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THE ASSOCIATION BETWEEN GOBIID FISHES AND BURROWING ALPHEID SHRIMPS

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INTRODUCTION

The association between gobiid fishes and burrowing alpheid shrimps was described for the first time by Longley & Hildebrand (1941) from southern Florida. The further study of this partnership was delayed until the introduction of mask and snorkel and SCUBA diving as a tool for collecting material and carrying out detailed behavioural and ecological studies in the marine environment. The first aspect studied was the taxonomy of the gobies, a discipline which still leads the research of this association, probably due to the gobies' diversity and richness in species and circumtropical distribution (Klausewitz, 1960; Lubbock & Polunin, 1977; Polunin & Lubbock, 1977; Yanagisawa, 1978; Hoese & Randall, 1982). The first ecological-behavioural studies were made by Luther (1958a,b) and Magnus (1967) in the Red Sea. In the northern Gulf of Elat, Red Sea, the present author has studied goby-shrimp associations for more than seven years, concentrating on communication, distribution and partner specificity (Karplus, 1970, 1976, 1979, 1981; Karplus, Szlep & Tsumamal, 1972a, 1974, 1981; Karplus, Tsumamal & Szlep, 1972b; Karplus & Vercheson, 1978; Karplus & Ben-Tuvia, 1979; Karplus, Tsumamal, Szlep & Algom, 1979; Goren & Karplus, 1983). In Hawaii a detailed quantitative study was carried out on the communication between two species of shrimps, and one species of goby using both sequence and information analysis (Moehring, 1972; Preston, 1978). Polunin & Lubbock (1977) carried out a field study in the Seychelles on the distribution and partner specificity of goby-shrimp associations. The ecology, population dynamics and partner specificity of goby-shrimp associations were studied in the Great Barrier Reef by Cummins (1979). The reproduction of goby and shrimp and the initial formation of the association, areas completely unknown, were studied in southern Japan by Yanagisawa (1982, 1984) following a laboratory study by Harada (1969). Data collected by individuals in different parts of the world gradually complemented one another to allow a more comprehensive understanding of these fascinating associations.

The aim of this review is to present in detail the present state of knowledge of the goby-shrimp association and to suggest areas of importance for future research.

TAXONOMY OF GOBIES AND ALPHEID SHRIMPS

The majority of the publications on goby-shrimp association are devoted to the taxonomy of the associated gobies which show great diversity and richness in genera and species (Fig. 1). Few associated gobies were described while traditional methods of collecting were employed. The usual indiscriminate massive poisoning of reef fishes for their collection is not effective for collecting associated gobies since these small fish are often overlooked in mass collections or hide in their holes where they either die or avoid the poison. The specific search by means of SCUBA diving for associated gobies in the last two decades in shallow and deep water has been most rewarding. Many new species are being discovered and described. The successful collection of associated gobies is practised by means of: an Hawaiian sling and a multipronged arrow (Randall, 1963), small baited hooks (Yanagisawa, 1976; Polunin & Lubbock, 1977), small amounts of poison injected in specific areas (Hoese & Randall, 1982), small dynamite cartridges (Klausewitz, pers. comm.), traps (Magnus, pers. comm.), "slurp gun" (Moehring, 1972), and hand nets after manually blocking the burrow entrance with a spade (Karplus, 1970). A special remote-operated spade was later developed for collecting live gobies for behavioural studies (Karplus & Vercheson, 1978).

Several problems exist in the classification of gobies which live in association with alpheids. Many of the nominal genera involved have not been adequately diagnosed. Consequently, in many cases, species have been placed in genera with which they have little affinity (Hoese & Steene, 1978). Generic and species synonymy have often added to the confusion. A total of 70 nominal species of gobiid fishes placed within 18 nominal genera have been reported as living in association with burrowing alpheid shrimps (Table I). In some of these genera, which contain several species, all members live in association with shrimps: e.g. *Amblyeleotris*—20 species, *Cryptocentrus*—18 species, *Ctenogobius*—6 species, *Vanderhorstia*—5 species, and *Stonogobius*—4 species. In a revision of the genus *Cryptocentrus* at present in preparation by Hoese, about 40 nominal species are described (Hoese & Steene, 1978). Already close to 100 species of associated gobies have been discovered, so it can be assumed that their actual number is probably closer to two hundred.

To date 13 species of alpheid shrimps have been reported as living in association with gobiid fishes (Table II). The majority of these species belong to the *Brevirostris* group. Only three species (*Alpheus crassimanus*, *A. randalli*, and *A. malabaricus*) belong to the *Edwardsii* group. Species of both these groups occupy burrows of their own construction in silty to sandy bottoms (Banner & Banner, 1982).

In many of the studies which either briefly mention goby-shrimp association or deal with them at length, the shrimp taxonomy only covers the family or generic level. The two main reasons for this are the difficulty experienced in shrimp collection, as they withdraw rapidly into their burrows when approached by a diver, and the great variability of shrimp morphology and coloration (Banner & Banner, 1982). Shrimps can be collected by means of: an Hawaiian sling and a multipronged arrow (Banner & Banner, 1980), small dynamite cartridges or traps (Karplus & Vercheson, 1978), injection of an irritating liquid heavier than water (a saturated solution of NaCl with CuSO_4)

into the burrow, forcing the shrimp to leave it (Weiler, 1976), hand nets after blocking the burrow entrance with a spade (Karplus, 1970; Moehring, 1972), or digging up the entire burrow system of small animals (Yanagisawa, 1984). The same remote-operated spade used for collecting gobies has been utilized here, (Karplus & Vercheson, 1978). Most of the above methods required patience, skill, and practice, rendering the collecting of associated alpheid shrimp a rather difficult task.

Banner & Banner (1982) discussed the colour, pattern, and structural variability of the Indo-Pacific goby-associated alpheid shrimps of the *Brevirostris* group. This variability makes the determination of species from dead specimens extremely difficult. Banner & Banner (1982) suggested that the answer for species distinctions lies not in museum work with dead specimens but in careful field observations correlated with laboratory studies on living animals. Several types of associated alpheid shrimp, differing with respect to coloration, ecology and behaviour, have been described from the Seychelles (Polunin & Lubbock, 1977), the Great Barrier Reef (Cummins, 1979), and the northern Red Sea (Karplus *et al.*, 1974). The last authors suggested that different types of Red Sea shrimp of distinct colour patterns (Fig. 2) living on different substrata, in different types of burrows and with different fish partners, may represent valid species. Species validity of these types of Red Sea alpheid shrimp was confirmed by Professor Miya in his morphological studies (Karplus *et al.*, 1981).

The actual number of goby-associated alpheid shrimp is probably several times larger than already reported. With the further collection of shrimps and clarification of the "type" status, more species will certainly be described.

DISTRIBUTION OF ASSOCIATIONS

The association between gobiid fishes and burrowing alpheid shrimp has been reported by numerous workers from many localities in tropical as well as subtropical waters. The present author has chosen one among all references for each locality as an example. These associations were found in the Red Sea (Klauswitz, 1960), the Persian Gulf (Palmer, 1963), and in the Indian Ocean, in Aldabra Atoll (Polunin & Lubbock, 1977), the Seychelle Islands (Polunin & Lubbock, 1977), South Africa (Smith, 1959), Moçambique (Macnae & Kalk, 1962), the Maldive Islands (Hoese & Randall, 1982), and Madagascar (Thomassin, 1971). These associations were also reported in the Pacific, in Palau (Bayer & Harry-Rofen, 1957), Fiji, New Caledonia, American Samoa (Lubbock & Polunin, 1977), Solomon Islands (Hoese & Randall, 1982), Hawaii (Preston, 1978), Malluca (Hoese & Steene, 1978), Indonesia (Hoese & Steene, 1978), Marquesas (Banner & Banner, 1980), Marshall Islands (Paulson, 1978), Great Barrier Reef (Cummins, 1979), New Guinea (Hoese & Randall, 1982), Japan (Yanagisawa, 1978), and the Philippine Islands (Hoese & Randall, 1982), as well as in the Atlantic in Florida and the Bahamas (Bohlke & Chaplin, 1968).

Some associated gobies are very widely distributed. For example, *Amblyeleotris steinitzi*, was first described from the Red Sea and the Marshall Islands (Klauswitz, 1974a), and later also recorded from the Seychelles (Polunin & Lubbock, 1977), southern Japan (Yanagisawa, 1978), and the

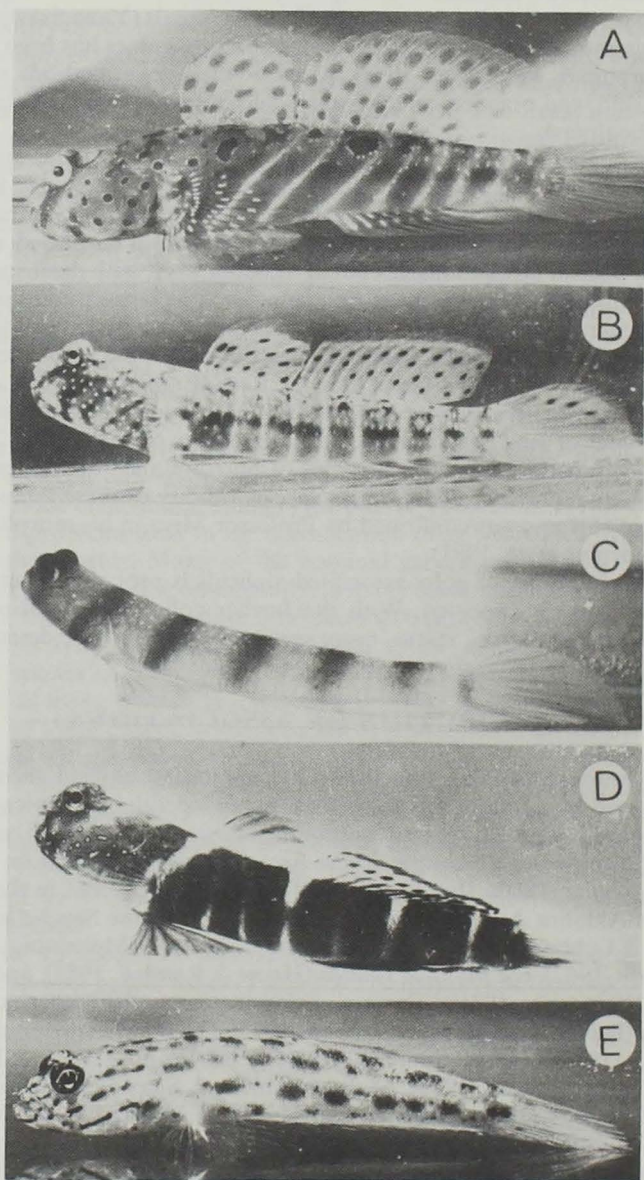


Fig. 1(A-E).—Species of gobies associated with shrimp in the northern Red Sea: A, *Cryptocentrus caeruleopunctatus*; B, *C. cryptocentrus*; C, *Amblyeleotris steinitzi*; D, *Cryptocentrus lutheri*; E, *Ctenogobiops maculosus*.

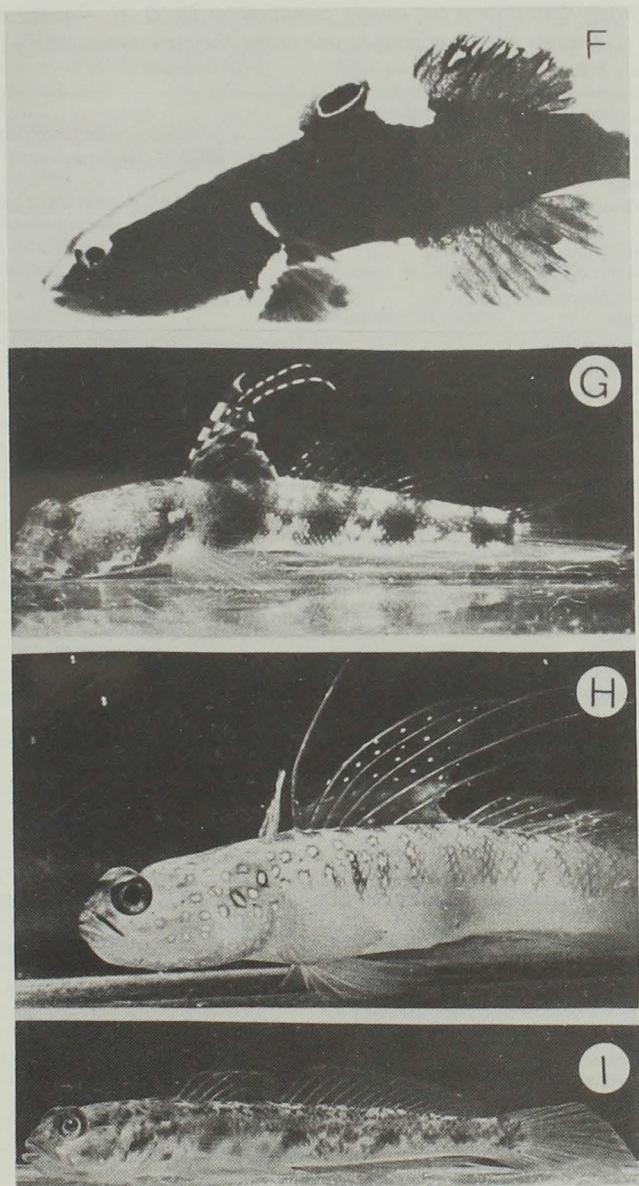


Fig. 1(F-I).—F, *Lotilia graciliosa*; G, *Eilatia latruncularia*; H, *Vanderhostia mertensi*; I, *V. delagoae*; from Karplus *et al.* (1981).

TABLE I

Species of gobies reported associated with burrowing alpheid shrimps: this table is largely based on a list kindly provided by Dr D. F. Hoese; where two species names appear in one entry they are synonyms

Species of goby	Reference
<i>Acentrogobius pflaumi</i>	Harada, 1969; Yanagisawa, 1978
<i>Gobius pflaumi</i>	
<i>Amblyeleotris aurora</i> Polunin & Lubbock, 1977	Polunin & Lubbock, 1977; Banner & Banner, 1980
<i>Amblyeleotris callopareia</i> Polunin & Lubbock, 1979	Polunin & Lubbock, 1979
<i>Amblyeleotris diagonalis</i> Polunin & Lubbock, 1979	Polunin & Lubbock, 1979
<i>Amblyeleotris fasciata</i>	Yanagisawa, 1976, 1978
<i>Zebreleotris fasciatus</i> (Herre, 1953)	
<i>Amblyeleotris fontanesii</i>	Hoese & Steene, 1978
<i>Gobius fontanesii</i> (Bleeker, 1852)	
<i>Amblyeleotris guttata</i>	Yanagisawa, 1978
<i>Pteroculiops guttatus</i> (Fowler, 1938)	
<i>Amblyeleotris gymnocephala</i>	Hoese & Steene, 1978
<i>Gobius gymnocephalus</i> (Bleeker, 1853)	
<i>Amblyeleotris japonica</i>	Miya & Miyake, 1969; Harada, 1969, 1971;
<i>Amblyeleotris japonicus</i> (Takagi, 1957)	Yanagisawa, 1976, 1978, 1982, 1984
<i>Amblyeleotris latifasciata</i> Polunin & Lubbock, 1979	Polunin & Lubbock, 1979
<i>Amblyeleotris macronema</i> Polunin & Lubbock, 1979	Polunin & Lubbock, 1979
<i>Amblyeleotris maculata</i> Yanagisawa, 1976	Yanagisawa, 1976, 1978
<i>Amblyeleotris ogasawarensis</i> Yanagisawa, 1978	Yanagisawa, 1978
<i>Amblyeleotris periophthalma</i>	Hoese & Steene, 1978
<i>Eleotris periophthalmus</i> (Bleeker, 1853)	
<i>Amblyeleotris randalli</i> Hoese & Steene, 1978	Hoese & Steene, 1978
<i>Amblyeleotris rhyax</i> Polunin & Lubbock, 1979	Polunin & Lubbock, 1979
<i>Amblyeleotris steinitzi</i>	Klausewitz, 1974a; Polunin & Lubbock, 1977; Yanagisawa, 1978; Cummins, 1979; Karplus <i>et al.</i> , 1981
<i>Cryptocentrus steinitzi</i> (Klausewitz, 1974)	Klausewitz, 1969; Banner & Banner, 1981
<i>Amblyeleotris sungami</i>	
<i>Cryptocentrus sungami</i> (Klausewitz, 1969)	Polunin & Lubbock, 1977
<i>Amblyeleotris wheeleri</i>	
<i>Cryptocentrus wheeleri</i> Polunin & Lubbock, 1977	
<i>Bathygobius curacao</i> Metzelaar	Karplus, pers. obs.
<i>Butis butis</i> Hamilton	Macnae & Kalk, 1962
<i>Cryptocentrus albidorsus</i>	Yanagisawa, 1978
<i>Mars albidorsus</i> Yanagisawa, 1978	
<i>Cryptocentrus caeruleomaculatus</i>	Yanagisawa, 1976, 1978
<i>Mars caeruleomaculatus</i> (Herre, 1933)	
<i>Cryptocentrus caeruleopunctatus</i>	Klausewitz, 1960, 1964; Clark <i>et al.</i> , 1968;
<i>Gobius caeruleopunctatus</i> (Ruppell, 1828)	Magnus, 1967; Zander, 1967; Banner & Banner, 1981
<i>Cryptocentrus cinctus</i>	Cummins, 1979
<i>Smilogobius cinctus</i> (Herre, 1936)	

TABLE I—continued

Species of goby	Reference
<i>Cryptocentrus cryptocentrus</i>	Luther, 1958a; Smith, 1959; Abel, 1960;
<i>Gobius cryptocentrus</i> (Valenciennes, 1837)	Klausewitz, 1960; Macnae & Kalk, 1962; Zander, 1967; Polunin & Lubbock, 1977; Banner & Banner, 1981; Karplus <i>et al.</i> , 1981 Polunin & Lubbock, 1977; Cummins, 1979
<i>Cryptocentrus fasciatus</i>	
<i>Gobiosoma fasciatum</i> (Playfair, 1866)	
<i>Cryptocentrus filifer</i>	Yanagisawa, 1978
<i>Gobius filifer</i> (Valenciennes, 1837)	
<i>Cryptocentrus inexplicatus</i>	Hoese, pers. comm.
<i>Smilogobius inexplicatus</i> (Herre, 1934)	
<i>Cryptocentrus insignitus</i>	Larson & Randall, pers. comm.
<i>Batman insignitus</i> (Whitley, 1956)	
<i>Cryptocentrus leucostictus</i>	Hoese, pers. comm.
<i>Gobius leucostictus</i> (Gunther, 1871)	
<i>Cryptocentrus lutheri</i> Klausewitz, 1960	Klausewitz, 1960; Palmer, 1963; Karplus <i>et al.</i> , 1981 Polunin & Lubbock, 1977
<i>Cryptocentrus malindiensis</i>	
<i>Iotogobius malindiensis</i> Smith, 1959	
<i>Cryptocentrus maudae</i> Fowler, 1937	Hoese, pers. comm.
<i>Cryptocentrus nigrocellatus</i>	Yanagisawa, 1978
<i>Mars nigrocellatus</i> (Yanagisawa, 1978)	
<i>Cryptocentrus niveatus</i> Valenciennes, 1837	Randall, pers. comm.
<i>Cryptocentrus obliquus</i>	Yanagisawa, 1976, 1978
<i>Smilogobius obliquus</i> (Herre, 1934)	
<i>Cryptocentrus shigensis</i> Kuroda, 1956	Hoese, pers. comm.
<i>Cryptocentrus strigiliceps</i>	Hoese, pers. comm.
<i>Mars strigiliceps</i> (Jordan & Snyder, 1901)	
<i>Ctenogobiops aurocingulus</i>	Lubbock & Polunin, 1977
<i>Aparrius aurocingulus</i> (Herre, 1935)	
<i>Ctenogobiops crocineus</i> Smith, 1959	Polunin & Lubbock, 1977; Lubbock & Polunin, 1977; Yanagisawa, 1978
<i>Ctenogobiops feroculus</i> Lubbock & Polunin, 1977	Lubbock & Polunin, 1977; Polunin & Lubbock, 1977
<i>Ctenogobiops maculosus</i> Fourmanoir, 1955	Klausewitz, 1960; Lubbock & Polunin, 1977; Clark <i>et al.</i> , 1968; Paulson, 1978; Karplus <i>et al.</i> , 1981
<i>Ctenogobiops pomastictus</i> Lubbock & Polunin, 1977	Lubbock & Polunin, 1977; Cummins, 1979
<i>Ctenogobiops tangaroai</i> Lubbock & Polunin, 1977	Lubbock & Polunin, 1977
<i>Eilatia latruncularia</i> Klausewitz, 1974	Klausewitz, 1974b; Karplus <i>et al.</i> , 1981
<i>Flabelligobius fourmanoiri</i> Smith, 1956	Randall, pers. comm.
<i>Gobionellus saepeplallens</i> Gilbert & Randall	Bohlke & Chaplin, 1968
<i>Gobionellus stigmalophius</i> Mead & Bohlke	Bohlke & Chaplin, 1968
<i>Gobius nudiceps</i>	Macnae, 1957
<i>Cattrogobius nudiceps</i>	
<i>Lotilia graciliosa</i> Klausewitz, 1960	Klausewitz, 1960, 1970; Banner & Banner, 1981; Karplus <i>et al.</i> , 1981 Yanagisawa, 1978, 1982
<i>Mahidolia mystacina</i>	
<i>Gobius mystacina</i> Valenciennes, 1837	
<i>Nes longus</i> Nichols, 1914	Longley & Hildebrand, 1941; Bohlke & Chaplin, 1968; Weiler, 1976
<i>Psilogobius mainlandi</i> Baldwin, 1972	Mochring, 1972; Preston, 1978
<i>Stonogobiops dracula</i> Polunin & Lubbock, 1977	Polunin & Lubbock, 1977; Banner & Banner, 1980; Hoese & Randall, 1982
<i>Stonogobiops medon</i> Hoese & Randall, 1982	Hoese & Randall, 1982

TABLE I—continued

Species of goby	Reference
<i>Stonogobiops nematodes</i> Hoese & Randall, 1982	Hoese & Randall, 1982
<i>Stonogobiops xanthurhinica</i> Hoese & Randall, 1982	Yanagisawa, 1976; Hoese & Randall, 1982
<i>Tomiyamichthys oni</i>	Yanagisawa, 1978, 1982, 1984
<i>Cryptocentrus oni</i> (Tomiyama, 1936)	
<i>Tomiyamichthys randalli</i> Goren & Karplus, 1983	Goren & Karplus, 1983
<i>Vanderhorstia ambanoro</i> Fourmanoir, 1957	Hoese, pers. comm.
<i>Vanderhorstia delagoae</i>	Macnae & Kalk, 1962; Klausewitz, 1964; Magnus, 1967; Banner & Banner, 1981; Karplus <i>et al.</i> , 1981
<i>Gobius delagoae</i> (Barnard, 1937)	Yanagisawa, 1978
<i>Vanderhorstia lanceolata</i> Yanagisawa, 1978	Klausewitz, 1974b; Yanagisawa, 1978, 1982, 1984; Karplus <i>et al.</i> , 1981
<i>Vanderhorstia mertensi</i> Klausewitz, 1974	Polunin & Lubbock, 1977; Yanagisawa, 1978; Cummins, 1979
<i>Vanderhorstia ornatisissima</i> Smith, 1959	Harada, 1969; Yanagisawa, 1978
<i>Vireosa hanae</i> Jordan & Smith, 1959	Polunin & Lubbock, 1977
<i>Yongeichthys pavidus</i> Smith, 1959	
<i>Amoya signatus</i>	

TABLE II

Species of burrowing alpheid shrimp reported associated with gobiid fishes

Species of shrimp	Reference
<i>Alpheus bellulus</i>	Miya & Miyake, 1969; Harada, 1969, 1972; Yanagisawa, 1976, 1978, 1982, 1984; Karplus <i>et al.</i> , 1981
<i>Alpheus brevicristatus</i>	Harada, 1969; Yanagisawa, 1978
<i>Alpheus brevirostris</i>	Karplus <i>et al.</i> , 1981
<i>Alpheus djiboutensis</i>	Luther, 1958a,b; Klausewitz, 1960; Harada, 1972; Karplus <i>et al.</i> , 1972a,b, 1981; Karplus, 1970, 1981; Paulson, 1978; Banner & Banner, 1981, 1983
<i>Alpheus floridanus</i>	Weiler, 1976
<i>Alpheus crassimanus</i>	Macnae, 1957; Thomassin, 1971; Farrow, 1971
<i>Alpheus malabaricus</i>	Macnae & Kalk, 1962
<i>Alpheus ochrostriatus</i>	Karplus <i>et al.</i> , 1981
<i>Alpheus purpurilenticularis</i>	Karplus, 1981; Karplus <i>et al.</i> , 1981
<i>Alpheus randalli</i>	Banner & Banner, 1980; Hoese & Randall, 1982
<i>Alpheus rapacida</i>	Macnae & Kalk, 1962; Magnus, 1967; Moehring, 1972; Preston, 1978; Yanagisawa, 1978, 1982, 1984; Banner & Banner, 1981, 1982
<i>Alpheus rapax</i>	Macnae & Kalk, 1962; Magnus, 1967; Moehring, 1972; Polunin & Lubbock, 1977; Preston, 1978; Banner & Banner, 1981, 1982; Karplus <i>et al.</i> , 1981
<i>Alpheus rubromaculatus</i>	Karplus <i>et al.</i> , 1981

Great Barrier Reef (Cummins, 1979). Other species like *Eilatia latruncularia* and *Tomiyamichthys randalli* have so far only been described from the northern Red Sea (Klausewitz, 1974b; Goren & Karplus, 1983). One should be very cautious when speculating about endemism because the collection of

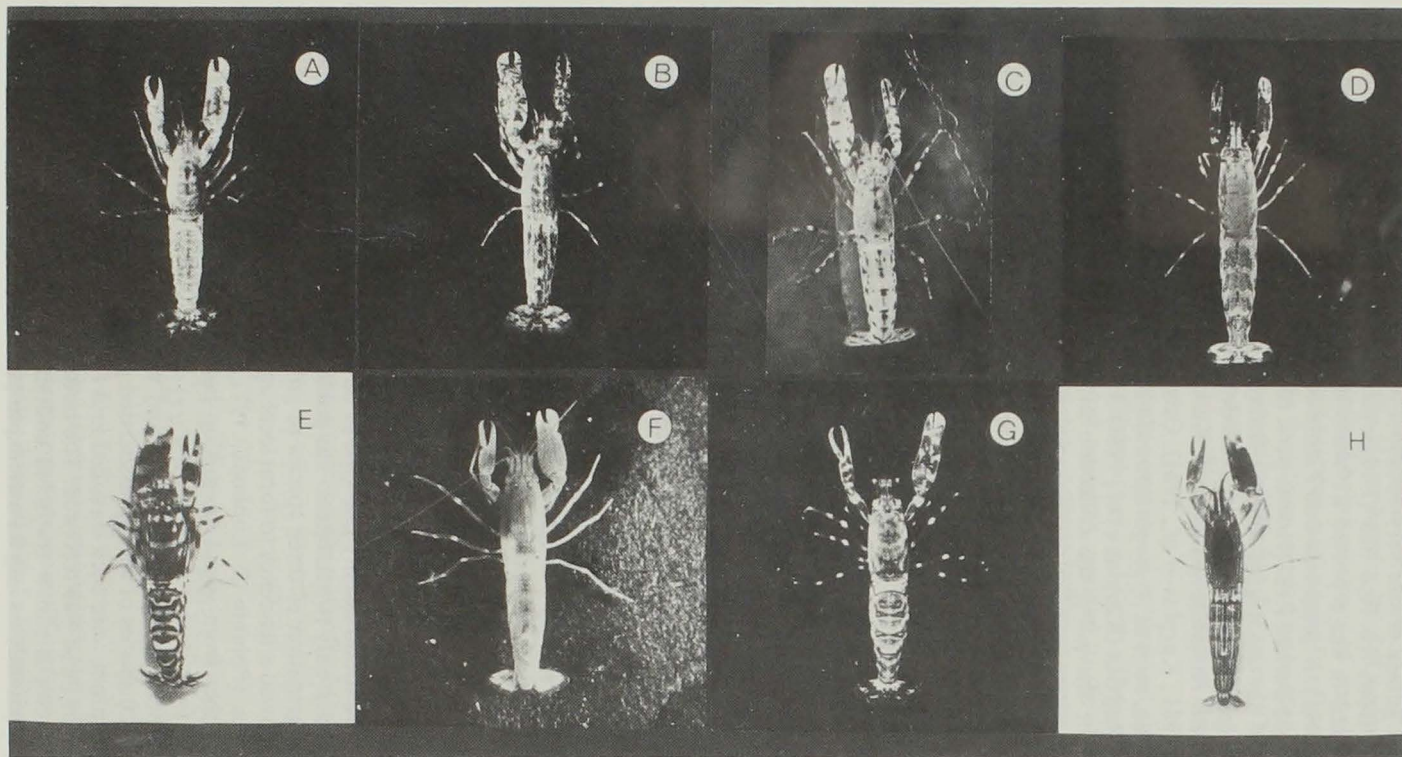


Fig. 2.—Species shrimp associated with gobies in the northern Red Sea: A, *Alpheus purpurilenticularis*; B, *A. rapax*; C, *A. rubromaculatus*; D, *A. brevirostris*; E, *A. bellulus*; F, *A. ochrostriatus*; G, *A. djiboutensis*; H, *Alpheus* sp.; from Karplus *et al.* (1981).

associated gobies is still very sporadic and patchy, *Lotilia graciliosa*, first described from the Red Sea (Klausewitz, 1960) was known only in that locality until it was reported 21 years later in the Fiji Islands (Banner & Banner, 1981). *L. graciliosa* and *Eilatia latruncularia* were recently observed in the Great Barrier Reef (Hoese, pers. comm.).

Some of the associated alpheid shrimps have a very wide distribution. *Alpheus rapax*, for example, was recorded from the Red Sea, Moçambique, Hawaii, and Australia (Macnae & Kalk, 1962; Preston, 1978; Banner & Banner, 1981; Karplus *et al.*, 1981). Other species were only recorded from a single area, such as *A. purpurilenticularis* that has so far only been reported from the Red Sea (Karplus *et al.*, 1981). In the case of the shrimp, even more so than for the goby, the collection of animals is very limited and their identification complex, so that no conclusion can be drawn from the available record on the distribution and endemism of associated shrimps.

ECOLOGY OF ASSOCIATIONS

The species of gobiid fishes and alpheid burrowing shrimps in the associations live in various kinds of sediments, ranging from silty mud to coral rubble, in the intertidal zone down to a depth of more than 50 m, and in a variety of habitats, *e.g.*, mud flats and sea-grass beds (Polunin & Lubbock, 1977; Yanagisawa, 1978). The ecology of these associations is usually treated very superficially, either as an appendix to taxonomical studies, as a single element within a much larger ecological system, or as a background to behavioural studies. Most of these studies are of a general descriptive nature usually concerned with a single association, or more often, with a single species of goby. They refer to depth range, the character of the sediment and occasionally to the type of habitat. These studies have not attempted to analyse qualitatively or quantitatively differences between sympatric association.

Polunin & Lubbock (1977) were the first to deal with the problem of habitat specificity of shrimp-associated gobies. In their study, carried out in the Seychelle Islands, they examined the distribution of 13 species of associated gobies in a small bay on the northwestern coast of Mahe. Seven different sandy habitats were defined in this protected bay that contained both well-developed coral reefs and extensive sandy habitats, extending from the intertidal zone to lower than 30 m depth. A marked degree of habitat segregation was exhibited by the different species of gobies. Five out of the 13 examined species were found in only one type of habitat while four additional species were found in only two habitats. The publication reported more generally on habitat segregation of three species of gobies at Aldabra Atoll. Most goby species showed a tendency to form local aggregations, frequently made up of one species (Polunin & Lubbock, 1977). This phenomenon could have resulted either from social interaction between gobies, from habitat segregation, or from both.

In southern Japan, depth range and substratum specificity were investigated in 20 species of shrimp-associated gobies (Yanagisawa, 1978). Depth and substratum were each classified into four categories and the occurrence of gobies in these was recorded. The bottom substratum inhabited by each gobiid species is rather restricted and similar, among the localities, each species apparently having its own depth preference.

The ecology of six species of gobies and their four types of shrimp partners was studied at One Tree Reef, in the Great Barrier Reef (Cummins, 1979). The specificity of the substratum defined by proportions of gravel and sand, was found to be almost entirely lacking. No single species of goby and no type of shrimp was segregated from the others, according to Pielou's (1969) index of segregation, and to the nearest neighbour distances. These results contrast with the local aggregations and marked level of habitat segregation reported for species of gobies from Lizard Island, Great Barrier Reef (Polunin & Lubbock, 1977).

The distribution of several sympatric species of gobies and shrimps was studied in the northern Red Sea (Karplus *et al.*, 1981). The vertical distribution was analysed by a series of transects, parallel to the shore set at depth intervals of 2 m, down to a depth of 20 m. Different species of gobies and shrimps exhibited a different vertical distribution as regard both depth range and relative abundance. In shallow and in deep water, the species of shrimps differed whereas, as far as the gobies were concerned, the same species were found, their number decreasing with depth. In the shallow water of a sandy lagoon, four species of shrimps were found in local aggregations, with little overlap in different sub-habitats (Fig. 3). These sub-habitats were defined by the distance from the reef and the character of the sediment (mean grain size and sorting). It is difficult to evaluate the independent effect of these variables as the two are intercorrelated. The preference of different shrimp species for different types of sediment could depend on differing diets, or on a different structure of the fine hairs of the chela which are used in sediment transport. A similar segregation of burrowing alpheid shrimps in specific habitats has been described for several associated (Macnae & Kalk, 1962) and free living species (Nolan & Salmon, 1970). *A. bellulus* from Japan (Yanagisawa, 1982) and *A. floridanus* from Puerto Rico (Weiler, 1976) were both, however, reported to live on a wide range of substrata. In contrast to shallow-water shrimps, deep-water shrimps in the Red Sea do not show segregation in different sub-habitats, probably due to the more uniform character of the sediment at that depth.

In contrast to the Red-Sea burrowing shrimp of shallow water, the associated gobies show less habitat specificity and occur in different habitats depending on the species of their shrimp partner. This may possibly be due to the fact that these gobies do not burrow, and unlike the shrimps, do not feed on organic material found in the sediment or on epifauna and interstitial animals (Magnus, 1967; Harada, 1969). Burrowing fish, like burrowing alpheid, show a stronger attachment to a specific type of substratum (Rao, 1939; Colin, 1972; Webb, 1974).

BURROW STRUCTURE, CONSTRUCTION, AND DYNAMICS

BURROW STRUCTURE

The burrow structure can be divided into two components, the structure and number of its openings and its subterranean structure (Karplus *et al.*, 1974).

The typical shape of the burrow opening of a goby-associated shrimp is

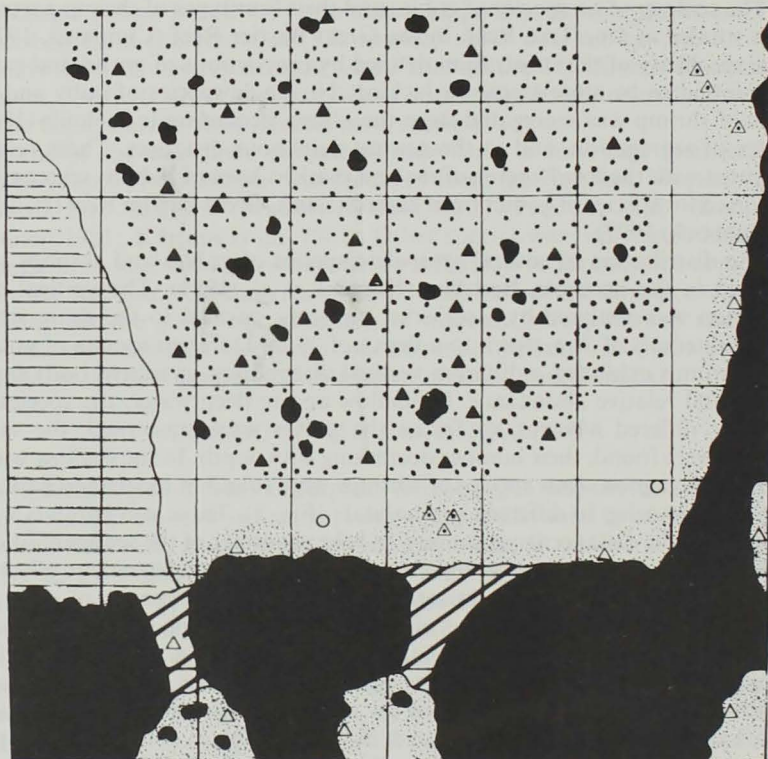


Fig. 3.—Distribution of associated gobies and shrimps in the lagoon of the Elat Nature Reserve: each square is 1×1 m; coarse stippling, coarse sediment; fine stippling, fine sediment; blank, intermediate sediment; black, living and dead corals; horizontal rules, stones; sloping rules, tunnels in the reef; ▲, *Alpheus purpurilenticularis* and *Amblyeleotris steinitzi*; △, *Alpheus rubromaculatus* and *Lotilia graciliosa*; △, *Alpheus rapax* and *Ctenogobiops maculosus*; ○, *Alpheus djiboutensis* and *Cryptocentrus lutheri*; from Karplus *et al.* (1981).

asymmetrical, its roof and sides being embedded by the shrimp in coral and shell fragments to prevent the collapse of its walls. It has a sandy floor leading to a shallow sloping ramp consisting of sand transported from within the burrow; the ramp is often used by the goby as a lookout post. This type of burrow opening has been described in connection with *A. djiboutensis* (Luther, 1958a; Karplus *et al.*, 1972a, 1974), *A. crassimanus* (Farrow, 1971), *A. bellulus* (Yanagisawa, 1984), and *A. purpurilenticularis* (Karplus, 1979). The structure of the burrow opening of different species is not necessarily similar. Various types of burrow openings have been found in the northern Red Sea for different goby-associated shrimp (Karplus *et al.*, 1974). In addition to the typical asymmetrical burrow opening, two symmetrical ones, an elevated tube-like opening and a funnel-like opening have also been described (Fig. 4). The

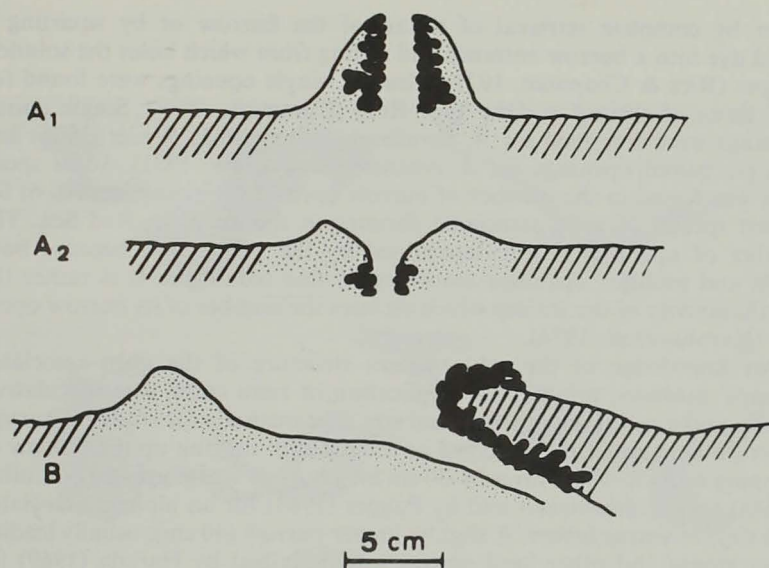


Fig. 4.—The three basic structures of burrow openings of goby-associated shrimps in the northern Red Sea: A1, symmetrical tube-like opening; A2, symmetrical funnel-like opening; B, asymmetrical opening; dotted areas, sand transported by shrimp; hatched area, undisturbed sediment; black patches, coral, shell, and stone fragments; from Karplus *et al.*, 1974).

appearance of symmetrical and asymmetrical openings depends largely on the substratum. Mainly asymmetrical openings are found in the burrows of *A. djiboutensis* and *A. purpurilenticularis* located in coarse and intermediate sand while symmetrical openings, embedded on all sides in coral fragments are more frequently found in the burrows of *A. rapax* (tube-like) and *A. rubromaculatus* (funnel-like), both located in fine sediments.

A detailed analysis of the burrow opening structure of four different types of shrimps was carried out at One Tree Reef (Cummins, 1979). Each burrow entrance was classified according to four categories (*e.g.* angle of descent) and seven different points were measured (*e.g.* width of entrance). Numerical and non-numerical attributes of the burrows were simultaneously analysed using multivariate techniques. No single feature or combination of features was diagnostic of any one type of shrimp although two groups, each comprising two types of shrimps, could be distinguished.

A shallow and narrow groove stretching from the burrow opening has been described for several shrimp species. A short (20–30 cm) and rather deep (10 cm) groove was described for *A. djiboutensis* (Luther, 1958a), a somewhat longer (40–50 cm) and shallow one (1–2 cm) for *A. purpurilenticularis* (Karplus, 1979), while a shallow (2–3 cm) and very long (up to 80 cm) groove was described for *A. bellulus* (Yanagisawa, 1984). These grooves facilitate the activities of the shrimp outside their burrows (Karplus, 1979).

The number of openings of a single burrow can be accurately determined

either by complete retrieval of a cast of the burrow or by squirting a liquid dye into a burrow entrance and noting from which holes the solution escapes (Rice & Chapman, 1971). Usually, single openings were found for four types of shrimp at One Tree Reef (Cummins, 1979). Single paired openings were described for *A. floridanus* (Shinn, 1968; Weiler, 1976) and multiple paired openings for *A. crassimanus* (Farrow, 1971). Some specificity was found in the number of burrow openings (ranging from 1–6) for several species of goby-associated shrimps in the northern Red Sea. The number of openings is not determined by the substratum because both single and multiple openings are found in fine sediments. It is rather the specific activity of the shrimp which dictates the number of its burrow openings (Karplus *et al.*, 1974).

Our knowledge of the subterranean structure of the goby-associated shrimps' burrows, prior to the application of resin casts, was speculative, usually under-estimating their actual size. The methods for studying burrow structure were either not specified or consisted of digging up the burrow or pumping water into it. Only a 20–30 cm long burrow was suggested by Luther (1958a) for *A. djiboutensis* and by Palmer (1963) for an alpheid associated with *Cryptocentrus lutheri*. A slightly longer burrow (40 cm), usually leading under stones and other hard objects was described by Harada (1969) for *Alpheus bellulus*. Following unsuccessful attempts to dig out the associated goby and shrimp, Smith (1959) concluded that the burrows were deep. The burrows of two shrimps probably *A. rapax* and *A. rapacida* were described as shallow, at least 70 cm long, parallel to the surface, and occasionally branching off (Magnus, 1967).

The exact study of the structure of infralittoral burrows of crustaceans only started about twenty years ago when polyester and epoxy resins became available. Resin casts are superior to those made of plaster of Paris whose use is limited to the intertidal zone. The resins have several virtues: an ability to harden underwater, a controllable viscosity, strength, impregnation of substratum and possible "freezing" of burrow producers and co-habitants (Farrow, 1971).

The burrow structure of eight different species and four types of associated shrimps has been investigated by the application of epoxy and polyester resins—*A. crassimanus* (Farrow, 1971), *A. djiboutensis*, *A. purpurilenticularis* and *A. rubromaculatus* (Karplus *et al.*, 1974), *A. floridanus* Weiler, 1976), *A. rapax* (Karplus *et al.*, 1974; Preston, 1978), *A. rapacida* (Preston, 1978), *A. bellulus* (Yanagisawa, 1984), tapestry, pink, banded and pale shrimp types (Cummins, 1979).

Goby-associated shrimps usually have shallow burrows branching off irregularly and in close contact with hard objects like coral and stone boulders within the sediment (Fig. 5). Due to the tendency of sand to collapse, these hard objects were used to support the subterranean burrow structure determining to a high degree their irregular structure and their lack of species' specificity. The effect of the substratum on the burrow structure has been demonstrated for *A. crassimanus* (Farrow, 1971). When located in a coarse substratum with hard objects, it had an irregular burrow structure but, when located in muddy silts, the burrow had a regular dichotomous branching pattern.

The burrow casts retrieved from sediment lacking supporting objects had

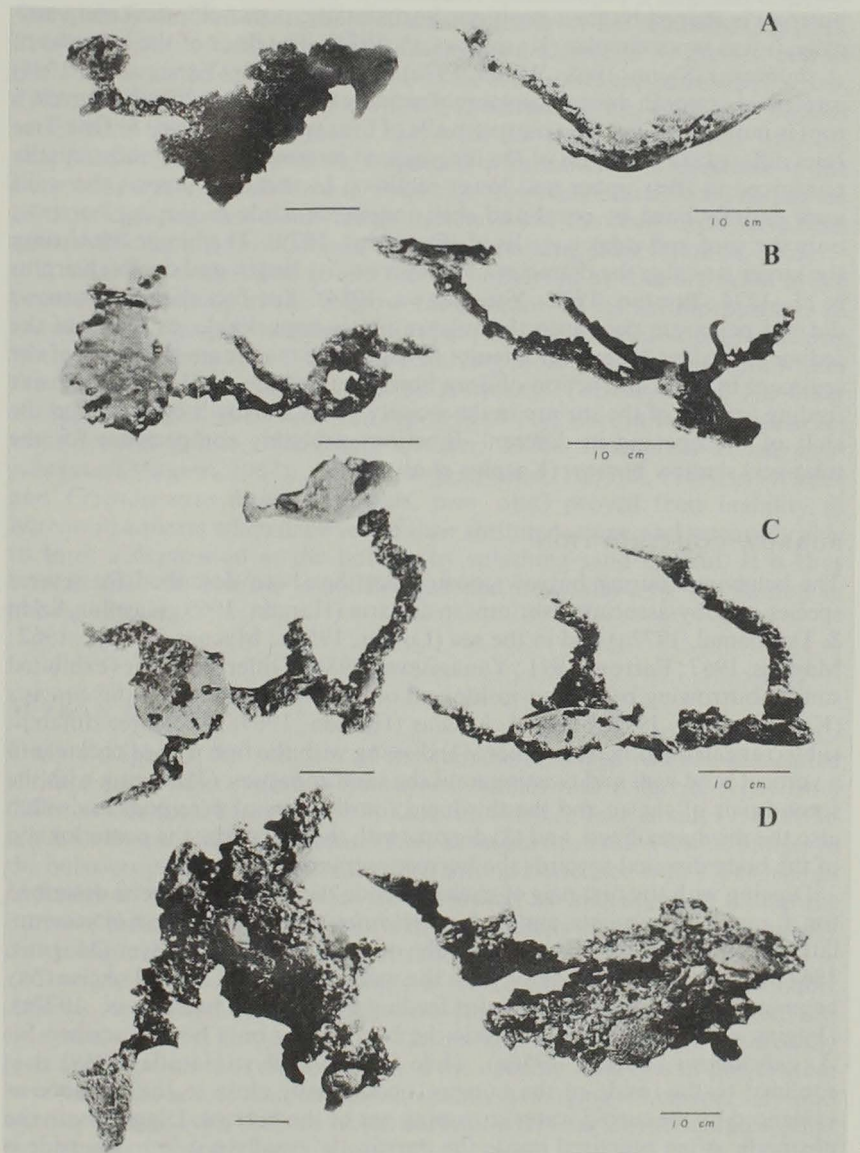


Fig. 5.—Resin casts of burrows of young *Alpheus bellulus*: A, B, and D, associated with *Amblyeleotris japonica*; C, associated with *Stonogobius* sp.; scale bars are 10 cm; from Yanagisawa (1984).

an even diameter at different points, while the diameter of a burrow leading under rocks or corals was irregular with occasional chamber-like enlargements (Karplus *et al.*, 1974; Yanagisawa, 1984). The cross section of the burrows is shaped by their position: horizontally, it was elliptical and vertically, it was more circular (Karplus *et al.*, 1974). The floor of the burrows of *A. floridanus* (Shinn, 1968; Weiler, 1976) and *A. bellulus* (Yanagisawa, 1984) is relatively smooth due to transport of sand by the shrimp, while the burrow's roof is more irregular. The burrow walls of four types of shrimps at One Tree Reef differed from the rest of the investigated burrows by being substantially reinforced in their upper and lower sections. In vertical burrows the walls were entirely lined by coral and shell fragments while in sloping burrows, only the roof and sides were lined (Cummins, 1979). The larger the shrimp the larger was also the diameter of its burrow, its length and depth (Karplus *et al.*, 1974; Preston, 1978; Yanagisawa, 1984). The fact that the burrows did not penetrate deep into the substratum is remarkable, as many of the sediment-feeding organisms attempt to utilize the maximum thickness of the sediment in the construction of deep burrows (Farrow, 1971). The intensive feeding activity of the shrimp in the vicinity of the burrow's opening and the shift of the opening in different directions probably compensates for the relatively shallow burrow (Karplus *et al.*, 1974).

BURROW CONSTRUCTION

The behaviour during burrow construction has been described for several species of goby-associated shrimps in aquaria (Harada, 1969; Karplus, Szlep & Tsurumal, 1972a) and in the sea (Luther, 1958a; Macnae & Kalk, 1962; Magnus, 1967; Farrow, 1971; Yanagisawa, 1984). Different species exhibited similar burrowing behaviour inside and outside the burrows. *A. djiboutensis* (Karplus *et al.*, 1972a) and *A. bellulus* (Harada, 1969) used three different subterranean digging techniques: (1) digging with the first pair of chelae into a vertical sand wall and twisting until the sand collapses, (2) digging with the second pair of chelae and the third and fourth pairs of pereopods and often also the third maxiliped, and (3) digging with the pleopoda, the posterior end of the body directed towards the burrow entrance.

Digging with the first pair of chelae outside the burrow has been described for *A. rapax*, *A. rapacida*, and *A. purpurilenticularis* in the process of accumulating sediment in the burrow from the outside upper intact layer (Magnus, 1967; Karplus, 1979). Digging with the walking legs and second chelae may be practised outside the burrow for feeding purposes (Karplus *et al.*, 1972a). Digging with the pleopoda outside the burrow has only been described for *A. djiboutensis* (Luther, 1958a), while in *A. bellulus* (Harada, 1969) it is confined to the inside of the burrow, occasionally close to the entrance as evidenced by the turbid water streaming out of the burrow. Digging with the pleopoda, often practised inside the burrow, is usually not found outside it because during that activity the shrimp's head is directed towards the entrance and the alpheid's rapid withdrawal is hindered (Magnus, 1967).

The transport of sand grains and small stones from the inner parts of the burrow is done by the first pair of the strongly compressed chelae. The two chelae join together to form a kind of spade broadened by rows of long hairs fringing the dorsal and ventral margins of both chelae (Magnus, 1967; Miya

& Miyake, 1969). Small amounts of sediment are lifted and transported on the chelae while large amounts of sediment remain on the ground and are moved by the chelae, acting as a bulldozer. Occasionally a large flat object—like a shell—is used for a more efficient transfer of the sediment (Magnus, 1967). Twiglets of corals and shell fragments are grasped by the first pair of chelae and carried out of the burrow to the area above the entrance (Farrow, 1971; Magnus, 1967; Yanagisawa, 1984; Karplus *et al.*, 1972a). *A. bellulus* seizes coral and shell fragments only with the small chela, never with the snapping chela but secures the fragments with the latter's assistance in the burrow aperture to reinforce it. Plasticity, however, is attributed to the use of these chelipeds since individuals that have lost the small chela have been observed to handle this material with the remaining chela (Harada, 1969).

A single, non-identified gobiid fish was observed at Aldabra Atoll in the process of assisting in the burrow construction of its shrimp partner, *A. crassimanus*. This goby enlarged the upper part of the dichotomous branching burrow in the form of a U-tube by removing mouthfuls of mud from within the burrow and ejecting them at the periphery (Farrow, 1971). No other shrimp-associated goby has been reported to take part in burrow construction. Several gobies, *Nes longus* (Weiler, 1976), *Cryptocentrus caeruleopunctatus* (Magnus, 1967), *Amblyeleotris japonica* (Harada, 1969), *A. steinitzi* and *Cryptocentrus lutheri* (Karplus, pres. obs.) proved their inability to burrow in aquaria when deprived of their shrimp partner, and were only able to form a depression at the bottom by splashing sand around. It is thus evident that the burrow is constructed and maintained by the shrimp in almost all cases.

BURROW DYNAMICS

Daily changes in the position of the burrow openings of goby-associated shrimps have been reported for several species and different types from different localities (Magnus, 1967; Karplus, Szlep & Tsumamal, 1974; Polunin & Lubbock, 1977; Cummins, 1979; Yanagisawa, 1982, 1984). Changes in the burrow openings of a non-identified shrimp associated with *Ctenogobiops feroculus* at Aldabra Atoll were demonstrated by indicating on a map the burrow positions on two consecutive days, as well as the changes in frequency distribution of nearest neighbour distances (Polunin & Lubbock, 1977).

Changes in the burrow openings of two species of shrimps, probably *Alpheus rapax* and *A. rapacida*, were studied in the northern Red Sea (Magnus, 1967). The positions of the burrow entrances were marked by inserting two iron rods on both sides of the opening. Changes of the position were continuous and unidirectional, usually averaging 40 cm per day and were correlated with the size of the shrimp, character of the sediment, and occurrence of obstacles within it.

The changes in the position of the burrow openings of *A. bellulus* associated with *Amblyeleotris japonica* were studied in Japan (Yanagisawa, 1982, 1984). Individual burrows were identified at localities of high densities by the tagging of the associated goby that seldom exchanged its shrimp partner. The burrows were also identified by the combination of the sides of the large chela of both male and female shrimps and by their size and coloration. The distance of

daily shift of the entrance reached 160 cm. There was no regular shift pattern but the positions of a burrow were confined, over several months, to a limited range usually with a horizontal extent of about a half to two square metres.

The dynamics of burrow openings of several sympatric species of burrowing goby-associated shrimps have been studied in a shallow lagoon in the northern Gulf of Elat (Karplus *et al.*, 1974). Burrows were not studied in densely populated areas to avoid confusion. The burrow openings were marked with iron rods, similarly to Magnus (1967) and their daily changes in position—distance and angle—were recorded for ten days, but several marked burrows were occasionally examined over a period of six months. The maximal daily changes of the burrow entrance position, which ranged from 30 to 80 cm were species specific, as also was the relatively small area to which the openings were confined. The daily displacement of the burrows of the different species was correlated with their type of substratum and their proximity to large coral boulders. The coarser the sediment the larger the change while the closer to the reef wall or large coral boulders the smaller the daily shift in position. The changes in the burrow structure are apparently restricted to the upper shallow parts of the burrow, while the deeper parts, often leading under and between large boulders, remain stable (Karplus *et al.*, 1974).

A comparative study of the changes of the burrow opening of four types of shrimps was carried out at One Tree Reef (Cummins, 1979). Maximal daily shifts were type-specific and ranged from 50 to 160 cm. Each burrow usually had three openings but usually only one was open at any time. The entrance of each burrow recurred at exactly the same position, even when the recordings were made after a period of two years.

Three different mechanisms for shifting the burrow opening have been described for different species. According to Magnus (1967), the shift resulted only from the feeding activity of the shrimp which removed substratum from the area overlying the burrow, thus continuously shifting the opening backwards. The bigger the shrimp the more substratum was removed. The shift of the burrow is due to the activities of both partners according to Karplus *et al.* (1974). The irregular multidirectional shift results from the activity of *Amblyeleotris steinitzi* wedging its head through the substratum to create a new opening. *Alpheus purpurilenticularis* follows and enlarges the new opening while the old one rapidly collapses (Fig. 6). The fixed changes in the position of the burrow openings of the Australian types (Cummins, 1979) probably result only from the activity of the shrimp. Both the upper and lower parts of the burrow are reinforced by coral fragments, so they are stable and the shrimp is only alternately clearing or blocking them with sediment, thus reforming the openings at the same positions.

The change in the position of the burrow opening is important for both shrimp and fish. The shrimp thereby gains access to additional suitable substrata outside the burrow. The territorial fish not only protects its shelter against intruders but is actively controlling the mobile system of burrow openings, spacing them out and thus controlling the density of the associations. *Amblyeleotris steinitzi* reacted to a camera placed on a tripod in front of its burrow by shifting the entrance 25 cm away from the camera (Karplus, pers. obs.). Similarly, instead of having to abandon its burrow because of a

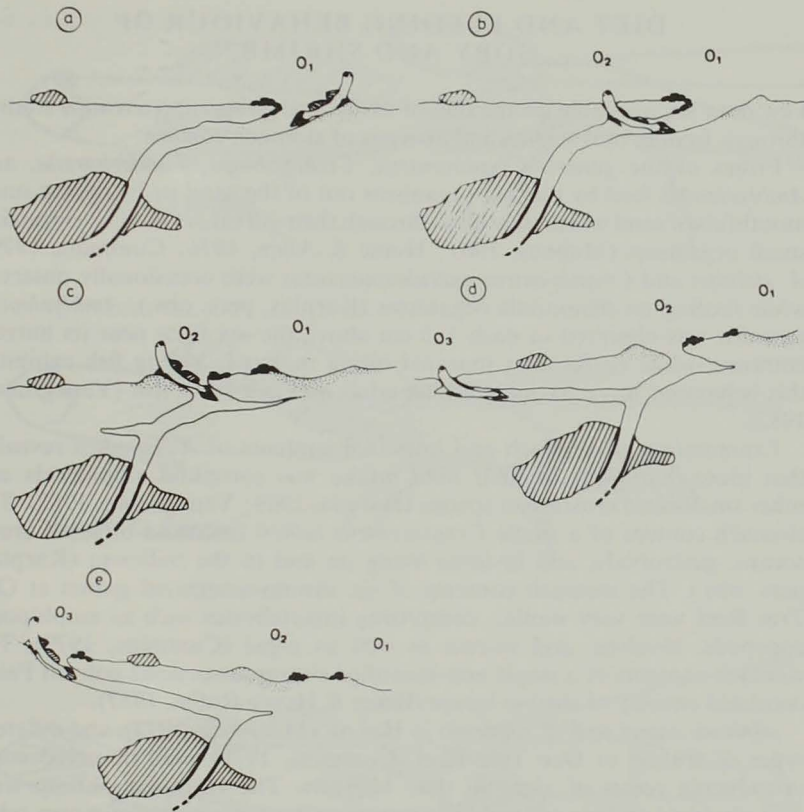


Fig. 6.—Dynamics of the upper burrow system in the association of *Amblyeleotris steinitzi* with *Alpheus purpurilenticularis*: a, fish located in front of burrow opening (O₁); b, formation of new burrow opening (O₂) by fish; c, opening O₁ collapsed, opening O₂ functional; d, formation of additional opening (O₃) by fish; e, openings O₁ and O₂ collapsed, opening O₃ functional; from Karplus *et al.* (1974).

territorial conflict with its dominant neighbour, a goby can form a new opening further away. During the reproductive season, the fish has to reach its partner and is thus exposed to predators. The shift of the burrow opening towards the partner may reduce the danger.

A detailed study of the daily changes of burrow entrance features was made at on One Tree Reef (Cummins, 1979). Some individuals of each type of shrimp showed the same structure for five days, while others showed a daily variation in the structure of the entrances. Daily fluctuations occurred in the number of burrow openings of several Red Sea shrimps. A complete blockage of all the openings was occasionally observed; this lasted for 1 to 3 days, after which a significantly greater shift occurred indicating intensive subterranean digging activity, even though no activity was observed on the surface (Karplus *et al.*, 1974).

DIET AND FEEDING BEHAVIOUR OF
GOBY AND SHRIMP

Few data are available on the diet of associated gobies and shrimps studied through feeding movements and analysis of stomach content.

Fishes of the genera *Cryptocentrus*, *Ctenogobiops*, *Vanderhorstia*, and *Amblyeleotris* feed by picking organisms out of the sand or by taking small mouthfuls of sand which they filter through their gill rakers thereby extracting small organisms (Magnus, 1967; Hoese & Allen, 1976; Cummins, 1979). *A. steinitzi* and *Cryptocentrus caeruleopunctatus* were occasionally observed while feeding on planktonic organisms (Karplus, pers. obs.). *Amblyeleotris japonica* was observed to dash 1–5 cm above the sea floor near its burrow entrance, while performing repeated biting motions. Young fish exhibited this behaviour more frequently than adult and sub-adult fish (Yanagisawa, 1982).

Examination of stomach and intestinal contents of *A. japonica* revealed that more than 90% of their food intake was corophiid amphipods and other small-sized crustacean species (Harada, 1969; Yanagisawa, 1982). The stomach content of a single *Cryptocentrus lutheri* consisted of small crustaceans, gastropods, and bivalves living on and in the sediment (Karplus, pers. obs.). The stomach contents of six shrimp-associated gobies at One Tree Reef were very similar, comprising invertebrates such as amphipods, copepods, bivalves, and worms as well as algae (Cummins, 1979). The stomach contents of a single non-identified shrimp-associated goby at Palau consisted entirely of shrimp larvae (Bayer & Harry-Rofen, 1957).

Alpheus rapax and *A. rapacida* in Hawaii (Moehring, 1972), and different types of shrimp at One Tree Reef (Cummins, 1979) were observed while introducing pieces of algae in their burrows. The Hawaiian shrimp were also observed to snip off and take into their burrows pieces of worm tubes protruding around the burrow entrances (Moehring, 1972). Digging in the sediment with the first pair of chela and the subsequent introduction of the sediment into the burrow has been described for *A. purpurilenticularis* (Karplus, 1979), *A. rapax* (Karplus, 1976), *A. djiboutensis* (Karplus, 1976), and probably *A. rapacida* (Magnus, 1967). Only the upper undisturbed sediment layer, approximately 5–10 mm thick, probably rich in organic materials, was introduced in this way; sediment previously removed from the burrow was never re-introduced (Magnus, 1967). The granulometric character of the undisturbed sediment, close to the burrow opening of *A. floridanus* did not differ significantly from that ejected from the burrow (Weiler, 1976). A comparison between the undisturbed sediment and the one removed from the burrow, as regards its organic content and composition, would be of interest but has never been determined. The stomach contents of *A. bellulus* consist of fairly large amounts of unidentified materials and some nematodes, copepods and amphipods, so that the diet is assumed to consist mainly of detritus, epi- and interstitial fauna (Harada, 1969).

The interrelationship between the feeding behaviour of goby and shrimp is of interest. Several authors have stated that the goby seeks food in the sediment excavated by the shrimp (Abel, 1960; Farrow, 1971; Hoese & Steene, 1978) or eats small invertebrates which are disturbed by the sediment ejected from the burrow (Magnus, 1967). In both cases, the goby benefits

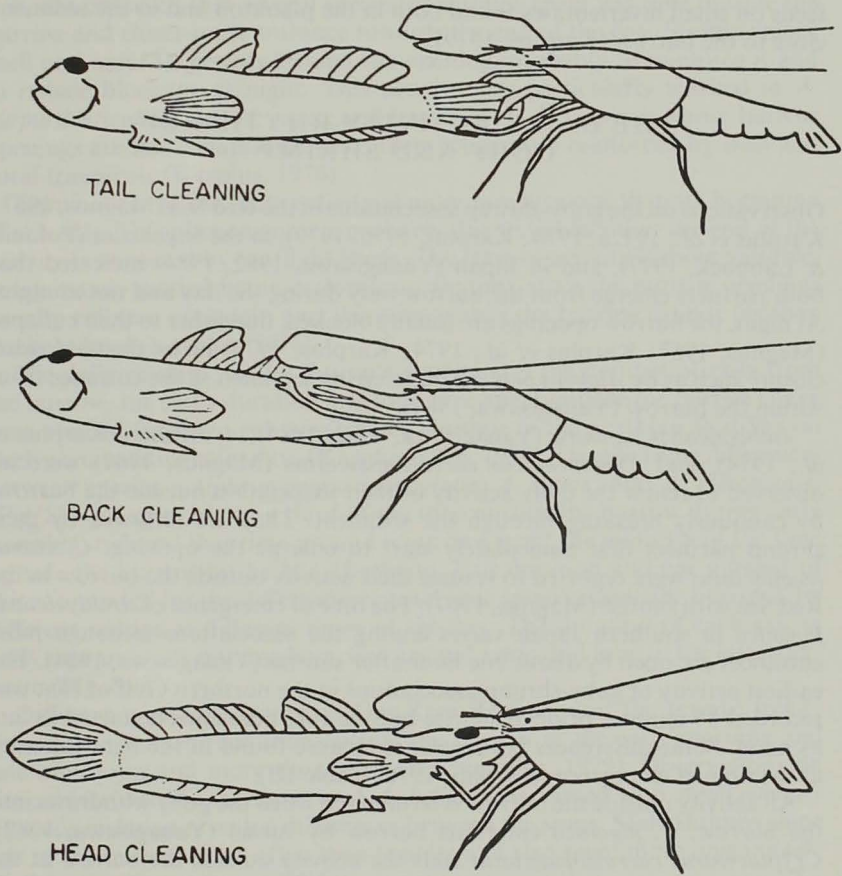


Fig. 7.—*Alpheus djiboutensis* cleaning *Cryptocentrus cryptocentrus* (from Karplus *et al.*, 1972a).

from the digging activity of the shrimp. A mutual benefit involving feeding has been described for *A. djiboutensis* cleaning its fish partner *Cryptocentrus cryptocentrus* (Fig. 7). During the cleaning process, the shrimp's first pair of chelae were placed on the fish while its second pair moved repeatedly from the fish to the mouth region of the shrimp (Karplus *et al.*, 1972a).

Possible predation of the goby on its shrimp partner's larvae was suggested by Bayer & Harry-Rofen (1957) as well as by Herald (1961). This conclusion is based on a single animal and the shrimp larvae were not identified. Detailed stomach content analysis of the goby during the reproductive season of the shrimp as well as observation of the interactions between gobies and shrimp releasing larvae in artificial burrows could clarify this issue.

Despite some possible overlap in the diet of gobies and shrimp (*e.g.* both eat polychaetes), the shrimp is basically a detritus-feeder, whereas the goby

feeds on small invertebrates found both in the plankton and in the sediment close to the burrow (Karplus, 1979).

THE DAILY ACTIVITY RHYTHM OF GOBY AND SHRIMP

Observations on the goby-shrimp associations in the Red Sea (Magnus, 1967; Karplus *et al.*, 1972a, 1974; Karplus, 1976, 1979), in the Seychelles (Polunin & Lubbock, 1977), and in Japan (Yanagisawa, 1982, 1984) indicated that both partners emerge from the burrow only during the day and not at night. At night, the burrow openings are usually blocked, due either to their collapse (Magnus, 1967; Karplus *et al.*, 1974; Karplus, 1979) or to their intended closure such as by *Alpheus bellulus* transferring sediment to the entrance from within the burrow (Yanagisawa, 1984).

Amblyeleotris japonica (Yanagisawa, 1982, 1984), *A. steinitzi* (Karplus *et al.*, 1974), and *Cryptocentrus caeruleopunctatus* (Magnus, 1967) were all observed to renew the daily activity of their association outside the burrow, by cautiously breaking through the sediment. They are followed by their shrimp partners that immediately start to enlarge the opening. *C. caeruleopunctatus* were reported to resume their activity outside the burrow in the Red Sea with sunrise (Magnus, 1967). The time of emergence of *Amblyeleotris japonica* in southern Japan varies among the associations although most entrances are open by about one hour after sunrise (Yanagisawa, 1984). The earliest activity of goby-shrimp associations in the northern Gulf of Elat was recorded 35 minutes prior to sunrise but, on rare occasions it started as late as noon. Some differences between species were found in the light intensity at the time of emergence (Karplus, 1976; Table III).

All activity outside the burrow is terminated when the goby withdraws into the burrow. *A. japonica* enters its burrow by sunset (Yanagisawa, 1982). *Cryptocentrus caeruleopunctatus* ends the activity outside the burrow at the latest 20 minutes after sunset (Magnus, 1967). Some differences of light intensity at the final retreat of the goby into the burrow were found for three sympatric Red-Sea species (Karplus, 1976; Table III).

TABLE III

Initiation and termination of activity of three species of gobies in the northern Red Sea in relation to light intensity: figures show number of gobies at start of activity and at final retreat into burrow in parentheses

Light intensity, lux	<i>Amblyeleotris steinitzi</i>	<i>Cryptocentrus lutheri</i>	<i>Ctenogobiops maculosus</i>
< 150	1 (2)	1 (5)	13 (19)
150-300	4 (5)	2 (11)	2 (4)
300-450	2 (9)	7 (1)	1 (1)
450-850	1 (3)	3 —	2 —
850-2500	4 —	4 —	3 —
2500-5000	3 —	2 —	1 —
> 5000	3 —	2 —	1 —

It was observed that several species of shrimps spent less time outside the burrow and closer to its entrance towards the end of the day. Shrimps place shell and coral fragments around the opening, probably to reinforce it and to reduce blockage at night. This activity was particularly marked in *A. purpurilenticularis* and *A. rapax* and less so in *A. djiboutensis* whose burrow openings are less collapsible due to their being more reinforced by shell and coral fragments (Karplus, 1976).

Termination of the daily activity is more synchronous than its beginning (Table III). This phenomenon is probably due to the fact that the end of the activity is triggered by low light levels. The start of activity is more variable, being mainly guided by an endogenous rhythm, since the burrow openings usually collapse overnight and the goby within the burrow cannot perceive the light level (Karplus, 1976).

The daily rhythm of the shrimp's activity (*i.e.* the number of exits from the burrow, the exit's duration and total time spent outside the burrow) have been studied for three goby-associated shrimps in the northern Red Sea on twelve consecutive calm days (Karplus, 1976, 1979). Despite some differences between species—*Alpheus purpurilenticularis*, *A. rapax*, and *A. djiboutensis* (Fig. 8)—all spent about a third of the time outside the burrow during early morning, reduced that time around noon and spent the majority of the time outside the burrow in the late afternoon. Exit duration and not number of exits accounted for the differences in total time spent outside the burrows, by different species at different times of the day. The duration of each exit in early morning was intermediate, low around noon and long in the late afternoon (Fig. 8).

Different types of shrimps at One Tree Reef showed the reverse trend: these shrimps spent less time outside the burrow in the early morning and late afternoon and more time at noon (Cummins, 1979). Observations on the activity outside the burrow of *A. bellulus* associated with *Amblyeleotris japonica* in Japan revealed differences between the sexes. Male shrimps came out of the burrow more often than females and also spent more time outside the burrow (Yanagisawa, 1984).

Magnus (1967) was the first to report on the introduction of sediment into the burrow by Red Sea goby-associated shrimps and on the changes in this activity throughout the day, its being most pronounced in early morning and late afternoon. Changes in the sand transport and digging activity of several goby-associated shrimps has been investigated in the northern Red Sea (Karplus, 1976). Despite specific differences between species (Fig. 9)—*A. purpurilenticularis*, *A. djiboutensis*, and *A. rapax*—all left their burrows in the morning and noon mostly loaded with sediment and coral fragments while, in the late afternoon, they left their burrows mainly with empty chelae. Digging with the first pair of chelae was slight in the morning and noon and pronounced in the late afternoon. The frequency of entrances into the burrow with chelae loaded with sediment was very low in the morning and increased substantially in the late afternoon. The high frequency of exits in the morning with chelae loaded with sediment is probably due to the clearance of the subterranean burrow which collapsed at night. Feeding related digging outside the burrow is mainly practised in the late afternoon and is followed by sediment introduction into the burrow. This sediment, rich in organic material will probably be consumed when activity outside the burrow is terminated.

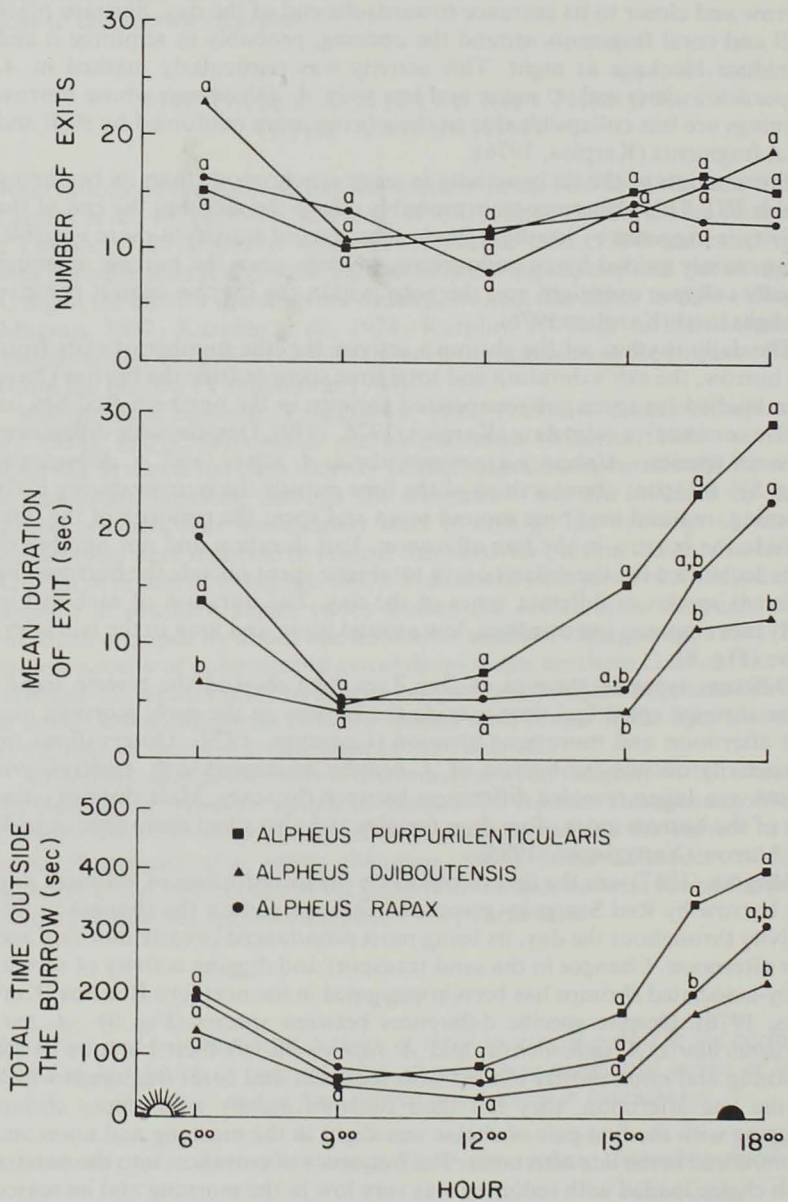


Fig. 8.—The daily activity rhythm of three goby-associated prawns in the northern Red Sea measured during periods of 10 min: sunrise and sunset are shown; significant differences in activity ($\alpha = 0.05$) at any given hour are indicated by different letters (a, b); from Karplus (1976).

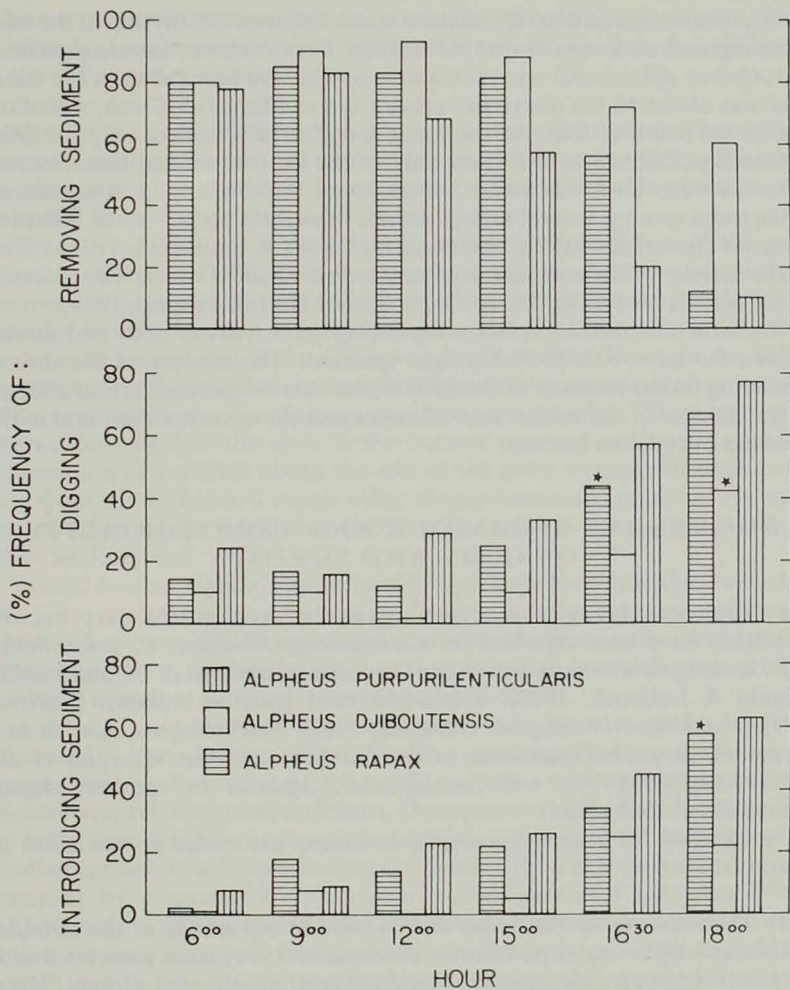


Fig. 9.—The daily rhythm of transporting sediment from within the burrow, digging and introducing sediment into the burrow by three goby-associated shrimps in the northern Red Sea measured during periods of 10 min: all cases, except those marked with an asterisk, showed significant deviation from random distribution of activity compared with no activity; from Karplus (1976).

Differences between species in shrimp activity outside the burrow are probably related to the relative importance to their diet of the sediment outside the burrow.

In southern Japan, during rough weather, red tide, and water temperatures below 15 °C, the burrow remained closed and their residents stayed inside it all day (Yanagisawa, 1982, 1984). In the northern Red Sea, when the sea is rough no activity was recorded in shallow water, while at 8–10 m or more depth the activity outside the burrow continued (Karplus, 1976).

Associations located in very shallow water followed the rhythm of the tides superimposed on a regular diurnal rhythm. *Cryptocentrus caeruleopunctatus* and *Alpheus djiboutensis* were still active outside the burrow when the water level was about 10 cm above the substratum at Marsah-Murach, a shallow bay 20 km south of Elat. As the water level further receded, only the goby remained positioned in the lower part of the burrow funnel, but retreated when the water level was about 3–5 cm above the substratum. Associations of the same species, several metres distant in slightly deeper water, followed a regular diurnal activity rhythm (Karplus, 1976). A similar effect of the tides on the activity of the associations found in very shallow water, was observed on the reef flat at Heron Island, Great Barrier Reef (Cummins, 1979).

The main environmental factor regulating the activity of goby and shrimp outside the burrow is probably light intensity. The activity of the shrimp depending on the presence of the goby at the burrow entrance is also affected by the collapse of the subterranean burrow and the occurrence of food in the sediment outside the burrow.

AGGRESSIVE BEHAVIOUR AND TERRITORIALITY OF GOBY AND SHRIMP

The occurrence of aggressive interactions between gobies over burrow ownership have been reported for *Ctenogobius feroculus*, *C. pomastictus*, and *Vanderhorstia ornatissima* in the Seychelles (Lubbock & Polunin, 1977; Polunin & Lubbock, 1977), a non-identified goby at Aldabra (Farrow, 1971), *Vanderhorstia delagoae* (Magnus, 1967), *Amblyeleotris steinitzi* and *Cryptocentrus caeruleopunctatus* in the northern Red Sea (Karplus *et al.*, 1974; Karplus, 1979), and *Amblyeleotris japonica* in southern Japan (Yanagisawa, 1982, 1984).

Competition for burrow ownership in shrimp-associated gobies is due to several factors.

(1) *The reduction of number of burrows due to the pairing of the shrimps:* *Alpheus bellulus* starts its benthic life alone and very soon associates with a small *Amblyeleotris japonica*. Within several months the shrimp finds a mate and the number of burrows is thus reduced by half. Intense competition then occurs between the gobies over the remaining burrows, since the goby is only paired as an adult for short periods of time (Yanagisawa, 1982, 1984).

(2) *Competition for the larger burrows:* A large *Cryptocentrus caeruleopunctatus* possessing a relatively small burrow was observed to take over a larger burrow possessed by a small goby (Karplus *et al.*, 1974). The positive size correlation between goby and shrimp (Palmer, 1963; Klauswitz, 1964; Karplus *et al.*, 1974; Cummins, 1979; Yanagisawa, 1984) is probably due to competition for the larger burrows.

(3) *Periodical desertion of burrows:* *Vanderhorstia delagoae* and *V. ornatissima* are two species with a loose attachment to their shrimp partners. They often leave their burrow during feeding excursions within their wide

home range which comprises the territories of several associations. They often try to take shelter in the nearest burrow when endangered (Magnus, 1967; Polunin & Lubbock, 1977).

Most of the gobies form temporary pairs during the reproductive season. One of the fish in the pair has to abandon its own burrow which will rapidly be taken over by another one (Yanagisawa, 1982). After leaving its mate, this goby will have to acquire a new burrow.

The burrow entrance is the centre and most protected part of the goby territory (Karplus, 1979). Usually a single or a pair of gobies occupies one burrow and protects its surroundings. In areas of high density *Amblyeleotris japonica* were sometimes reported to occupy several burrows at the same time and to protect their surroundings against intruders (Yanagisawa, 1982). Aggressive interactions between neighbouring gobies are usually frequent but of lower intensity than in disputes over burrow ownership. These aggressive interactions regulate the shift in the burrow opening and territory. Little information is available about the size of the goby territory defined as the area from within which it expels other shrimp-associated gobies of the same and of other species. Moehring (1972) suggested that the goby size and sex affect territory size.

Several distinct types of agonistic behaviour have been described for gobies which are competing for a burrow or during a conflict between neighbours. These behaviours include aggressive acts with physical contact (*e.g.*, mouth fighting and biting) and without physical contact (*e.g.*, lateral display, circling, tail beat) as well as submissive acts (*e.g.*, head down).

A detailed field study on aggressive interaction between gobies has been presented by Yanagisawa (1982, 1984) for *A. japonica*. Prolonged fighting and circling were performed mainly by males whereas such encounters between females were relatively rare and short. Dominance was apparently determined by body size. Size is not always decisive in competition for burrows as, in another species, *Vanderhorstia delagoae* in search of a burrow avoids burrows occupied by a smaller *Cryptocentrus caeruleopunctatus* (Magnus, 1967). Although threat displays and body contact are common in aggressive interaction between *Amblyeleotris japonica*, sometimes the subordinate fish surrender their burrows to the approaching dominant ones, even without exhibiting any defensive behaviour. The size differences between the opponents in these cases probably are very large (Parker, 1974; Maynard-Smith & Parker, 1976). The reverse situation is encountered in disputes between fish of similar size, which can be severe and often terminate in the winning of the resident.

A detailed laboratory study of aggressive interactions, using sequence and information analysis, was carried out on *Psilogobius mainlandi* (Moehring, 1972). Staged encounters between pairs of gobies were analysed from recordings on an hour-long video tape. The effect of size of interacting gobies suggested that large gobies have larger territories than small gobies, while females have larger territories than males. Agonistic behaviour occurs more frequently between large gobies and less frequently between small ones. Contrasting with *Amblyeleotris japonica*, interacting females perform more aggressive acts than the other two sex combinations. Dominance positions of interacting gobies are more definitely and rapidly established in interactions

between large and small gobies than between gobies of similar size. Only large females dominate males, while the males dominate the females of similar size.

No interactions at all outside the burrow were observed between shrimps of adjacent burrows (Karplus, pers. obs.). Yanagisawa (1984) suggested that, while digging a burrow underground *Alpheus bellulus* can encounter other individuals of the same sex, and as they cannot tolerate each other, they fight, attempting to expel the other individual. That may be one of the reasons for the lack of either or both chelae occasionally observed in shrimps in the sea.

The agonistic interactions between shrimps were investigated in a single laboratory study, involving two species, *Alpheus rapax* and *A. rapacida* (Moehring, 1972). Staged encounters between pairs were studied from recordings on an hour-long video tape using sequence and information analysis. Several aggressive (*e.g.*, lunge, snap, chelae spread) and submissive acts (*e.g.*, avoid) were described. The size, sex, and species of shrimp were found to affect the frequency of aggressive interactions, the establishment of dominance and the efficiency of information transmission.

REPRODUCTION OF GOBY AND SHRIMP

The reproductive behaviour of shrimp-associated gobies was completely unknown up to the last few years. Palmer (1963) stated that it was not known whether the gobies utilized the shrimps' burrows for spawning. Magnus (1967) suggested that the gobies may use burrows uninhabited by shrimps for spawning because the burrowing activity by shrimps would prevent adequate development of the goby eggs.

In a recent detailed field study, many aspects of the reproductive behaviour of a shrimp-associated goby *Amblyeleotris japonica* were finally revealed (Yanagisawa, 1982). Males of this species were usually ready to form pairs from May until September. During this period, males moved cautiously over the substratum, rarely venturing more than 3 m from their burrows. Females were rather passive and sometimes refused to pair themselves, indicating this by nudging the male's belly. Paired males were sometimes attacked and replaced by single males. The competition of males in this species may be accounted for by the fact that only a small percentage of females were gravid at one time, while most adult males were apparently sexually active throughout the breeding season. At most, only about 7% of all the associations were paired during July and August. All males that were presumed to have successfully fertilized eggs, were those that were larger and socially dominant. Most males, however, paired only once in several weeks, always with one female at a time, suggesting that there is no monopolization of reproduction. Established pairs were maintained for several days and no aggressive interactions were observed between the mates. Males spent more time than females inside the burrow, and retreated before their mates in case of danger, staying afterwards much longer inside than the females. These differences may be related to the stronger attachment of the male to the burrow. A 77-mm female was observed to lay an egg mass containing about 20 000 ellipsoid eggs 1.1 mm long. After spawning, the females leave the

burrow or position themselves at its entrance, while the males spend from four to seven days inside the burrow taking care of the eggs.

Among the large individuals of several species of gobies, pairs were recorded during several months. *Vanderhorstia delagoae* and *Amblyeleotris steinitzi* paired in the Red Sea from April until November, and *Ctenogobiops maculosus* and *Eilatia latrucularia* from April until December (Karplus, pers. obs.). In Japan *Vanderhorstia mertensi* and *Amblyeleotris japonica* were reported to pair from May until September (Yanagisawa, 1982). Other species, in the same and in different localities, paired throughout the entire year: in Japan *Tomiyamichthys oni* (Yanagisawa, 1982); in Hawaii, *Psilogobius mainlandi* (Preston, 1978); and in the Great Barrier Reef, *Cryptocentrus fasciatus*, *C. cinctus*, *Amblyeleotris steinitzi*, and *Ctenogobiops pomasticus* (Cummins, 1979).

The formation of pairs and their stability in the goby-associated shrimps was completely unknown due to their spending a large part of their lives underground and the difficulty in collecting and tagging them. Yanagisawa (1984) has overcome some of these difficulties in his study on the reproductive behaviour of *Alpheus bellulus* associated with *Amblyeleotris japonica*, by identifying individual prawns, by size, coloration, and the side of the large chela. Pairs of shrimps are always heterosexual. The size of the mates is positively correlated, although in adult pairs the female is slightly larger than the male. The proportion of ovigerous females was highest from mid-July to mid-August although they were sighted early in July and as late as December. The number of eggs carried by a female was positively correlated with her size and its maximal number was close to 4500. Juvenile shrimp settled on the substratum from late July to early October. The shrimps mature and participate in reproduction within one year of their settlement. At the start of their benthic lives, they are single but, with growth gradually form pairs, 50% pairing four to six months after settlement whereas the adults are mostly paired. Pairs are probably not formed on the surface, as shrimps have never been witnessed to venture far enough from their burrow entrances to reach the adjacent entrances in daytime, and at night the entrances are all plugged with sand. Yanagisawa (1984) suggested that shrimps could obtain their mates underground. Although the distance between two adjacent burrow entrances usually exceeds 50 cm, the subterranean extensions of a burrow are wide enough to come close to the adjacent burrows. A single shrimp can establish a pair when the resident of an adjacent burrow is a single one of the opposite sex. The adult shrimp's pair-bond is usually stable; some pairs were observed for more than several months, within a maximum range of two square metres (Fig. 10). Yanagisawa (1982) suggested that the permanency of the pair-bond and the timing of its formation depends on the degree to which movement between units of habitat is difficult and on the availability of mates. In the absence of clues pointing to the number of potential mates, as in the case of *Alpheus bellulus* and the difficulty of acquiring a mate subterraneously, the shrimp's preferred method is to establish a pair-bond with a mate, even at a very early age and to maintain it for a long time. In a number of obligatory goby-shrimp associations, cases have been reported of shrimp living in heterosexual pairs; *Alpheus* sp. associated with *Cryptocentrus caeruleopunctatus* and *Vanderhorstia delagoae* (Magnus, 1967); *Alpheus purpurilenticularis* with *Amblyeleotris steinitzi*

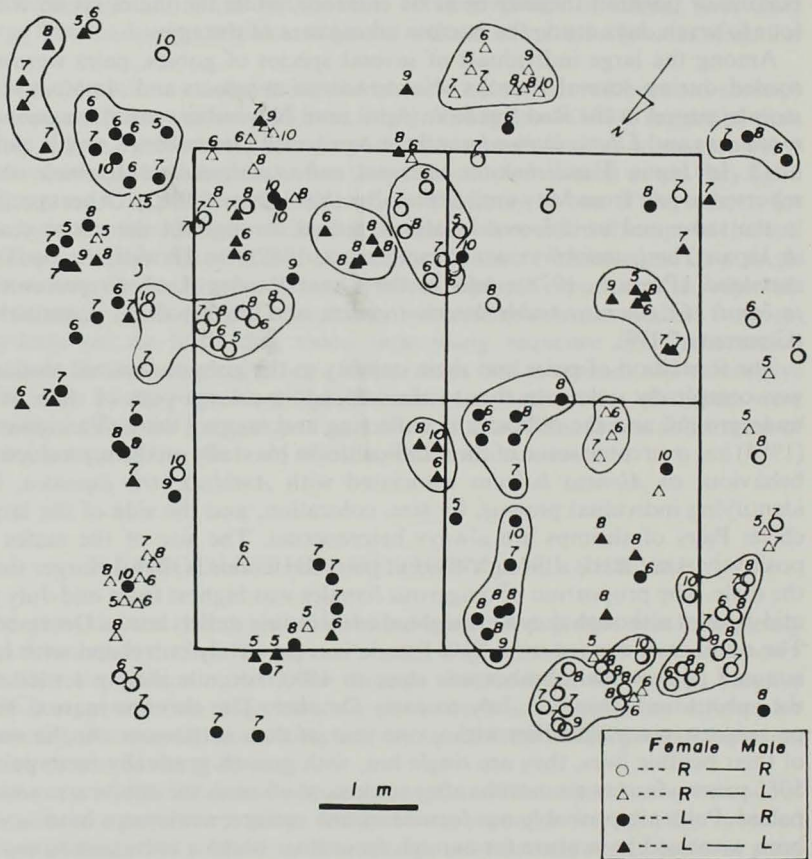


Fig. 10.—Map of the entrances of the burrows out of which a pair of adult *Alpheus bellulus* were observed to come: numbers indicate the month observed; a patch of entrances enclosed with a line indicate a stable association whose members did not change during the observation period; R, large chela on the right side; L, large chela on the left side; from Yanagisawa (1984).

(Karplus, 1979), and *Alpheus rapacida* with *Psilogobius mainlandi* (Preston, 1978).

The pair formation of *Alpheus rapacida* in large finger bowls has been studied in the laboratory (Moehring, 1972). Only shrimps of opposite sexes paired. Females communicate to males more information per act and with greater efficiency than males to females. Pair formation in this species probably also takes place underground, as suggested for *A. bellulus*, since it was never observed to leave the burrow vicinity.

A. rapax living in a more facultative type of association with *Psilogobius mainlandi* travel by themselves over the substratum on very hot days when the tide is low. They live in burrows in groups of three, two females and one

male, or in pairs consisting of two females or of a male and a female (Preston, 1978). A stable heterosexual pair of this species may not be essential, as mates can be more easily obtained by moving to an adjacent burrow (Yanagisawa, 1984).

POPULATION STRUCTURE AND DYNAMICS

The study of the population structure of goby-shrimp associations and its seasonal fluctuations is complex since it involves both recruitment and pair formation of two different organisms, as well as the formation of new associations, and the changes in established ones.

No data are available from field studies on the sex-ratio of shrimp-associated gobies as these fish usually lack a conspicuous sexual dimorphism. The only shrimp-associated goby known to possess marked sexual dimorphism is *Cryptocentrus caeruleopunctatus*. In this species, the males are larger than the females, their fins are longer and they possess a conspicuous dark caudal fin, while the females' caudal fin is greenish-grey (Klauswitz, 1960). In a monospecific aggregation of this species in the northern Red Sea, numbering more than thirty adults the sex ratio did not deviate significantly from 1 : 1 (Karplus, pers. obs.).

The population structure and dynamics of *Alpheus bellulus* and *Amblyeleotris japonica* were studied in southern Japan (Yanagisawa, 1982, 1984). In this area, the climate is subtropical with a rather severe winter, and consequently seasonality exists in breeding and growth. The growth pattern of *Alpheus bellulus* was estimated by measuring animals collected monthly. The shrimps mature and participate in reproduction within a year after settlement. Based on the largest size obtained and their growth pattern, it is suggested that the adult population is composed of one-year and two-year groups. The growth pattern of *Amblyeleotris japonica* was also estimated from monthly collections (Yanagisawa, 1982). Within one year of settlement, the fish participated in reproduction, and the adult population was composed of one- and two-year old individuals. The number of juvenile *A. japonica* associated with shrimps, compared with that of adults, changed with time. Immediately following settlement, during September and October, juvenile gobies were several times more numerous than adults. Their number decreased by about 60% during the first three months following settlement, partially due to the shrimps' pair formation. The entire population of settled fish decreased by about 80% in a single year. Juvenile *Amblyeleotris japonica* settled where adult gobies were present but also as in peripheral areas where no adults were seen (Yanagisawa, 1982, 1984). Similarly, juvenile *Cryptocentrus lutheri* and several other species of this genus were reported as settling in areas already occupied by adults, as well as in shallow areas largely covered by stones and not inhabited by adults (Zander, 1967; Karplus, Szlep & Tsurnamal, 1981).

Synchronization of the breeding seasons of *Amblyeleotris japonica* and *Alpheus bellulus* increases the likelihood of co-occurrence of non-paired juveniles of both species. The establishment of the association, as early as possible after settlement, must be essential to avoid predation: e.g., the case of a prawn

with a carapace length of 1.7 mm reported associated with an *Amblyeleotris japonica* of 8.7 mm standard length. Yanagisawa (1982) suggested that since juvenile shrimps, whose burrows have not been occupied by fish were detected, it can be assumed that a post-larval shrimp starts digging a small burrow as soon as it settles on the bottom. A non-associated goby, exploring the bottom, may encounter such a burrow and form a partnership with its occupant. Despite the synchronization of breeding seasons, disproportional settlement of gobies and shrimps in any one area at a given time will inevitably occur, resulting in considerable mortality of the surplus animals (Yanagisawa, 1984).

The population structure of goby-shrimp associations was relatively stable at One Tree Reef, Great Barrier Reef (Cummins, 1979). The frequency of the pairings did not vary seasonally, neither did the ratio of juveniles to adults. This stability of the population structure in the relatively uniform tropical climate, contrasts with its seasonal fluctuations in the subtropical climate of southern Japan (Yanagisawa, 1982, 1984).

A long term study of the stability of individual partnerships was carried out at One Tree Reef (Cummins, 1979). In this analysis a large number of burrow entrances were mapped and the details of individuals within each partnership (*i.e.* size, species, paired or single) were recorded at a mean interval of 3.5 months. A large percentage of the shrimps whose individual histories were traced, were found in the second recording as being associated with a different individual of the same or of a different species of goby (Fig. 11). As these gobies were usually fully, or almost fully, grown, it can be assumed that many of them do not have life-long associations with a particular shrimp. Several mechanisms causing the turnover of gobies in individual burrows were suggested: displacement of original gobies by bigger or other species, leaving a burrow voluntarily to find a mate or a preferred shrimp partner, and death through disease or predation. Approximately half of the shrimps, which could not be traced from the first recording, were probably recruited juveniles, associated with juvenile gobies. The other half were adult shrimps, probably unrecorded in the first census due to having been subterranean at that time. It was later found that some of these shrimps had actually been recorded previously.

Experimental removal of gobies from marked burrows was also carried out at One Tree Reef (Cummins, 1979). Of the 14 studied burrows, 12 were recolonized by adult gobies within a mean of two weeks, by either the species of goby preferred by each type of shrimp or by one of the generalist species. A non-preferred species of goby recolonized a burrow for several days only, thereafter leaving it again. This experiment demonstrated the recolonization of burrows, the sequential changes of fish partners of individual shrimps, and the ability of shrimps to survive at least several weeks without gobies. At any one census, a number of burrows having no goby occupant are consequently not recorded. Magnus (1967) has suggested that there is a vast population of subterranean shrimp which is not active outside the burrows due to the lack of fish partners. The renewal of the shrimp's activity outside the burrow, after making contact with a goby, has been documented (Magnus, 1967; Karplus, 1981; Yanagisawa, 1984), but the proportion of the subterranean prawns in the entire population is unknown.

In addition to fluctuations in the population structure, occasional disasters

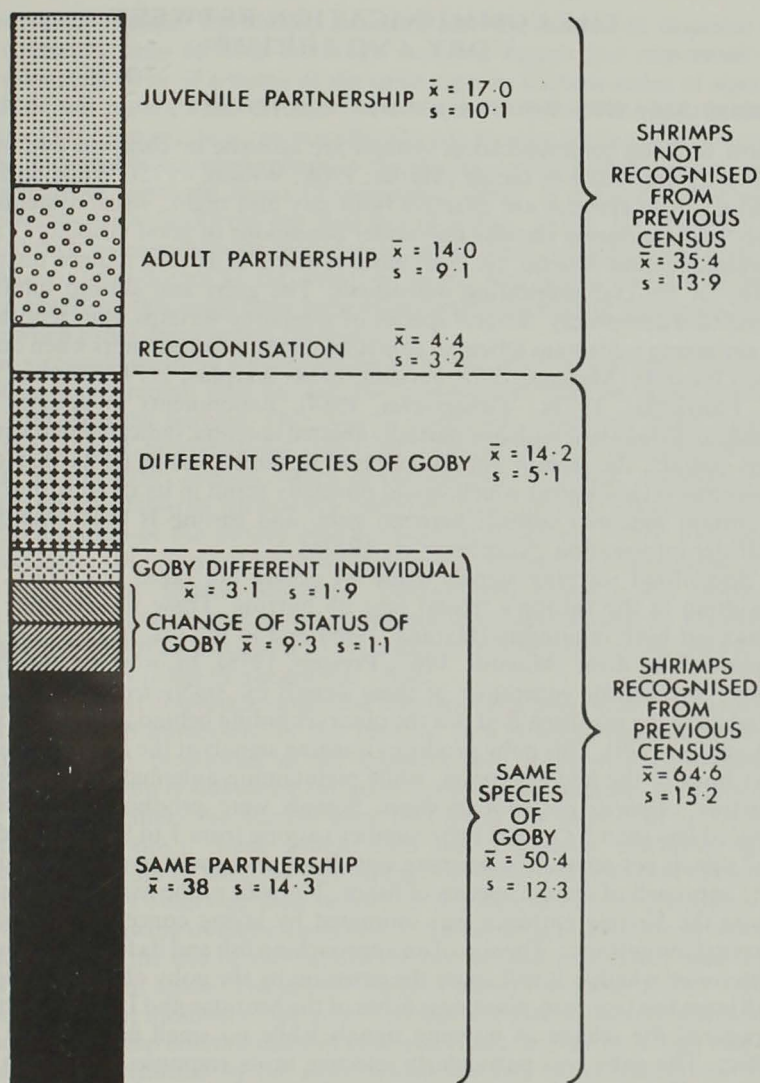


Fig. 11.—The fate of marked associations expressed in percentages following a 3.5-month interval at One Tree Reef, Great Barrier Reef (from Cummins, 1979).

like a typhoon (Yanagisawa, 1982) or very strong winter storms (Karplus, pers. obs.) may completely destroy entire populations. These catastrophes probably occur due to the removal of the bottom sediment inhabited by the gobies and shrimps.

THE COMMUNICATION BETWEEN
GOBY AND SHRIMP

COMMUNICATION UNDER NATURAL CONDITIONS

Most warning communication systems are acoustic or chemical and only a minority are visual or tactile (Marler, 1968; Wilson, 1975). While chemical and acoustic systems are effective both day and night, visual systems can only operate during the day and under conditions of good visibility. Tactile communication systems are even more restrictive, as they require the proximity of the communicating individuals. The goby and shrimp fulfill this condition completely. Several species of symbiotic shrimps were reported as maintaining a constant antennal contact with their fish partners when outside their burrows (Magnus, 1967; Preston, 1978; Karplus, 1979; Karplus, Szlep & Tsumamal, 1972a; Yanagisawa, 1984). Experiments in aquaria with *Alpheus djiboutensis* with one partially ablated antenna, indicated that without this contact, the shrimp did not respond to the retreat of its partner *Cryptocentrus cryptocentrus* which would normally result in its rapid withdrawal. Constant antennal contact between goby and shrimp is thus essential to transfer information (Karplus *et al.*, 1972a).

Specialized warning signals made by gobies are rapid tail flicks, often resulting in the shrimp's retreat into its burrow. These signals have been observed both in aquaria (Harada, 1969) and in the sea, in response to an approaching diver (Magnus, 1967; Preston, 1978). In order to understand their function the generation of these signals by *Amblyeleotris steinitzi* was studied in the northern Red Sea the observer hiding behind a fibreglass shield (Karplus, 1979). This goby produces warning signals at the rate of 7.4 signals per hour in the late afternoon, while maintaining antennal contact with its partner, *Alpheus purpurilenticularis*. Signals were produced in series (*i.e.* spaced less than 5 s apart) their number varying from 1 to 9, with a mean of 1.7 signals per series. The warning signals are given selectively in response to the approach of certain species of fishes. The trail of the fish and its distance from the burrow entrance was estimated by laying concentric iron circles around the entrance. The size of an approaching fish and its feeding behaviour determine whether it will cause the emission by the goby of warning signals. All large fish (*e.g.* non-piscivorous fishes of the Scaridae and Labridae families) triggered the release of warning signals while no small fish had the same effect. The goby was particularly selective in its response to medium sized fishes. The majority of warning signals were triggered by approaching goatfishes. These medium sized fish that are not predators, threaten the goby or the shrimp as they can block access to the burrow entrances completely by stirring the sediment in their search for food. Medium sized piscivorous fish from different families (*e.g.*, *Parapercis hexophthalma*, *Pterois volitans*) also triggered the release of warning signals. Medium sized fishes which were neither piscivorous nor sediment diggers (*e.g.*, *Chaetodon chrysurus*, *Acanthurus nigrofuscus*) did not trigger the goby's warning signals even when they moved very close to the burrow entrance.

The efficiency of the goby-shrimp communication system can best be studied under natural conditions. The shrimp responded differently (*i.e.*, either retreating or not retreating into the burrow) to a series of signals than

to individual signals. The shrimp retreated into the burrow in response to approximately only 60% of the single warning signals but responded to approximately 90% of a series of the same signals. Certain series of signals which do not generate the shrimps' retreat seem to have been made in situations of little danger, (*e.g.*, an intruder already leaving the burrow vicinity).

The emission of warning signals in the sea by *Amblyeleotris japonica* was reported from Southern Japan (Yanagisawa, 1984). It is hard to compare these results with data from the Red Sea (Karplus, 1979). The majority of the tail flick warning signals recorded in Japan were probably produced in response to interference by the observer. In the Red Sea, a shield was used by the observer; this could have been important since 90% of all signals were given when fishes approached the burrow.

The strongest warning signal, produced by the goby and always resulting in the shrimp's retreat into the burrow, consisted in its own rapid retreat, head first, into the burrow. This type of signal was described much earlier than the tail flick, in studies of a variety of goby-shrimp associations (Luther, 1958a; Smith, 1959; Herald, 1961). In the northern Red Sea, *Amblyeleotris steinitzi* retreated into its burrow at a rate of 0.3 time per hour always inducing the rapid retreat of the shrimp into the burrow (Karplus, 1979). The same fishes causing the release of warning signals, also induce, at closer range, the goby's 'head-first' retreat. Similarly, *Amblyeleotris japonica* was reported from southern Japan to retreat into its burrow when approached by *Therapon jarbua*—a piscivorous fish—and to react rather indifferently to the approach of non-predatory fishes (Yanagisawa, 1984).

Periods without antennal contact are very short but may occur in situations when the shrimp moves out of the burrow, in a shallow straight groove, towards its goby positioned at the groove's end. Even without antennal contact, the shrimp is still under the goby's protection, because in an emergency, the goby enters the burrow head first using the groove in its retreat (Karplus, pers. obs.). Some insight into the completely unknown subterranean behaviour of the goby and shrimp following this retreat of the goby may be gained by observing their behaviour in artificial burrows (Karplus *et al.*, 1972a). Following its entry, head first, *Cryptocentrus cryptocentrus* moved rapidly towards the end of the burrow, turned around and slowly and cautiously moved out again. The deeper *Alpheus djiboutensis* had moved inside the burrow, at the moment of the goby's retreat, the less the shrimp retreated.

The goby-shrimp communication system is characterized by a high rate of warning signals emitted by the goby, and a low rate of its retreat into the burrow. Only when certain species of intruding fish cross a critical distance, and a high level of danger is thus reached, does the goby retreat. There is therefore, a zone within which the goby is aware of low danger, and transmits warning signals to the shrimp, without itself retreating into the burrow. For the alert goby, the disadvantage of being exposed to low danger, while staying outside the burrow is small and is compensated by the advantage of longer access to food. The shrimp, which has poor vision (Luther, 1958a; Magnus, 1967), and is completely dependent on the goby outside the burrow, has the advantage of being warned by tail flick signals in case of danger of low intensity, and of danger of high intensity by the goby's retreat.

A guarantee for safety signal has been described both in aquaria (Karplus *et al.*, 1972a) and in the sea (Magnus, 1967; Yanagisawa, 1984), but has been

less investigated. This signal consists in a slow undulation of large amplitude of the tail of the goby. This signal was emitted at the rate of 8.2 times per hour by *Amblyeleotris japonica* when touched by the antenna of *Alpheus bellulus*. This signal seems to have the function of eliciting the emergence of the shrimp, especially in cases of the shrimp remaining in the burrow for a long time. The goby only rarely exhibited this signal when the shrimp was engaged in constant activity in and out the burrow (Yanagisawa, 1984).

WARNING SIGNAL GENERATION IN RESPONSE TO PREDATORS AND MODELS OF PREDATORS

The ability of *Amblyeleotris steinitzi* to discriminate between predatory and non-predatory fish has been tested in a series of controlled field experiments which also took into account the level of activity of the shrimp (Karplus, 1979). A transparent box was used in this experiment to present different species of fish. *A. steinitzi* produced a larger number of warning signals, over 15 minutes, when exposed to *Parapercis hexophthalma*, a piscivore, than when exposed to *Acanthurus nigrofuscus*, a fish feeding mainly on algae, and when faced with the empty box (Fig. 12). No difference was found in the number of exits of the shrimps, thus the different signalling rates were probably the result of recognition of an enemy by the goby and not the different levels of activity of the shrimp. It is possible that the very young goby responds initially by emitting signals and retreating into its burrow at the approach of all types of fish. Only by a process of habituation does the goby cease to respond to common medium-sized, non-predatory and non-digging fishes (Karplus, 1979).

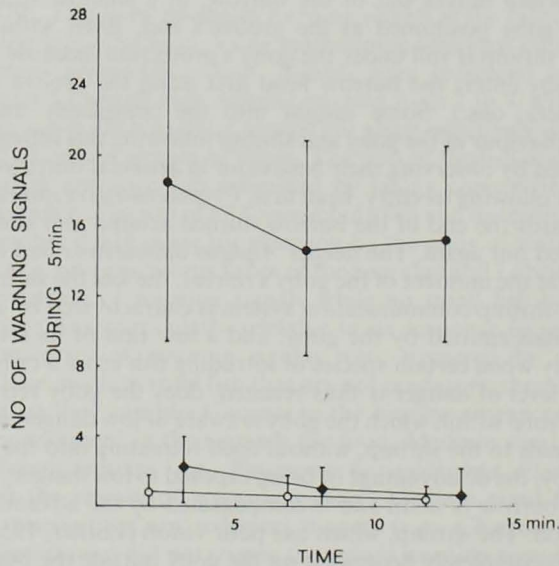


Fig. 12.—The number of warning signals of *Amblyeleotris steinitzi* given in response to *Parapercis hexophthalma* (●), *Acanthurus nigrofuscus* (■), and an empty box (○): results are means \pm standard deviation; from Karplus (1979).

The rate of signal emission by a goby in the presence of the same piscivore (*i.e.*, *Parapercis hexophthalma*) is negatively correlated with the distance between goby and the piscivore, and the duration of its exposure and positively correlated with the level of movement of the piscivore. That same fish when presented to the goby in a movement restricting box, caused the release of fewer warning signals than when the fish was presented in a spacious box where it could perform frequent movements (Karplus, 1976, 1979).

Various aspects of the reaction of *Amblyeleotris steinitzi* to a piscivore (*i.e.*, *Parapercis hexophthalma*), other than the generation of warning signals, changes with the distance between the two. Exposure to the piscivore from a very short distance caused the immediate retreat, head first, of the goby. Close to the piscivore, the goby head colour became white, whereas at a greater distance from the same piscivore or following longer periods of exposure, its head colour was dark. The advantage of these colour changes is probably that, during the white phase, the goby is less conspicuous to predators as it blends well with the light-coloured sand. The conspicuous black colour phase is probably advantageous in intraspecific interactions (*e.g.*, mate location). Because the white head coloration is positively correlated with the release of warning signals (Fig. 13), the tendency to escape is probably the motivation underlying the generation of warning signals.

The release of warning signals by the goby *Amblyeleotris steinitzi* in response to the approach of two-dimensional models of two different sizes of a piscivore of the Serranidae family has been investigated in the northern Red Sea (Karplus & Ben-Tuvia, 1979). The close approach of the model causes the retreat of the goby. The point reached by the model at the moment the goby enters its burrow was defined as the critical point. For both models, a negative correlation was established between the number of warning signals and the distance from the critical point. Thus, as in the previous study, a high level of escape tendency seems to underlie the generation of warning signals.

A comparative study of the response of three shrimp-associated gobies to a small two-dimensional predator model has been carried out in the northern Red Sea (Karplus, 1976; Karplus & Ben-Tuvia, 1979). *Amblyeleotris steinitzi* associated with *Alpheus purpurilenticularis* and *Ctenogobiops maculosus* associated with *Alpheus rapax* had similar responses to the model, with respect to the large mean number of signals generated (20.8 and 14.9, respectively). Both also showed a negative correlation between the number of signals and the distance from the critical point. Both these species entered their burrows head first at similar critical distances (*i.e.* distance between the critical point and the burrow entrance). *Cryptocentrus lutheri* associated with *Alpheus djiboutensis* differed greatly from the previous two species by a lower mean number of warning signals (2.5) and a lack of relationship between the number of signals and the distance from the critical point. Nine out of ten of this species' entrance into the burrows were of the tail-first type and their critical distance was approximately three times longer than in the other two species. The key to understanding the differences in signal generation of these three species lies in the way they enter their burrows. Head-first entries of fishes into the burrows or shelters appear to have been induced by stronger stimulation than tail-first entries (Magnus, 1967; Colin, 1971; Karplus *et al.*, 1972a; Fishelson, 1975). The low frequency of signals produced by *Cryptocentrus lutheri* is probably the result of its habit to withdraw into its

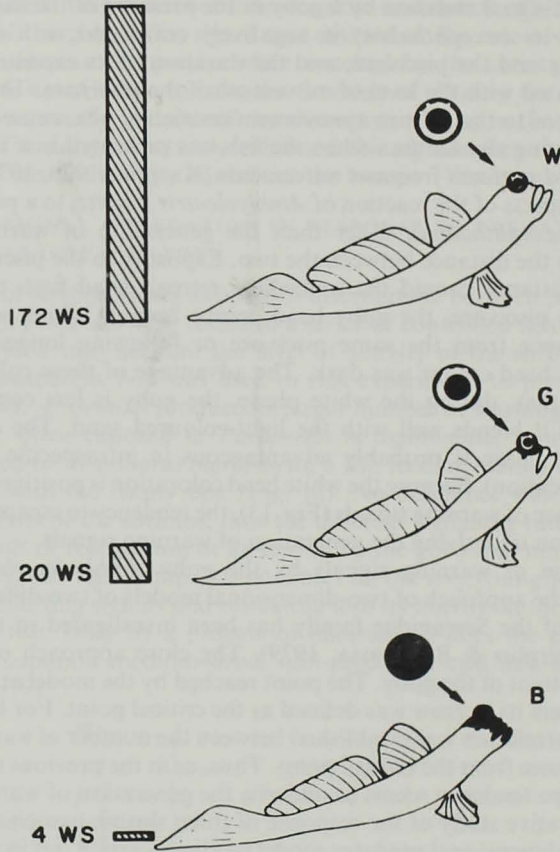


Fig. 13.—Head coloration and warning signals of *Amblyeleotris steinitzi*: WS, the tail-flick warning signal; W, white head; G, grey head; B, black head; from Karplus (1979).

burrow, tail first, when the danger is still distant. *Amblyeleotris steinitzi* and *Ctenogobiops maculosus* remain outside their burrow even when the danger is close. They thus attain a high level of tendency to escape and generate numerous warning signals prior to entering the burrow, head first.

SEQUENCE AND INFORMATION ANALYSIS

The statistical analysis of the sequence of goby-shrimp acts provides an objective evaluation of bi-directional communication. This method was often applied to the study of both vertebrate and invertebrate communication (Hazlett & Bossert, 1965; Altmann, 1965; Dingle, 1969; Max-Westby, 1975) but has so far only been used twice in the study of goby-shrimp communication (Preston, 1978; Karplus, 1979). While the sequence of acts of a pair of courting or fighting individuals can be visualized as a closed system

with only two actors, by definition, the warning systems are always open and include a third party—a source of disturbance. This inherent feature causes some difficulties both in obtaining sequences of goby-shrimp acts and in interpreting the results.

The communication between *Psilogobius mainlandi* and two species of shrimp *Alpheus rapax* and *A. rapacida* has been studied in shallow areas of Kaneohe Bay, Oahu, Hawaii (Preston, 1978). Observation was carried out in shallow waters, at low tide by slowly approaching the association, the observer constituting the source of disturbance. Thirteen different acts of the goby and seven acts of the shrimp were defined and their communicatory value as inhibiting or directing a given response were analysed on the basis of two act contingency tables. Of special interest were the four warning signals of the goby which directed the retreat of the shrimp. From weakest to strongest, these signals were: "withdraw", "tail flick", "tail beat", and "flee". Both species of shrimps often responded to the "tail flick" by the "sit" act—remaining motionless at the burrow entrance, a method of concealment which requires less energy than the withdrawal. This type of response to a warning signal had not previously been described for any goby-associated shrimp. Some differences in the response of the two species of shrimps to the same communicatory acts of the goby are probably related to the morphology of the shrimp. Because of differences in the length of the antennae of the two species of shrimps, two slightly different communication systems may have evolved. With its long antennae, *A. rapax* can dig at a relatively greater distance from a goby and still maintain contact with it. Its antennae distinctly detect the difference between a generalized movement of a goby and a "tail flick". On the other hand, with its relatively short antennae, *A. rapacida* has more body contact with the goby, and cannot usually distinguish between the generalized and specialized movements of the goby (Preston, 1978).

Generalized information, was calculated by Preston from the observed inter-phyletic two-act sequences, according to the methods used by Hazlett & Bossert (1965), Dingle (1969, 1972), and Steinberg & Conant (1974). More information was transmitted per act by *A. rapax* than by *A. rapacida*, but the latter produced more acts per encounter. The same amount of information was thus transmitted by the two species of shrimps to the goby. The fact that only one bit of information was transmitted per encounter supports the assumption that one 'yes-no' message was issued to the goby in each encounter. More transmission would probably be wasteful. Shrimp signals apparently informed gobies of whether or not an actively digging shrimp was present, that is, whether or not warning signals were necessary in the event of danger. Warning signals were unnecessary and therefore not made, when the shrimp was inside the burrow. The amount of information transmitted by the goby to the two species of shrimps was in both cases similar, and the goby act "tail flick" contributed the most to information transmission (Preston, 1978).

The sequence of the acts of the goby *Amblyeleotris steinitzi* and the shrimp *Alpheus purpurilenticularis* have been recorded in a shallow lagoon in the

northern Red Sea, when faced by a living predator—*Parapercis hexophthalma*—kept in a transparent box (Karplus, 1979). Twelve acts of the goby and five acts of the shrimp were defined. The main findings of this study were similar to those of Preston (1978). The communicatory acts of the goby—rapid body movements and special warning signals—directing the retreat of the shrimp are of interest. The first one occurs both in the absence and presence of the shrimp while the special warning signals—“tail flick” and “tail beat”—are only made in the shrimp’s presence. Some of the rapid body movements—“head-first entry”, “tail-first entry”, and “partial-tail entry”—are connected with situations of danger, while quick short movements either to collect sediment or to change position, are not. The shrimp probably responds to the last group because of the similarity of those signals to the

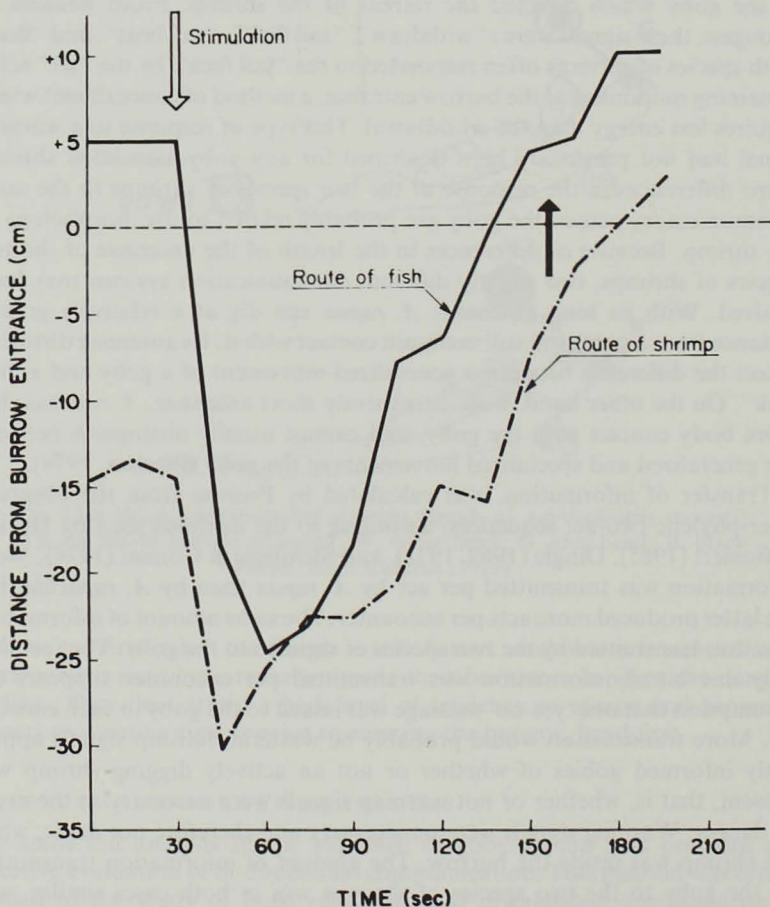


Fig. 14.—The head-first retreat of *Cryptocentrus cryptocentrus* into an artificial burrow: the black arrow indicates the area where pushing of the goby by *Alpheus djiboutensis* was performed; from Karplus *et al.* (1972a).

initial part of the first ones. Also of interest is a rare act of the shrimp, its pinching of the goby. A similar behaviour was frequently observed in the subterranean parts of an artificial burrow. *Alpheus djiboutensis* pushed the goby *Cryptocentrus cryptocentrus* out in order to allow the shrimp's activity outside the burrow (Fig. 14). This act was carried out using the first pair of chelae and was usually directed at the tail of the goby. In rare cases when the goby did not respond, the shrimp intensified the pushing and snapped once or twice with its big chela, thus adding the acoustic channel to the goby-shrimp communication system (Karplus *et al.*, 1972a). Pinching outside the burrow appears to represent an extension of subterranean pushing.

The validity of chi square tests, as used in the analysis of the goby-shrimp contingency tables to measure communication and the application of information theory may be questioned. Each dyade in the table should have been independent, while actually a large variable number of dyades are contributed by the same individuals (Moehring, 1972). The contingency table should be analysed as one entity thus the separate analysis of rows is probably not valid statistically. The assumption that these acts are similar is incorrect since at least the "tail flick" of *Amblyeleotris steinitzi* was demonstrated to be a graded signal (Karplus *et al.*, 1979b). Changes in the goby's response to the source of disturbance with distance and time affects the goby-shrimp interactions (Karplus, 1979). This contradicts assumption of stability when sequence and information analysis is made. The study of goby-shrimp communication using sequence analysis did not take into consideration the duration of acts which may have been crucial to their outcome (Hazlett & Bossert, 1965).

Even with these violations and limitations part of which cannot be overcome, the quantitative methods applied proved to be an important tool in the objective analysis of communication systems.

FILM ANALYSIS

Film analysis is necessary for understanding the goby-shrimp communication, since only through it can the details of rapid and complex interactions be clarified. Regretfully, this method has only been applied once in order to study the interactions between *A. steinitzi* and *Alpheus purpurilenticularis* in a shallow lagoon in the northern Red Sea (Karplus *et al.*, 1979). No cross-species comparisons were therefore made. Five different measurements of the tail-flick warning signal of this goby—amplitude, speed, number of components, length (*i.e.* total distance traversed by the caudal fin—TDT), and duration—were analysed. The conspicuous nature of this signal, compared with all other tail movements, provides it with coding characteristics (Wiley, 1973). These features increase the efficiency of the signal without making too much use of redundancy, which is harmful in any alarm system. The tail-flick warning signal belongs also to the category of graded signals which are characterized by different levels of intensity. They convey more information, than the discrete signals which are generated either in a simple on-or-off manner or display a typical intensity as a result of a wide range of stimulations (Morris, 1957; Wilson, 1975).

Filming also provided the means of analysing the exact variable response of a shrimp to a warning signal (Fig. 15). The combined principal component factor analysis with a stepwise multiple regression analysis was made to define

which of 18 independent variables (*e.g.*, shrimp chelae either empty or loaded with sediment, the speed of the shrimp, and its direction) are important in determining the shrimp's response. The structure of the preceding and actual warning signals and the area of contact of the antenna accounted for approximately a third of the differences in the shrimp's retreat response. The most important signal variable was its length (TDT). The neurophysiological mechanism, underlying the action of the mechanoreceptors on the shrimp's antenna responding to the minute vibrations of the goby's fins, are yet unknown but their study would be interesting.

The feedback mechanism by which the goby regulates the intensity of the warning signal, according to the shrimp's response is one of the most complex aspects of this communication system. Upon lack of response from the shrimp, the fish increases the intensity of its signal (measured by TDT), while upon the rapid retreat of the shrimp, the fish decreases the signal intensity. The goby's regulation of the intensity of the warning signal according to the shrimp's response is possible, since the mean time interval between two consecutive signals of a series (1.6 ± 1.1 s) is significantly longer than the mean latency of the shrimp's response (0.5 ± 0.4 s).

The antennal contact between shrimp and goby (Figs 16 and 17) described in field (Magnus, 1967; Karplus, 1979) and laboratory studies (Harada, 1969; Karplus, Szlep & Tsurumal, 1972a) has been further investigated by filming. The areas of contact between shrimp and goby changed according to the position of the shrimp, relative to that of the goby. When the shrimp was behind the goby, both its antennae pointed forward and touched the goby's caudal fin with one of them. When the shrimp was parallel to the goby, one antenna was bent sideways touching the second dorsal fin, while the other still pointed forward. When the shrimp was further away from the burrow than the goby, one antenna pointed backwards, touching the goby's pectoral fin while the other was still directed forward. Warning signals are given with various fins including the caudal, second dorsal, anal and pectoral fins according to the area of antennal contact. In each case, however, the caudal fin is involved in signalling (Fig. 18). The possibility of signalling with several fins enables the shrimp to move further away from the goby while still being protected through the warning system.

The goby's head-first retreat into its burrow is so rapid that without film analysis only a cloud of sand can be perceived during its occurrence. The goby's retreat is made in two stages. In the first short stage (0.16 s), the goby turns towards the burrow opening in a loop, its tail and head almost meeting. In the second, longer and less uniform stage (0.52 ± 0.19 s), the goby enters head first into the burrow. This retreat causes the shrimp to withdraw very rapidly (93.7 ± 54.9 mm/s) at a latency of only 0.16 s. The mean maximal speed of entering a burrow, in response to a series of warning signals, was only 16.5 ± 7.2 mm/s with a latency of 0.51 ± 0.36 s. The head-first retreat of the goby thus constitutes the strongest warning signal not only because it always induces the shrimp's retreat but also due to the extreme retreat speed of the shrimp and the shrimp's very short latency to respond. Because the goby's head-first retreat takes place under circumstances of extreme danger as during direct attack by a predator, any delay in the shrimp's response or any weak response on its part will cause it to be devoured and led to a direct negative selection of shrimps exhibiting this behaviour.

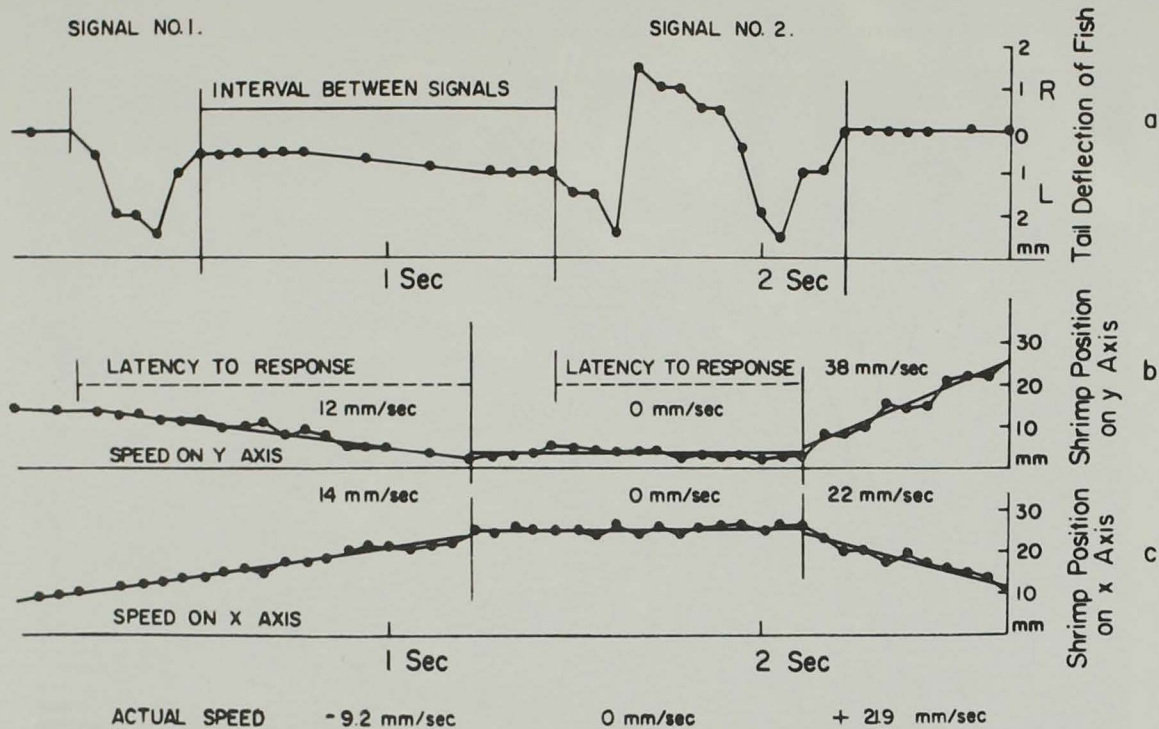


Fig. 15.—Graphical presentation of the interaction between the tail-flick warning signal of *Amblyeleotris steinitzi* and the response of *Alpheus purpurilenticularis*: a, the movement of the caudal fin of the goby, R, right and L, left; b, the movement of the shrimp on the Y axis ($\times 2$); c, the movement of the shrimp on the X axis ($\times 2$): from Karplus *et al.* (1979).

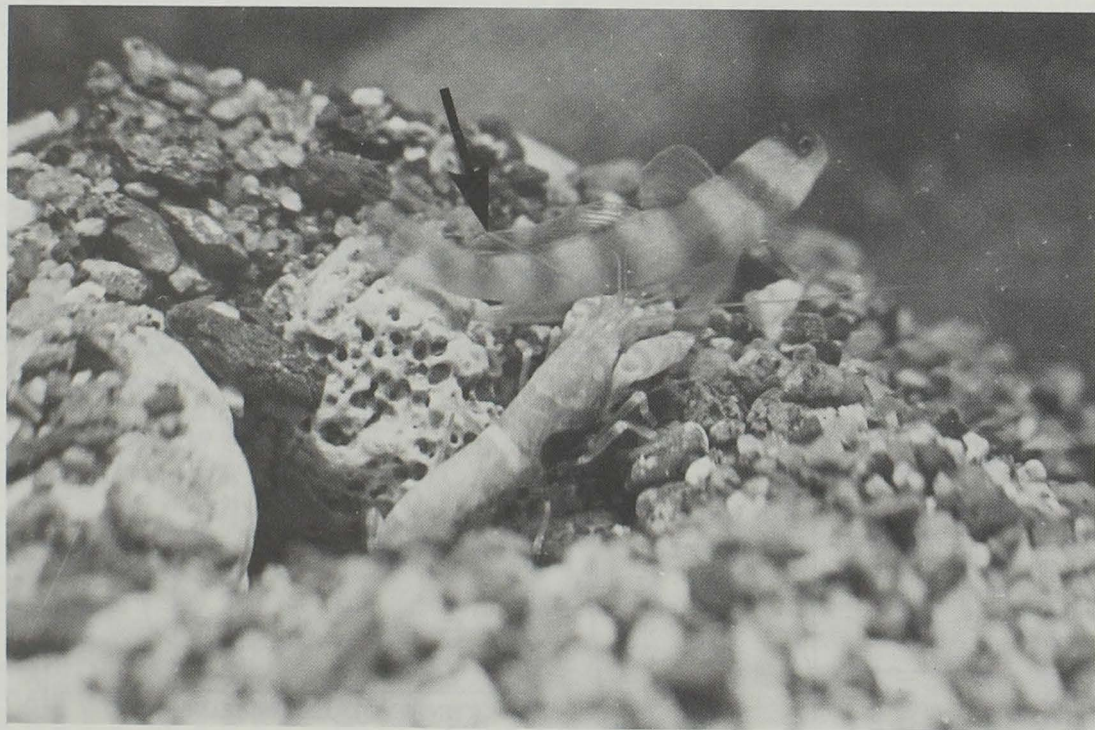


Fig. 16.—*Alpheus purpurilenticularis* maintaining antennal contact with *Amblyeleotris steinitzi* (from Karplus, 1979).

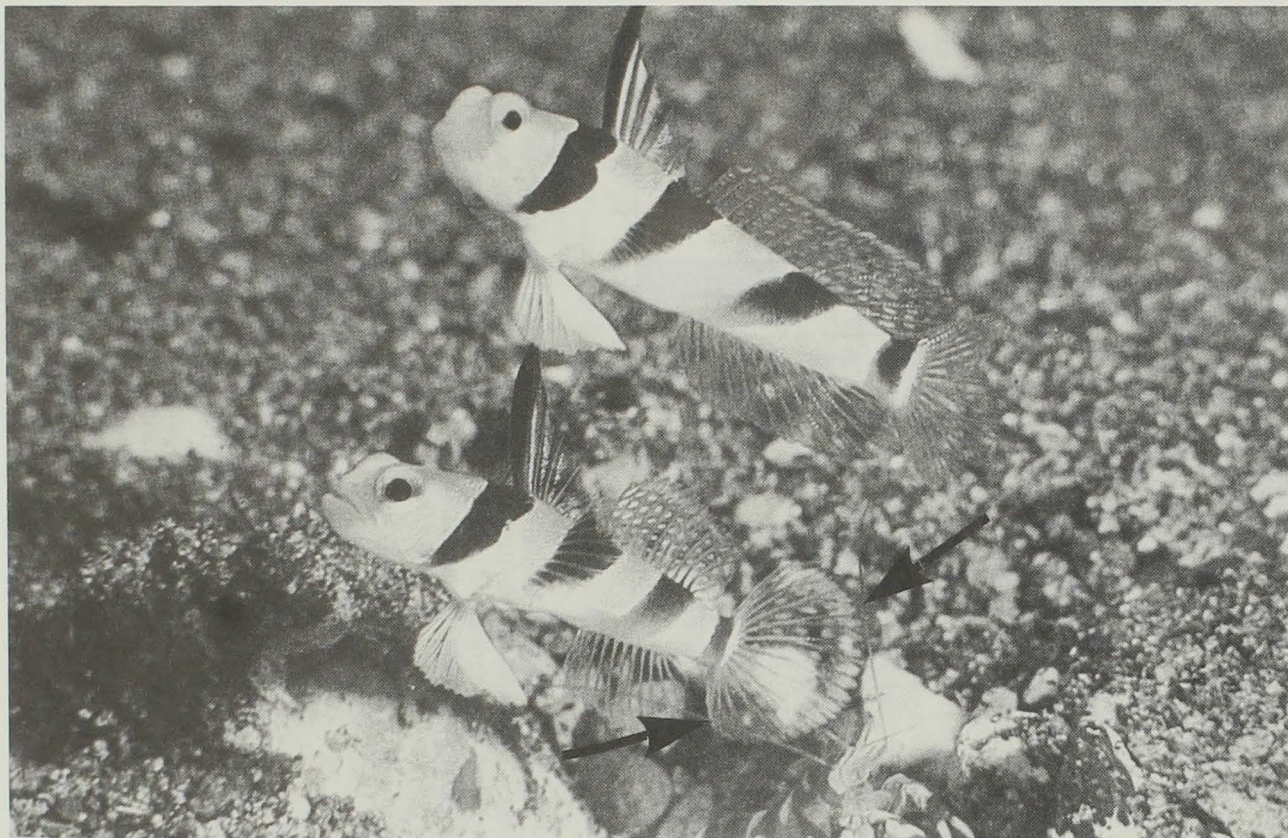


Fig. 17.—*Alpheus randalli* maintaining antennal contact with *Stonogobiops nematodes* (from Hoese & Randall, 1982).

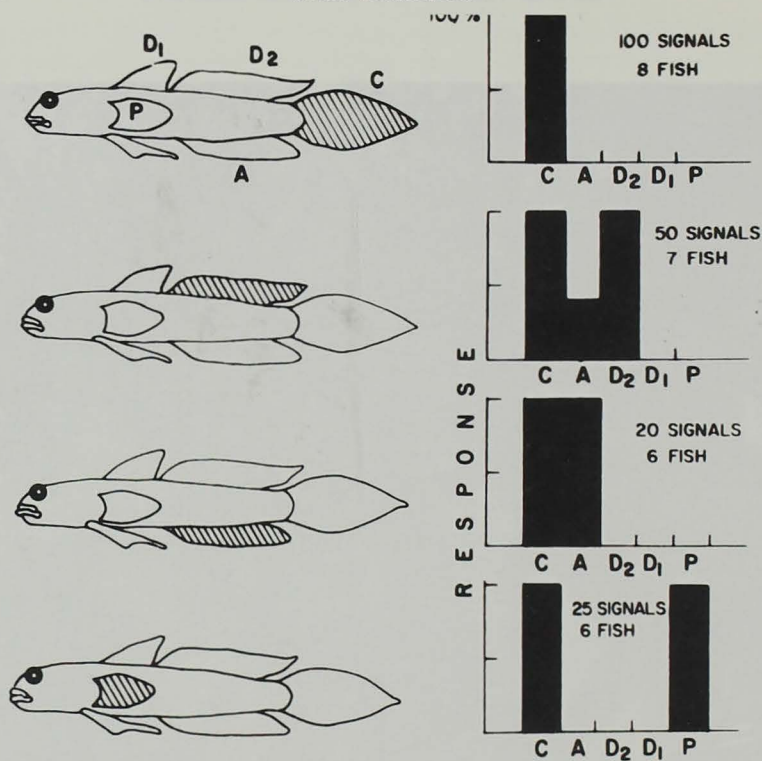


Fig. 18.—*Amblyeleotris steinitzi*: fins taking part in signalling and the areas of antennal contact: left, the area of contact (stippled); right, the frequency (%) in which various fins took part in signalling; C, caudal fin; A, anal fin; D₁, first dorsal fin; D₂, second dorsal fin; P, pectoral fins; from Karplus *et al.* (1979).

PARTNER SPECIFICITY OF GOBY-SHRIMP ASSOCIATIONS

FIELD OBSERVATIONS

The joint occurrence of several different species of alpheid shrimp and gobiid fishes in the same area, poses several questions with respect to the degree of partner specificity, its regulating mechanism, and function.

Specificity was initially studied by examining the occurrence or non-occurrence of certain species of gobies and shrimp in the same burrow. Harada (1971) concluded that, in southern Japan, goby-shrimp associations are non-specific since all possible combinations between four species of gobies and two species of shrimp were found. In a more recent publication, Yanagisawa (1978) stated that some specificity was found in the combinations between gobiid fishes and snapping shrimp. Little of that is known, however, because

the majority of these shrimps in southern Japan were either not collected or not identified.

Polunin & Lubbock (1977) examined the composition of 170 associations in the Seychelles. They concluded, based on the number of partners, that different species of gobies and shrimps differed with respect to partner specificity. The use of the occurrence or non-occurrence of certain species of gobies and shrimps in a burrow, as the sole criterion for specificity, may be misleading, because the composition of the associations may result from a random independent distribution over burrows of both species.

Partner specificity of six species of goby and four types of shrimp has been investigated in the sandy lagoon of One Tree Reef, Great Barrier Reef (Cummins, 1979). Chi square analysis was used to determine whether the distribution of goby species across types of shrimps differed significantly from a random one. Preference for a certain partner was also studied by a partial correlation of the number of gobies of each species and the number of shrimps of each type within local populations. Three species of gobies were associated both as juveniles and adults with a single "preferred" type of shrimp while, in one species of *Amblyeleotris*, only the adults were partner specific. One species of goby, was equally associated with two types of shrimps, and another species was associated at random with all the types of shrimps.

Partner specificity of goby-shrimp associations was further investigated in the northern Red Sea in a combined field and laboratory study (Karplus, Szlep & Tsuramal, 1974, 1981; Karplus, 1981). The composition of over 750 associations was analysed following Pielou's (1969) method for analysing associations of pairs of species found in discrete units. The following three questions were posed.

- (1) Does a species of goby occur together with a species of shrimp in the same burrow?
- (2) Is the number of co-occurrences significantly different (more or less) than would be expected from a random distribution of both species over burrows?
- (3) What is the strength of the association between two species, measured using Pielou's (1969) correlation coefficient?

Partner specificity differed greatly in deep and shallow waters. In deep water, no evidence of partner specificity was found whereas, in shallow water, three different types of specificity occurred, as follows.

Type I: co-occurrences of goby and shrimp in the same burrow, with a positive correlation coefficient.

Type II: co-occurrences of goby and shrimp in the same burrow, with a negative correlation coefficient.

Type III: no co-occurrence of goby and shrimp in the same burrow, correlation coefficient negative.

In shallow water, each of four different shrimp species occurring in a different microhabitat formed a very strong association (highly positive correlation coefficient) with a single species of goby of a different genus. Each of these shrimp species had a negative correlation coefficient with all the other gobies (Fig. 19).

Species of gobies which had a wide depth range were associated with

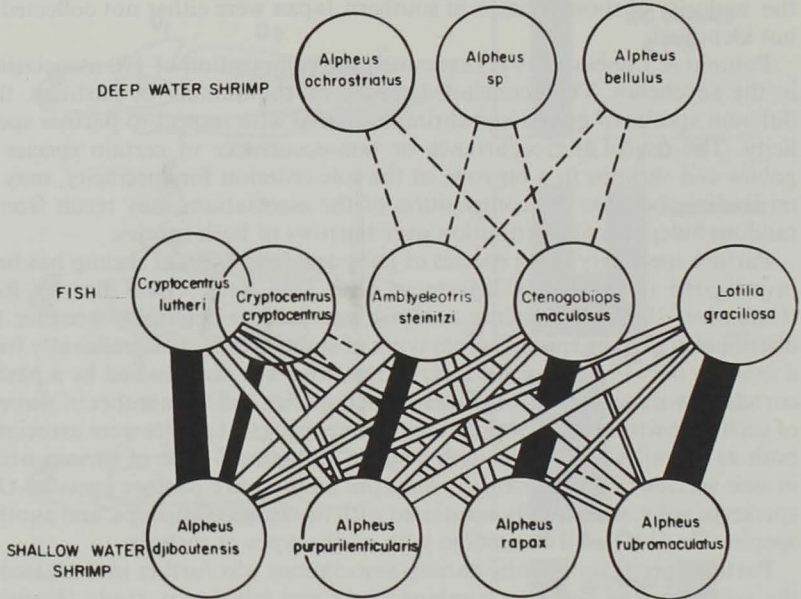


Fig. 19.—A diagrammatic representation of the strength of the association between alpheid shrimp and gobiid fish in the Elat Nature Reserve: black line, dependent occurrence of goby and shrimp in the same burrows and a significant positive correlation coefficient; white line, dependent occurrence of goby and shrimp in the same burrows and a significant negative correlation coefficient; broken line, independent occurrence of goby and shrimp in the same burrows; from Karplus *et al.* (1981).

different shrimp species in shallow and deep waters (Fig. 20). The same species formed random associations with deep-water shrimps and highly specific associations with shallow-water shrimps (Karplus, 1976). The segregation of shrimp to different habitats, usually inhabited by several shrimps of the same species, increased the probability of a goby moving away from its partner to re-enter the burrow of a shrimp of the same species. The non-occurrence of a certain species of shrimp and goby in the same burrow at Marsah-Murach, despite the spatial distribution facilitating it, suggested the involvement of a behavioural mechanism in the regulation of partner specificity (Karplus *et al.*, 1981).

LABORATORY EXPERIMENTS

Laboratory experiments on goby-shrimp partner specificity have been carried out on species found in the northern Red Sea (Karplus, 1981). Although only a few species were studied, they were selected to represent the three different types of specificity (Karplus *et al.*, 1981).

Species of gobies and shrimps of the first type of specificity were mutually attracted. The goby was visually attracted to the shrimp and the shrimp

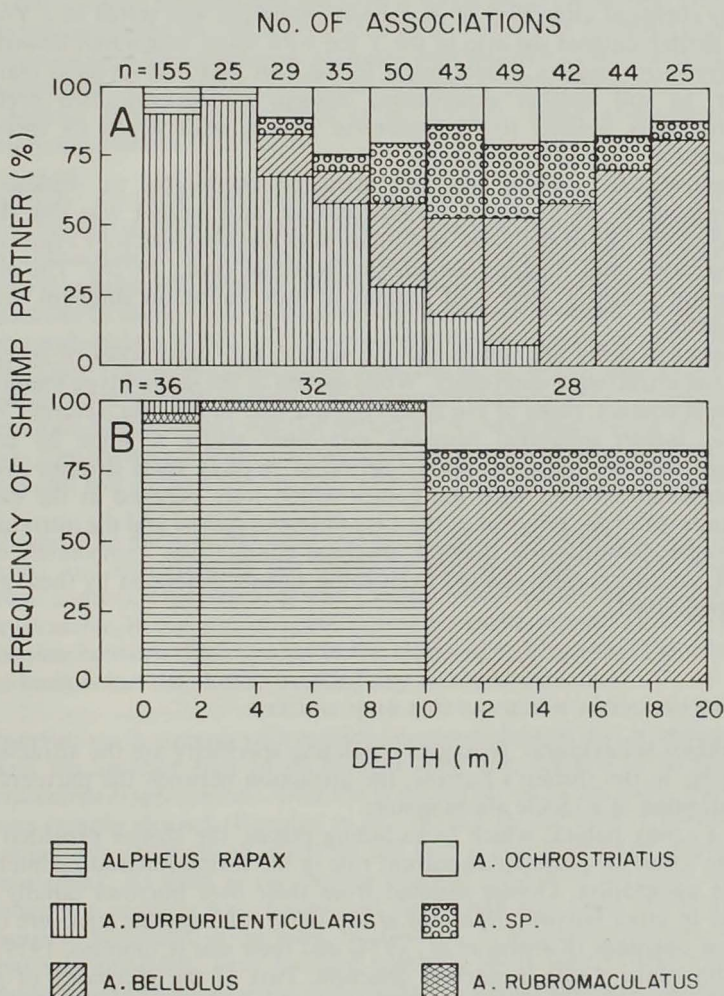


Fig. 20.—Changes with depth in the composition of shrimp partners of two gobiid fishes in the northern Red Sea: A, *Amblyeleotris steinitzi*; B, *Ctenogobius maculosus*; from Karplus (1976).

was chemically attracted to the goby (Karplus, Tsumamal & Szlep, 1972b; Karplus, 1981). The visual attraction of *Amblyeleotris steinitzi* was tested in a white elongated Perspex box which had two identical, water-tight transparent cells at each end. The attraction of this goby to its preferred shrimp partner, *Alpheus purpurilenticularis*, was demonstrated by the longer time it spent near the cell containing that shrimp, instead of near the empty cell, the longer time its head touched that cell and the longer time it attempted to enter it. In another experiment, *Amblyeleotris steinitzi* preferred *Alpheus purpurilenticularis* to *A. djiboutensis* with the latter of which its specificity relationship was of the second type.

The chemical attraction of *A. purpurilenticularis* was tested in a Y-maze. This shrimp entered the arm of the Y fed with water which had flowed over *Amblyeleotris steinitzi*, preferring it to the arm that had received plain sea water. In still another experiment, *Alpheus purpurilenticularis* preferred *Amblyeleotris steinitzi* to *Cryptocentrus lutheri*, with which its specificity relationship was of the third type.

Amblyeleotris steinitzi was not attracted chemically to *Alpheus purpurilenticularis*, its preferred shrimp partner, and neither was this shrimp attracted visually to this goby. A similar result was obtained for *Cryptocentrus cryptocentrus* and *Alpheus djiboutensis* (Karplus *et al.*, 1972b). The mutual attraction between goby and shrimp is thus based on different sensory modalities.

Species of goby and shrimp of the second and third types of specificity were not attracted to each other. While species of the second type maintained antennal contact, those of the third type did not. In aquaria, several *Cryptocentrus lutheri* inhabited burrows excavated under a stone by several *Alpheus purpurilenticularis*. Over a period of 30 days, these shrimps avoided any antennal contact with the gobies which were perched at the burrow entrance. After the removal of the *Cryptocentrus lutheri* and the introduction of several *Amblyeleotris steinitzi*, antennal contact was immediately established, and the shrimp reacted to warning signals generated by these gobies (Karplus, 1981).

THE MECHANISM REGULATING SPECIFICITY

The major behavioural processes regulating specificity are the attraction of the goby to the shrimp's burrow, the attraction between the partners, and the adoption of a tactile alarm system.

In a sandy habitat which lacks hiding places, the shelter provided by a shrimp's burrow plays an important rôle in the formation and maintenance of the association. Gobies isolated from their own burrows rapidly took shelter in other burrows (Karplus *et al.*, 1974). The specific structure of the burrow openings (Karplus *et al.*, 1974) and their size (Cummins, 1979) also possibly plays a rôle in partner selection. Part of the specificity of goby-shrimp association at One Tree Reef was controlled, according to Cummins (1979), by the size of the partners. Species of large gobies were associated with larger types of shrimp that also constructed larger burrows. Large individuals of one of the goby species, which as adults associated only with large types of shrimp, had associated, as juveniles, with all four types of shrimp, including two small types. A somewhat similar phenomenon was observed in Marsah-Murach. The very large *Cryptocentrus caeruleopunctatus* males only associated with *Alpheus djiboutensis* which attained the largest size and made the largest burrows of all goby-associated shrimps in that bay. The smaller juveniles and females of this species also associated with other smaller shrimp species (Karplus, pers. obs.). The strong negative phototactic response of the goby and shrimp (Karplus *et al.*, 1972b) may also have facilitated the maintenance of these associations.

The following behavioural interactions were suggested as regulating the different types of partner specificity (Karplus, 1981).

First type. In these partnerships the goby is attracted to the shrimp's burrow, the shrimp and goby are mutually attracted and maintain antennal contacts. Examples include the association between *Amblyeleotris steinitzi* and *Alpheus purpurilenticularis* (Karplus, 1981) and between *Cryptocentrus cryptocentrus* and *Alpheus djiboutensis* (Karplus *et al.*, 1972b). These associations are common and stable.

Second type. In these partnerships, the goby is attracted to the shrimp's burrow but the shrimp and goby were not mutually attracted although antennal contacts were maintained. For example, the association between *Amblyeleotris steinitzi* and *Alpheus djiboutensis* and between this same goby and *A. rapax* can be cited. These associations were rare and unstable. *Amblyeleotris steinitzi* and *Alpheus djiboutensis* were observed only once in the same burrow and for only two weeks. After this time, the goby left *A. djiboutensis* and moved to its preferred partner, *A. purpurilenticularis*. Also *Amblyeleotris steinitzi* and *Alpheus rapax* did not remain in the same burrow for more than a week. The shrimp in these partnerships did not, however, avoid antennal contact and was outside the burrow, with the goby present at the entrance.

Third type. The goby in this case was attracted to the shrimp's burrow but the goby and shrimp were not mutually attracted and did not maintain antennal contact. One example was *Cryptocentrus lutheri* and *Alpheus purpurilenticularis*. It was not possible during an entire month, to form a real association between these species in the laboratory. The goby was attracted to the burrow but the shrimp avoided any antennal contact.

Observations in aquaria with artificial burrows showed that *A. djiboutensis* blocked the anterior part of its burrow after the removal of its partner, *Cryptocentrus cryptocentrus*. After the re-introduction of the goby, the opening was rapidly cleared (Karplus *et al.*, 1972a). In the field, *Ctenogobius maculosus* was observed to insert its tail into a partly blocked opening of *Alpheus rapax*. As soon as the shrimp touched the tail of the goby with its antennae, the opening was cleared and the shrimp was again active outside the burrow. Similarly, in the field, burrows of *A. purpurilenticularis*, whose partner was removed, were blocked within a short time. These openings probably remained closed when approached by gobies such as *Cryptocentrus lutheri*, with which *Alpheus purpurilenticularis* avoids antennal contact.

Habitat selection of the goby cannot be a major mechanism regulating specificity, because it can only affect the initial stage of the contact between goby and shrimp. No partnership can be formed between certain species of goby and shrimp even if the goby seeks shelter in the shrimp's burrow because the shrimp will avoid any antennal contact with these species and will not leave its burrow nor clear its entrance while the goby is positioned at the opening. The segregation of shrimps in different habitats was probably important in the evolution of partner specificity. Species of shrimp with no clear habitat segregation show a lack of partner specificity. In the initial stages of the evolution of these associations, while they were still facultative, the distribution of the shrimps probably determined to a great extent the composition of the associations. Only later, with the gradual evolution of an obligatory and mutualistic relationship, did the behavioural interactions

between goby and shrimp become more important and a behavioural mechanism regulating partner specificity evolved.

The specificity of goby-shrimp associations is probably of importance at the level of the species but not of the individual. The spontaneous and rapid exchange of burrows and of shrimps between *Cryptocentrus caeruleopunctatus* of different sizes (Karplus *et al.*, 1974), the transitional occupation of several burrows by *Amblyeleotris japonica* (Yanagisawa, 1982) and *Vanderhorstia delagoae* (Magnus, 1967), as well as the immediate formation of associations between isolated partners in aquaria (Karplus *et al.*, 1972a; Karplus, 1981) support this assumption.

Polunin & Lubbock (1977) suggested that a species' specific communication system between goby and shrimp would enhance the efficiency of transmission but reduce the number of available hosts. A non-specific communication system could have a lower transmission efficiency but a higher number of potential partners. The testing of this hypothesis would be most interesting as it could provide us with some understanding of the function of partner specificity. Although species' specific differences in communication systems of several Red Sea associations were found (Karplus, 1976), the present state of knowledge on goby-shrimp communication systems does not allow us to test this hypothesis.

THE EVOLUTION OF GOBY-SHRIMP ASSOCIATIONS

The reconstruction of the evolution of a complex behavioural relationship is always complicated and speculative, but it can be aided by applying the comparative method. Comparisons between different populations of the same species, obligatory species with loose or tight relationships, and obligatory compared with facultative species may assist the reconstruction of the evolution of goby-shrimp associations.

The attachment between goby and shrimp, and the local conditions were correlated as relating to *Amblyeleotris japonica* in two localities in southern Japan. In one locality, with a high predator pressure and a low burrow density, the gobies spent more time in close proximity to the entrances, and seldom left the burrows. In this population, fewer floaters were found, and a single or pair of gobies occupied fewer burrows than in a population of low predator pressure and high burrow density (Yanagisawa, 1982).

Different species of shrimp-associated gobies differed in the degree of their attachment to their shrimp hosts (Magnus, 1967; Polunin & Lubbock, 1977). The goby *Vanderhorstia ornatissima* was often found in the Seychelles, far from its shrimp host, taking shelter in case of emergency in burrows of other gobies or in burrows of callinassid prawns. The loose relationship of this goby with its shrimp may be partly a result of its usual habitat, in which some protection from predators is provided by the abundant sea grasses. A similar loose relationship with its shrimp partner was described for another goby of this genus, *V. delagoae*, in the Red Sea (Magnus, 1967). Probably the highly cryptic colour and pattern of this fish facilitates this type of relationship.

Few species of gobies form facultative relationships with shrimp. *Vireosa hanae* occasionally hovers at about half a metre above the burrow entrance

of *Alpheus bellulus*, not maintaining contact with the shrimp. When *Vireosa hanae* retreated into the burrow, it caused the retreat of the shrimp and of *Amblyeleotris japonica* which often shared the same burrow (Harada, 1969; Yanagisawa, 1978). *Acentrogobius pflaumi*, a non-hovering goby does form facultative associations with *Alpheus brevicristatus*. Antennal contact was maintained by the shrimp with this goby, that often fled when approached by a diver instead of retreating into the burrow (Harada, 1969; Yanagisawa, 1978).

The behaviour of an obligatory fish partner *Nes longus* and a facultative one, *Bathygobius curacao*, both associated with a facultative shrimp partner, *Alpheus floridanus*, has been studied at Key Biscayne, South Florida (Karplus, unpubl. data). Continuous antennal contact was maintained between the two gobies and the shrimp while it was outside the burrow. The shrimp retreated into the burrow in response to tail-flick warning signals and head-first entry of *Nes longus*. *Bathygobius curacao* warned the shrimp only by head-first entry into the burrow, and gave no warning signals. *Nes longus* was continuously positioned in front of the burrow, in the shallow groove excavated by the shrimp, its tail directed to the entrance. *Bathygobius curacao* occasionally left the burrow entrance and moved in its vicinity, causing the shrimp to retreat when it emerged from the burrow during the goby's absence. The goby was often positioned very close to the burrow entrance but outside the groove. The emerging shrimp was, therefore, unaware of the goby's presence, failed to establish antennal contact and retreated. The time a shrimp spent outside its burrow differed when it was alone or when it was associated with a facultative or obligatory fish partner. *Alpheus floridanus* without a goby partner spent very short periods of time outside the burrow, usually only dropping the sediment very close to the entrance. When associated with *Bathygobius curacao*, it spent about 10% of the time outside the burrow and about 30% when associated with *Nes longus*.

The complex obligatory associations between non-burrowing gobies and burrowing alpheid shrimps probably evolved through loose facultative partnerships. The non-associated shrimp probably spent most of its time in the subterranean burrow, occasionally dumping sediment at the entrance. Non-associated gobiid fishes under intense predatory pressure in the sandy habitat, were probably protected mainly by their cryptic coloration and a few natural shelters. Some gobies started to take occasional shelter in burrows constructed by different groups of crustaceans, polychaetes, and echinuroids (MacGinitie, 1939; Luling, 1959; MacGinitie & MacGinitie, 1968; Schembri & Jaccarini, 1978). The habit of sheltering in burrows of alpheid shrimps was the most successful, since it evolved into a highly mutually beneficial partnership. The initial phases of this process were probably similar to the loose relationship existing between *Vireosa hanae* and *Alpheus bellulus*. This hovering goby occasionally takes shelter in the shrimp's burrow thereby warning it in case of danger, thus forming a mutually beneficial relationship. Antennal contacts were gradually established with species living on the substratum near the burrow entrance. The poor vision of the subterranean shrimp (Luther, 1958a; Magnus, 1967) probably determined the evolution of a tactile and not a visual communication system. The initial purpose of the antennal contact was probably only to inform the shrimp of the goby's presence at the entrance, the goby's retreat into the burrow probably being the only warning signal.

Such a relationship has been described for *Bathygobius curacao* associated with *Alpheus floridanus*. Magnus (1967) and Preston (1978) have both suggested that the tail-flick warning signal evolved from intentional movements of the goby, connected with its retreat to the burrow. There are numerous examples of communicatory movements which have evolved through a monovalent ritualization (Daanje, 1950; Andrew, 1956; Hjorth, 1966). It has been suggested that it was the escape tendency which motivated the generation of warning signals. An intermediate phase in the formation of the highly ritualized tail flick is probably the tail beat. This is still the dominant signal of *Psilogobius mainlandi*, and is emitted in cases of higher danger than the tail flick (Preston, 1978). The tail beat of *Amblyeleotris steinitzi* is only given on rare occasions, during massive body contact with the shrimp. Its dominant warning signal is the tail flick, a very effective graded and coded signal of short duration and small amplitude.

In the course of the evolution of an obligatory association between gobies and shrimps, they become mutually attracted and influence one another in many ways, as their interrelationship becomes mutual and complex. The shrimp provides the goby with a burrow to use as shelter in an emergency during the day, and as a resting place at night, as well as a place to deposit and guard its eggs with safety. The goby provides the shrimp with a tactile alarm system, enabling it to clear the burrow safely and to collect food outside the burrow. Warning signals can be emitted by the goby with several fins, depending on the area of the shrimp's antennal contact, their intensity being regulated by a feedback mechanism attuned to the shrimp's response. The goby determines every day the beginning of the shrimp's activity outside the burrow as well as the location of the burrow entrance by pushing its head through the substratum from within the burrow. Shrimp and goby also engage in a mutually beneficial cleaning relationship inside the burrow. In some associations the gobies were reported to feed outside the burrow on small crustaceans and polychaetes found in the sediment transported there by the shrimp. The synchronization of the breeding season of goby and shrimp facilitates the formation of the association from the very initial phases of their benthic life.

The partnership between goby and shrimp provides both of them with advantages over their, free-living relatives affecting their speciation distribution and abundance.

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