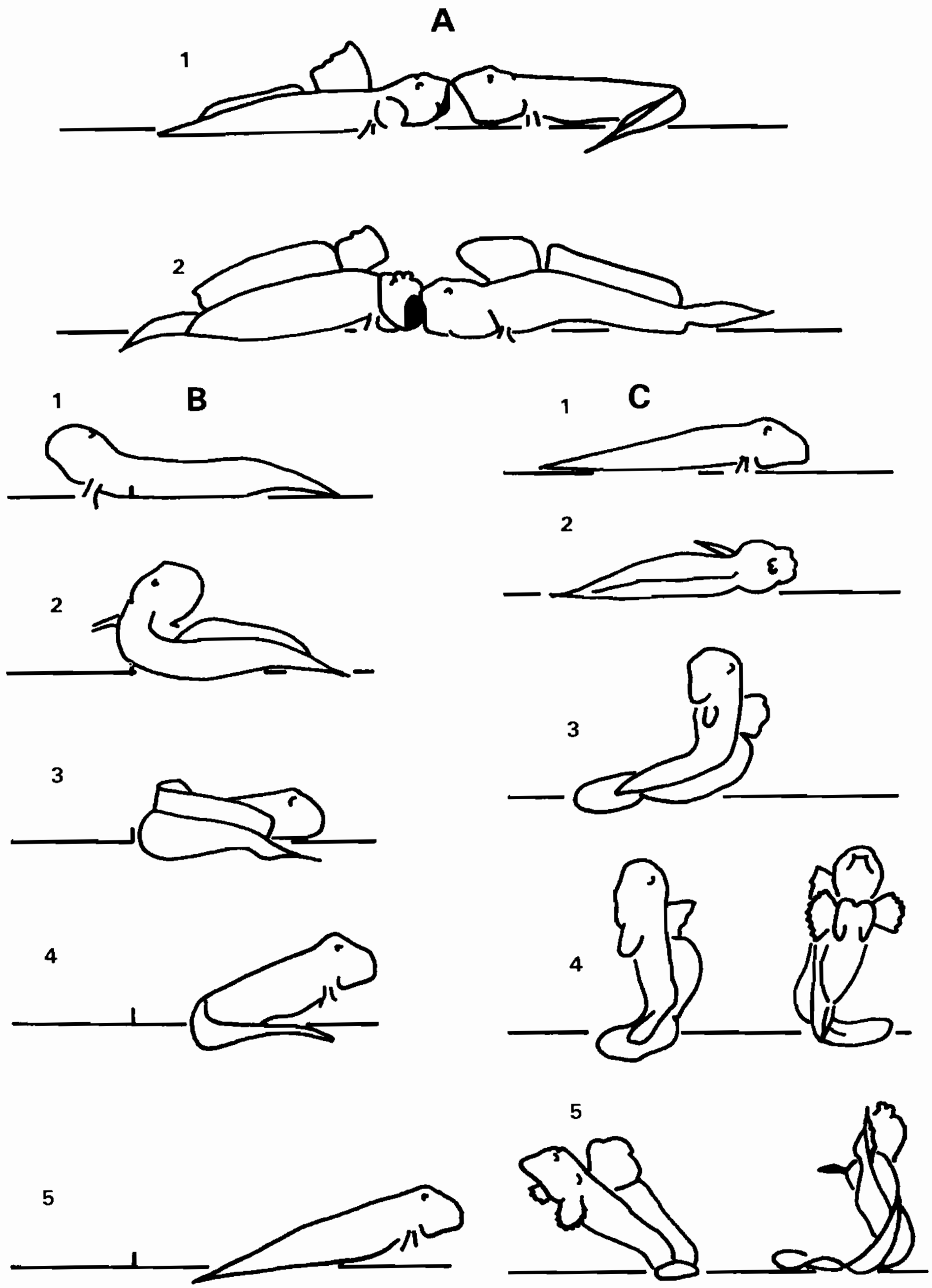

Fig. 6. Elements of agonistic and courtship behavior of *B. boddarti*. A, jostle; 1, the fish on the right is passively resisting the pushing of the other fish; 2, both fish are engaged in active pushing. B, 1–5, lateral flip sequence. C, 1–5, leap sequence in which the last two positions (4, 5) are shown from two aspects. The end of the leap is illustrated by pectoral waving (Fig. 7).

movement is signified by expansion of the second dorsal fin. The caudal fin is expanded as the fish rolls onto its side prior to the head and anterior trunk being thrown vertically into the air. In mid-leap the first dorsal fin is erected. At the height of the leap the pectorals, which are widely spread, are held at right angles to the body. On landing, only the pectorals remain erected. The leap is performed by a territorial fish when he is alone in his territory but at a time when neighboring fish are visible to him. Usually several leaps occur together in a bout of leaping. Males differ in the amount of leaping that is performed at any one time. For example, an analysis of 15 min of a videotape of about 30 territories showed that there were 13 leaping fish (Clayton & Vaughan 1986). This number of males in this area is probably accurate since territories are equally divided between males and females. Clearly, however, non-displaying males could not be identified. The number of leaps by each individual was extremely variable, ranging from 1 to 19 with a mean of 8 (S.D. 6·48).

(2) *Pectoral wave*. The basic action of a pectoral wave is the forward and backward movement of the erected pectorals (Fig. 7A). Usually a fin is held vertically throughout the full arc but in some cases the orientation may change. At the beginning of a wave, when the fin is laid back, the anterior face of the fin is directed obliquely upwards. As it moves forward it becomes vertical. A second variant involves the collapse of the fin during the back-stroke so that a point on the dorsal edge of the fin subscribes an ellipse as it moves through the complete movement. Occasionally the direction of this variant is reversed so that the fin moves the other way. Usually both pectorals move forward simultaneously, but in the elliptical variant of the movement alternation is not uncommon, especially if one fin reverses the direction of its movement. The pectoral wave always occurs after a bout of leaping but only when another fish is close by.

(3) *Tail-beat*. The tail and distal third of the body are thrown from side-to-side (Fig. 7B). The elevation of the tail and its shape are variable. When lifted clear of the ground the tail is often sharply wedge-shaped with collapsed fin rays. When the tail is not raised the rays may or may not be erected, but if tail-beating is performed in the pool the caudal fin is often fully spread. The beating occurs simultaneously with or following pectoral waving but only when another fish is close by.

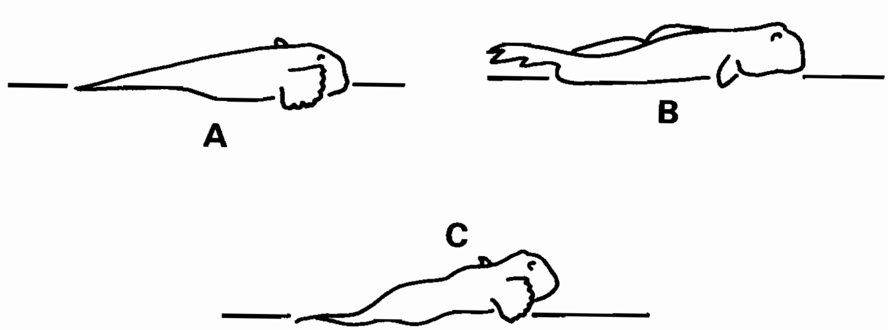

Fig. 7. Elements of courtship behavior of *B. boddarti*. A, pectoral wave. B, tail-beat. C, quiver.

(4) *Quiver.* The tail and the distal part of the body behind the pectorals are thrown into rapidly repeated lateral movements as a shallow sinusoidal wave passes along the body (Fig. 7C). The speed of the wave and the amplitude of the lateral movement are variable. As during tail-beating, the vertical position of the tail and its shape can change. Quivering can occur simultaneously with pectoral waving but both (either as separate events or when occurring together) can be interrupted by leaping. The recipient of the display essentially plays a passive role in the sequence: its continued presence being all that is required. If the recipient advances, the following behaviors occur.

(5) *Lead.* The male faces away from the advancing recipient of the display and moves into the pool toward the burrow entrance. Vigorous quivering and pectoral waving accompany leading and consequently the spread caudal fin of the male may waft across the head of the second fish. It is unlikely that this is a separate element of courtship. It simply results from the second fish's rapid and continuous approach towards the male which is only advancing in short bursts.

(6) *Follow.* The only active role played by the female in courtship is her slow advance towards the displaying fish. Crutching across the open margin or swimming in the pool and remaining stationary are her only responses.

(7) *Burrow entry.* The male enters the burrow to be immediately followed by the female. If the female's descent into the burrow is delayed the male will return to the surface, but an unsuccessful courtship attempt is always terminated before leading and following and once these have occurred burrow entry by both male and female always follows. Spawning has not been observed but the fish remain within the burrow for up to 45 min. Upon re-emergence the female returns to her territory whilst the male remains within his territory.

In *Boleophthalmus* courtship, aggression is expressed by head-up and/or gaping and by DC erection, the last occurring either on landing from a leap or as a separate display. In successful courtship these elements are conspicuous by their absence. The display of aggression by the male is not, however, the only reason for failure of courtship. The motivational and/or developmental state and even the sex of the recipient of the display must be considered. Another feature of the situation which appears to be independent of such factors is that displaying males rarely elicit severe antagonism in other fish. Leaping fish often find themselves in a neighbor's territory where, under normal circumstances, they would be attacked. At best, the sexually uninterested resident will ignore or avoid the intruder and at worst, respond by gaping. Chasing of the intruder has not been observed. This is not to say that leaping males cross territories to court distant fish. The male which finds itself in a neighbor's territory will return to its own as soon as possible.

A recipient of display can encourage further display simply by staying in the same place or by slowly advancing towards the male. Even if aggressive displays are incorporated in a male's display the gravid female, ready to lay her eggs, will still encourage his courtship and even a two second DC erection display in a T-formation fails to deter the female.

SEASONAL AND DIURNAL CHANGES IN ACTIVITY

The activity of *Boleophthalmus* is highly seasonal being correlated with the considerable seasonal and daily temperature changes so typical of the latitudes in which Kuwait is situated. Mean temperatures drop to 7·9°C in January (minimum −4°C) and reach 44·8°C in July (maximum 51·1°C) (Al-Kulaib 1975; Jones & Clayton 1983). The fish are usually active within the temperature range 13°C–40°C (Tytler & Vaughan 1983). Daily temperature changes, however, can be as high as 20°C and, irrespective of the time of the year, there is always some period of the day in which the fish are active. Darkness, high tide, inclement weather such as strong winds and rain, sand- or dust-storms all inhibit the fishes' activity.

In winter (December and January) the fish are largely inactive. Feeding is the main activity and little agonistic or constructive behavior is shown at this time. When the latter occurs it is haphazard and deposition can be anywhere in the territory. The fish are very sluggish and are relatively easy prey for the many migratory birds (see below) that feed on the mudflats. The territories fall into disrepair but are re-established when construction behavior and agonistic behavior, predominantly in territorial defense, re-appear in February. Silted systems are re-excavated, often emerging onto the surface at new locations. The territorial walls are repaired or built and, whilst there may be some new residents, the pattern of territories remains similar to the pre-winter situation (Clayton & Vaughan 1986). Construction behavior declines until by mid-May it has virtually ceased.

The breeding season begins in March but it is not until mid-April that the majority of males are displaying. Courtship continues until August by which time most territories have breached walls where fish have been moving between adjacent territories. Newly-hatched ambulatory (i.e. not pelagic larval stages) *Boleophthalmus* have been seen as early as mid-July but the majority appear later.

During October and November a second spate of construction behavior occurs during which the territorial boundaries are repaired. Agonistic behavior increases again but is noticeably absent during bouts of building.

The seasonal cycle is superimposed on and modifies the tidal cycle of activity. The tidal cycle in the northern Gulf is such that the highest tides are usually during the day in summer and at night in winter thereby partially protecting the littoral zone from temperature extremes (Jones & Clayton 1983). The fish are most active in the period after the tide has receded. Depending on the season, agonistic, construction and courtship behavior are all most frequent during this period. Feeding also occurs but is not restricted to this time and will occur at intervals throughout the day. Agonistic and courtship behavior, but not construction behavior, show a second peak of activity in the period immediately preceding the incoming tide. This period is necessarily shorter than that following the ebb tide. Construction behavior is limited to the earlier period either: (a) because the mud dries out when exposed and is difficult to excavate, or (b) because mud deposited prior to the incoming tide does not solidify and would be washed away.

FUNCTIONAL ASPECTS OF ACTIVITY PATTERNS

The form of locomotion adopted by the fish is clearly related to the situation and current behavior. Leisurely activities such as feeding and construction behavior are accompanied by rowing, reversing and crutching. In encounters with other fish (largely other *Boleophthalmus* but also *Scartelaos*) approaches are accomplished by fast crutching, swimming or skating. Avoidance is also achieved by these forms of locomotion but jumping with its fast and erratic changes of direction, is also commonly used. Simply because swimming and jumping are the fastest means of locomotion, they are the main way of avoiding predators. Any fast or sudden movement of an object immediately above the horizon elicit escape responses and *Boleophthalmus* are very slow to reappear from their burrows once disturbed. In most cases the horizon will be the fishes' territorial wall. This generalized escape response and slow re-emergence is probably adapted to the different hunting techniques of predators. Among the aerial predators which patrol up and down the mudflat parallel to the shore line, terns hunt by flying 2–3 m above the mudflat and diving down at potential prey. By contrast, gulls skim along the surface, sharply braking, wheeling and lunging to capture their fish. Ground predators such as bitterns, egrets and herons slowly stalk their prey and spear them with a rapid extension of their necks. The herons also stand immobile for long periods before striking.

These birds probably represent the main predators of littoral mudskippers (Mukherjee 1971a, 1971b) but the flood tide brings other predators. Sea snakes (*Hydrophis cyanocinctus*; Volsøe 1939) and Stonefish (*Leptosynanceja melanostigma*; pers. obser.) take *Boleophthalmus*. Cat sharks (probably *Chiloscyllium griseus*; Relyea 1981) also feed in the shallow water of the advancing tide. They are known to feed on bottom-dwelling molluscs and crustaceans but probably also catch mudskippers if they are out of their burrows.

Lying horizontally or vertically within the pool, the partially submerged fish remain stationary for long periods. Even during normal activity uninterrupted by inclement weather or the presence of a predator, the fish will remain in the pool. The horizontal position is typical of an animal between bouts of feeding or other activity whilst the vertical position is usually adopted when the fish emerges from its burrow after a period of enforced inactivity brought about by night or high tide.

Boleophthalmus can easily be distinguished from sympatric species of mudskipper by the side-to-side head movements performed during grazing. The action serves to skim off the surface layer of mud in which algae and diatoms are the predominant food items (Khoo 1966; Lim 1967; Pankow & Hug 1979; Sarker *et al.* 1980). Other organisms taken include polychaetes, copepods, nematodes and crustacean larvae (Mutsaddi & Bal 1969b). All dietary items, however, are subject to seasonal variation and for diatoms at least Mutsaddi & Bal (1969b) have demonstrated a close correlation between their availability and their occurrence in *Boleophthalmus*' gut.

Tearing and scraping of algal mats is confined to fish that inhabit land-water drainage channels where nutrient levels are sufficient to support such algal growths. During spring, clumps or sheets of algae (*Enteromorpha*, *Ulva*, *Sargassum* and *Laurentia* spp.) are also washed onto the mudflat and can be found in the territories. No *Boleophthalmus* have been seen to feed on this material although it is sometimes removed from blocked burrow entrances by the territorial fish.

Morphologically, *Boleophthalmus* is reasonably well adapted to an amphibious way of life and it is necessary to mention a number of these adaptations before discussing the behavioral ones. The fish extract oxygen from water through the gills and skin and also from air by periodic ventilation of the well vascularized opercular chambers (Biswas *et al.* 1979). Here this activity has been termed bulging. The gills of *Boleophthalmus* contain cells that secrete a water-binding mucus (Hughes & Datta Munshi 1979) which prevents dehydration without hindering gaseous exchange between the warm air or water and the blood (Singh *et al.* 1974). *Boleophthalmus* also has a mucous-covered and well vascularized skin (Salih & Al-Jaffery 1979) well suited to cutaneous respiration (Biswas *et al.* 1979; Tamura *et al.* 1976).

The behavior of *Boleophthalmus* complements these morphological features. The long periods in which fish remain in their pools ensures that the possible stress of dehydration is limited and, at least for juveniles with their relatively large surface areas, total exposure is rare. Territorial fish spend more time out of water feeding, chasing intruders and wall building. Provided the skin is moist and fish can return to water it is in no danger of becoming dehydrated. Pectoral fin flaps ensure that the bucco-pharyngeal region is kept moist and lateral rolls wet the whole body and obviate the need to re-immerse in water. Morphological adaptations of the eye give mudskippers excellent aerial vision as well as protecting them from dust and desiccation (Graham 1971). Clear secondary spectacles cover the eyes and eye retraction serves to remoisten them in the small water-filled cups that lie below the eyes. Like other gobies (Rice & Johnstone 1972), *Boleophthalmus* excavates a burrow by carrying mud in its mouth. By stating that *Boleophthalmus* merely pushes itself into the soft mud tail first, McNae (1968) implies a lack of construction behavior by this mudskipper. Certainly the construction behavior of *Periophthalmus* is better known (Stebbins & Kalk 1961; Brillet 1976; Kobayashi *et al.* 1971) but larger *Boleophthalmus* also live in burrows they have excavated (Mutsaddi & Bal 1969b; Khoo 1966; Salih & Al-Jaffery 1979). Errant, non-territorial individuals, however, do disappear into soft mud when danger threatens. When possible, they inhabit vacant burrows.

The polygonal mud-walled territories (Clayton & Vaughan 1982) are unique to Sulaibikhat Bay and probably depend on some, as yet unidentified, property of the mud or the tide for their existence. Equally intriguing, however, is their function and whilst this is the subject of continuing study some of the possibilities can be mentioned. The territories may be breeding ones, but whilst the territories are renewed seasonally the fish (single individuals of either sex) remain in essentially the same place all the time. Alternatively, the territories and the pools they contain may act as thermoregulatory devices (Tytler & Vaughan 1983) or as 'market gardens' for the fish. Admiraal & Peletier (1980) have shown how salinity, sulphide and temperature affect the distribution of diatoms on a temperate region mudflat. Although of a different order of magnitude, variations of these same factors are also important on tropical and subtropical mudflats. The territorial pools provide a microhabitat in which the extremes of the exposed mud are ameliorated. The territorial boundary walls also reduce agonistic behavior. Unless a fish is close to a wall (on an open margin) the height of the boundary wall is usually sufficient to exclude the fish from the view of a territorial resident (Clayton 1987).

The agonistic elements described here for *B. boddarti* agree with Lim's (1967) descriptions and are typical of many benthic fish. Head-up and spreading of the fins to their fullest extent are common among various shore fishes (Kinzer 1960; Gibson 1969; Wickler 1971; Wirtz 1978).

Intuitively it appears that D1, D2, D1 + 2, and DC erection represent increasing levels of aggression, but a more detailed analysis of the circumstances of these acts as well as those of biting, bulging and yawning is required before any definitive statements concerning their motivational control can be made. Functionally these behaviors serve as spacing mechanisms. Infringement of individual distance is the prime cause of agonistic encounters among errant individuals and the size of the contestants in such contests is often the deciding factor (Brillet 1975). Most of the territorial holders' agonistic behavior is directed towards evicting from their territory any errant individuals. By comparison the level of agonistic interaction between neighboring territorial fish is very low and the prime spacing mechanism is their construction behavior. Whilst agonistic behavior has been observed in both territorial and errant individuals, courtship behavior is confined to territorial fish; the male's conspicuous behavior serving to attract females to his territory. In common with many other benthic fish, the male's self-advertisement consists of stereotyped movements off the substratum which contrast markedly with the normal movements which are entirely substrate-bound (Gibson 1982). Thus leaping in *Boleophthalmus* is comparable with the vertical looping performed in the water column by blennies (Phillips 1977; Wirtz 1978) and gobies (Macdonald 1975; Yanagisawa 1982), and, more directly, with the leaping into the air performed in periophthalmid courtship (Brillet 1969, 1970). The similarities in the general patterns of behavior of all these shore fish may be regarded as convergent evolution in response to the same selection pressures (Wickler 1957).

Apart from being one of the clearest examples of Keenleyside's (1979) territorial mosaic category of territoriality, the *Boleophthalmus* system also presents some other interesting issues in reproductive biology. A territorial fish does not know the sex of its neighbors until the breeding season when the males identify themselves by leaping. The competition between males for females is severe. On average a fish has five neighbors only half of which will be of the opposite sex (Clayton & Vaughan 1982). Errant individuals may also be egg-laden and a territorial male can increase his fitness by fertilizing the eggs of both errant and territorial fish. Errant males do not possess a territory and do not exhibit leaping behavior. Such differential sexual activity is consistent with other polygynous mating systems (Wilson 1975). Usually, however, it is only the males that are territorial in such systems. Despite some decay of the walls at various times of the year, the fish remain in the same territory all the year round and it is likely that the fish derive some or all of the benefits already mentioned. During the breeding season, however, the possession of a territory by a female provides her with ready access to established territorial males.

The situation may be compared to that found in the ten-spined stickleback *Pygosteus pungitius* (Morris 1958). Individuals of both sexes establish territories in dense vegetation and it is only after this that they develop sexually. Because of the dense vegetation, it was argued, females without territories would be unable to find the males. In *Boleophthalmus* the problem is for females to reach the males. Errant individuals are chased from one territory to another and the choice of sexual partner must be necessarily hasty. With an established territory it is possible to spend some time in assessing the neighboring males: features assessed might be size of territory or length of courtship for example, and future study will be directed towards such problems.

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الصورة السلوكية لنطاط الوحل في المسطحات الطينية في الكويت

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الصفاة ١٣٠٦٠ ، الكويت

خلاصة

يصف هذا البحث الصورة السلوكية الأساسية لنطاط الوحل الشائع في المحيطين الهندي والهادي . وتتناول هذه الدراسة جماعة من هذه الأسماك تعيش في المسطحات الطينية في خليج الصليبخات . وتضم هذه الجماعة أفرادا اقليمية من الذكور والأناث ، أي أفرادا تبنى لأنفسها مناطق متعددة الأضلاع محددة بجدران من الطين وتدافع عن « أقاليمها » تلك ، كما أنها تضم أيضا أفرادا أصغر حجما تعيش جائلة أو لا تبنى لأنفسها مناطق محددة .

ويصف البحث أنماط السلوك غير الاجتماعي لحفظ الحياة ، وهو يتضمن سلوك الأغتذاء والاستجابات المنظمة لدرجة حرارة الجسم ، وعلى الأخص وضعي الرأس والزعانف ، وسلوك بناء الجدران الاقليمية . ويصف البحث أيضا الأوضاع الأساسية في سلوكي العدوان والغزل ، ويشبه سلوك الأفراد الجائلة سلوك الأفراد الاقليمية بصفة عامة ، باستثناء ما يتعلق ببناء الأقليم ونشاط الذكر في سلوك الغزل .

ونشاط هذا النوع من نطاط الوحل نشاط موسمي إلى حد بعيد ، ويرتبط ارتباطا وثيقا بالتغيرات الكبيرة في درجات الحرارة يوميا وموسميا . ويمكن تفسير كثير من أنماط سلوك حفظ الحياة في اطار التكيف لأسلوب حياة برمائية في تلك الظروف البيئية . أما أنماط السلوك الأخرى في العدوان والغزل فيمكن تأويلها بأنها تكيفات للضغوط الانتخابية التطورية في سمكة مرتبطة بمرتكز صلب .

كذلك يشير البحث أيضا إلى بعض المسائل في البيولوجية التكاثرية في هذا النوع الذي تتداخل فيه صور السلوك الاقليمية والاجتماعية على نحو فريد .