Symbiosis, 12 (1992) 275–291
Balaban, Philadelphia/Rehovot

Obligatory and Facultative Goby-Shrimp Partnerships in the Western Tropical Atlantic

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Received May 28, 1992; Accepted July 12, 1992

Abstract

The behaviour of an obligatory fish partner *Nes longus* and a facultative one *Bathygobius curacao*, when associated with a facultative shrimp partner *Alpheus floridanus*, was studied off key Biscayne, in southern Florida. Continuous antennal contact was maintained between the shrimp and the two gobies while outside the burrow. The shrimp retreated into the burrow in response to tail-flick warning signals and head-first entries of *N. longus*. *B. curacao* warned the shrimp only by head-first entries into the burrow and gave no special warning signals. The time a shrimp spent outside its burrow differed when it was free-living, or when associated with a facultative or obligatory fish partner. *A. floridanus* without a partner spent very short periods of time outside the burrow. When associated with *B. curacao*, it spent less than 10% of the time outside the burrow and about 30% when associated with *N. longus*. The goby-shrimp partnerships in the western tropical Atlantic are compared to those found in the Indo-Pacific region. The possible evolution of the goby-shrimp partnership is discussed.

Keywords: symbiosis, goby-shrimp associations, obligatory and facultative partnerships, evolution of partnership

1. Introduction

The partnerships between burrowing shrimp of the family Alpheidae and fishes of the family Gobiidae are mutualistic. The shrimp provides the fish, which is under a heavy predatory pressure in its sandy exposed habitat, with the refuge of a burrow that the fish uses as a temporary shelter during the day and as a permanent resting place at night. The fish provides the shrimp whose vision is poor, with a tactile alarm system to warn it from approaching predators. The goby's main warning signals consist of head-first entries into the burrow and tail flicks. These signals which cause the shrimp to retreat into its burrow are transmitted through the long antenna that are continuously positioned on the fish's body (Karplus, 1979, 1987; Karplus et al., 1979).

Behavioural and ecological studies on goby-shrimp partnerships were mainly carried out in the Indo-Pacific region, particularly in the Red-Sea (Luther, 1958; Magnus, 1967; Karplus, 1981; Karplus et al., 1981; Polunin and Lubbock, 1977) and off Japan (Harada, 1969; Yanagisawa, 1978, 1982, 1984). Little information is available about these partnerships in the Atlantic. Three species of gobies *Nes longus*, *Gobionellus saepepallens* and *Gobionellus stigmalophius* were reported to live in the western tropical Atlantic in association with a snapping shrimp (Bohlke and Chaplin, 1968; Longley and Hildebrand, 1941). *Alpheus floridanus* was reported from Laurel reef off Puerto-Rico to live in association with *N. longus* in a study devoted to the ecology of burrow-dwelling fishes (Weiler, 1976).

Most research on goby-shrimp associations focused on obligatory partnerships. The occurrence of facultative fish partners was briefly reported from Japan. The hovering goby *Vireosa hanae* uses rock crevices or shelters beneath stones as often as it utilizes shrimp burrows. The bottom dwelling *Acentrogobius pflaumi* forms a weak facultative relationship with the shrimp, often not taking shelter in its burrows but swimming away (Yanagisawa, 1978).

The aim of this study was to investigate the little known goby-shrimp partnerships of the Western tropical Atlantic while focusing on the differences between facultative and obligatory partners in order to provide a better understanding of the evolution of these complex and mutualistic partnerships.

2. Materials and Methods

The field study was carried out during November–December 1981, at the northwest point of Key Biscayne, (500–700 m east to the bridge connecting Key Biscayne with Virginia Key), Miami, Florida. This area forms the southern part of a narrow water channel connecting Biscayne Bay with the Atlantic Ocean. Behavioural observations were carried out in shallow water (50–100 cm) in a 50 m wide and 200 m long zone located about 30 m from the stony intertidal. This zone consisted of a sandy flat partly covered with dead and living turtle grass *Thalassia testudinum*. During the study, water temperatures ranged from 20–28°C. Mean current speed, measured 20 cm above ground with a flowmeter (General Oceanic, Inc.) ranged from 0–30 cm/sec. The current altered its course twice daily with the tide, moving in and out of Biscayne Bay. Cloud coverage ranged from 1/8 to 7/8.

Observations on activity of *A. floridanus* associated with two species of gobies were carried out with mask and snorkel over 8 days during five sessions evenly distributed over the entire day, i.e. 7^{00}–8^{00} (T_1), 9^{15}–10^{15} (T_2), 11^{30}–12^{30} (T_3), 13^{45}–14^{45} (T_4), 16^{00}–17^{00} (T_5); (sunrise–6^{30}, sunset–17^{30}). During each session shrimps associated with *N. longus* and *B. curacao* were each observed for 20 min. Every observation was carried out on different individuals which were haphazardly selected (i.e. first association to be encountered while shifting to different areas within the study zone). it was attempted to carry out daily observations on the same individuals found within marked burrows. This method was abandoned due to the short existance of specific partnerships between *B. curacao* and *A. floridanus*. Current speed, water temperature, depth and cloud coverage were recorded prior to each observation. Each observation period was preceded by a 10 min acclimation. Within the acclimation period which followed the approach to a distance of about 150 cm from the burrow entrance, shrimp were always observed to resume their regular activity outside the burrow. During each observation, the number of exits of the shrimp as well as their activity during exists such as exit with empty chelae or chelae loaded with sediment or plant material were recorded. Time spent outside the burrow was recorded for each exit with the aid of submerged stop watches. Means ($\pm$ standard deviations) were calculated and presented in the Results section. Also recorded were the shrimp activity of dumping sediment, digging in sediment or picking at plants. Finally it was noted whether the shrimp entered its burrow with its chelae empty, chelae loaded with sediment or while carrying plants. The position of the goby at the entrance and its retreats into the burrow were recorded as well as any interactions between goby and shrimp and among associated gobies.

The goby-shrimp tactile communication system was studied at a range of 30–40 cm with the aid of SCUBA. Observation on non-associated *A. floridanus* and *B. curacao* were carried out sporadically during the study.

Statistical analysis was carried out with SAS (1987) computer software. Descriptive statistics were computed from raw data. Differences between treatments were analyzed with the application of ANOVA and the Duncan multiple range tests on log transformed (i.e. number of shrimp exits, mean duration of exit, total duration of exit and duration of specific activities) and arcsin transformed (i.e. percentages of activities) data in order to increase the homocedasticity of the variance. A regression analysis was carried out on the data to determine the impact of observation time, current speed, temperature, depth and cloud coverage on number of shrimp exits and exit duration.

3. Results

Obligatory and facultative partners

The three species of gobies which were found in association with *Alpheus floridanus* Kingsley, 1887 in our study area were: *Nes longus* Nichols, 1914 *Gobionellus saepepallens* Gilbert and Randall and *Bathygobius curacao* Metzelaar (Fig. 1). The size, coloration, habitat and distribution of the fishes are given by Bohlke and Chaplin (1968). Similar information on *A. floridanus* is provided by Pierce (1950), Chace (1972) and Won Kim and Able (1988).

Two of the goby species, *N. longus* and *G. saepepallens* may be defined as obligatory partners. In our study area as well as in others (Bohlke and Chaplin, 1968) they were only found in association with shrimp. *G. saepepallens* was not further investigated due to its scarcity. *B. curacao* is a facultative partner. It was found both in association with a shrimp and free living. This species, common in shallow water in the Western Atlantic, has never before been reported in association with a shrimp. *A. floridanus* is a facultative partner. It was observed with all three species of gobies as well as in a free-living state (Table 1). The proportion of non associated shrimp is probably much larger than reported in Table 1. Free-living shrimp spend most of their time subterraneously and those not active outside the burrows during the survey were not recorded. The proportion of free-living *B. curacao* is probably also much higher than recorded. They are overlooked easily due to their small size and cryptic coloration. Associated ones, are spotted easily at the entrance of the shrimp's burrow.

Goby-shrimp communication

A. floridanus maintained an antennal contact with various parts of the body of both fishes while outside its burrow. Occasionally this contact was not maintained. This occurred when the partners were very close (several cm) to each other, when the shrimp was positioned parallel to the goby or while behind it and its two antenna were directed diagonally-sideways and forwards.

Upon close approach of a diver, *N. longus* performed rapid tail flicks with a typical small amplitude which were often accompanied by the retreat of the shrimp into its burrow. No special warning signals were ever observed

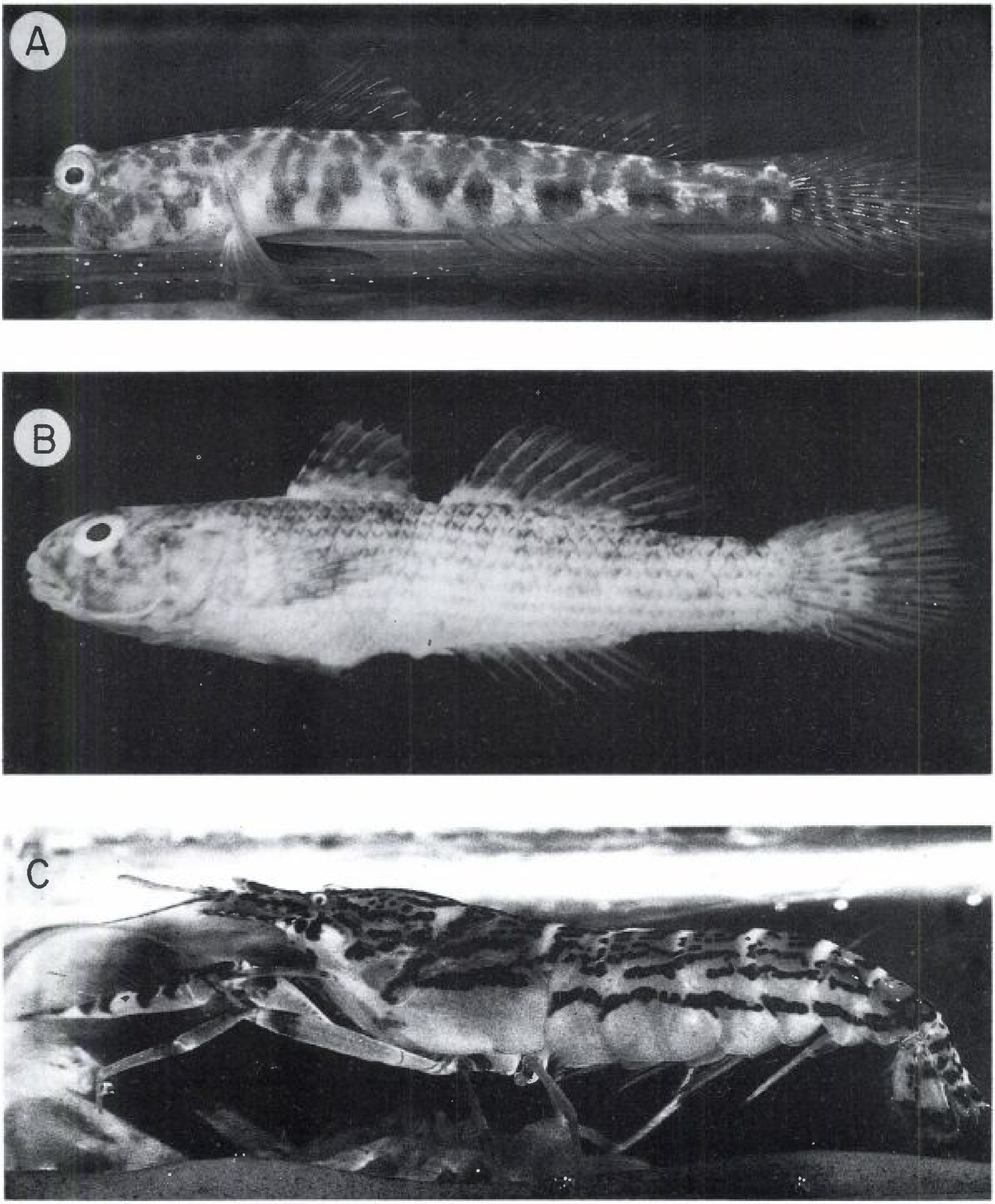

Figure 1. Species involved in mutualistic goby-shrimp partnerships off Key Biscayne, southern Florida. (A) *Nes longus*, (B) *Bathygobius curacao*, (C) *Alpheus floridanus*.

Table 1. Number of associated and non associated gobies and shrimp as found in a partial survey of the study area.

Shrimp partner	Fish partner *Nes longus*	*Gobionellus saepepallens*	*Bathygobius curacao*	No fish partner
Alpheus floridanus	42	4	33	5
No shrimp partner	–	–	10	

to be produced by the facultative partner *B. curacao*. Observations on the occurrence of the tail flick warning signals under natural conditions were not carried out due to low visibility. The structure of the tail flick warning signals of *N. longus* and their impact on the shrimp were investigated in the laboratory with the aid of film analysis and a mobile predator model (Karplus, in prep.).

The rapid head-first retreat of both species of gobies into their burrows caused by the very close approach of a diver consistently resulted in the rapid retreat of the shrimp into its burrow. The goby's head-first entries into the burrow were investigated while monitoring the daily activity rhythm of these associations. A total of 16 (1.2/hr) and 31 (2.7/hr) head-first entries were monitored for *N. longus* and *B. curacao* respectively. *Gerres cinereus*, a fish that digs in the sediment in search of food, caused a substantial fraction of the head-first entries (29% and 19% for *B. curacao* and *N. longus* respectively). Few head-first entries were caused by floating turtle grass and algae (13% and 6.5% for *B. curacao* and *N. longus* respectively). Single head-first entries were triggered by a large hermit crab, a blue crab *Callinectes sapidus* and a gray snaper *Lutjanus griseus*. The head-first retreat of the goby into the shrimp burrow observed under natural conditions consistently resulted in the immediate retreat of its shrimp partner, provided it was outside the burrow.

A. floridanus responded with retreat into its burrow to rapid body movements of its fish partner, though the latter remained outside the burrow. Four such incidents (0.3/hı) were recorded while it was associated with *B. curacao* and one (0.08/hr) while associated with *N. longus*. Some of these rapid movements of the goby were connected to food capture.

One of the major differences in the communication system between *A. floridanus* and its obligatory and facultative fish partners regards the aborted exits of the shrimp. Whenever an associated *A. floridanus* leaves its burrow without making a renewed antennal contact with its fish partner, it retreats into its burrow rapidly. These incidents occur five times more often when associated with *B. curacao* than with *N. longus* (2.5/hr versus 0.5/hr). Both species of gobies spend most of their time close to the burrow entrance and only seldom more than 30 cm away from it. All aborted exits, while associated with *N. longus*, occurred while this goby was more than 30 cm away from the burrow entrance. When associated with *B. curacao* only 3% occurred at this distance, 72% occurred when the goby was within 10 cm of the entrance and 25% while it was within 10–30 cm. The differences in the awareness of the shrimp to the presence of its fish partner may be due to the different positions these fish maintain at the entrance. *N. longus* consistently occupies the zone that is used by the shrimp during its exits (i.e. the shrimp activity zone, Fig. 2) and directs its tail towards the burrow opening. *B. curacao* spends only about 40% of its time in that zone and in the majority of cases its tail was not directed towards the burrow entrance (Fig. 3).

Resumption of shrimp activity outside the burrow after an aborted exit may follow the approach of the goby to the burrow entrance or the entrance and re-exit of the goby from the burrow. The shrimp may leave its burrow also without the goby returning to the burrow. In associations of *A. floridanus* with *N. longus*, the shrimp resumes its activity outside the burrow only in the presence of the goby. Most renewed exits (83%) of the shrimp follow the approach of the goby to the burrow entrance and 17% follow the entrance and re-exit of the goby from the burrow. In associations of *A. floridanus* with *B. curacao*, a large fraction of exits (40%) are resumed in the absence of the goby, 30% of the renewed exits follow the approach of the goby and 30% follow the entrance and re-exit of the goby. *A. floridanus* in association with *B. curacao* spends a relatively long time (5.3±4.3 min) inside its burrow following an aborted exit. It resumes its activity outside the burrow rapidly when associated with *N. longus* due to the short absence of this goby from the shrimp's activity zone at the burrow entrance.

Shrimp activity outside the burrow

The number of exits of *A. floridanus* from its burrow when associated with *N. longus* and *B. curacao* is presented in Fig. 4A. There was a highly significant difference in the number of exits of the shrimp dependent on its fish partner, lack of effect of time of day and lack of interaction between fish species and time (Table 2). The shrimp left its burrow three times more often when associated with *N. longus* than when associated with *B. curacao*. There was no effect of depth, cloud coverage, temperature, current speed and time of the day on the number of exits of *A. floridanus* when associated with *N. longus*, but a significant effect of time and depth on the number of exits when associated with *B. curacao*. The following equation ($r^2 = 0.43$) summarizes the impact

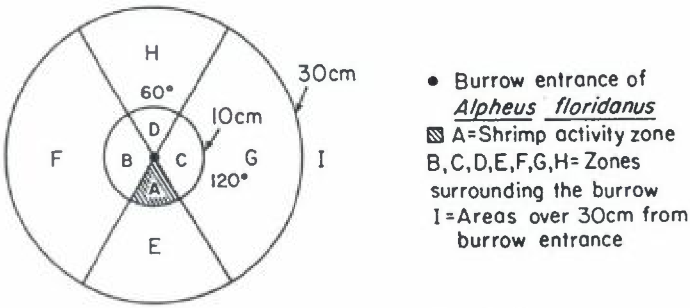

Figure 2. Schematic view of the area surrounding the burrow entrance

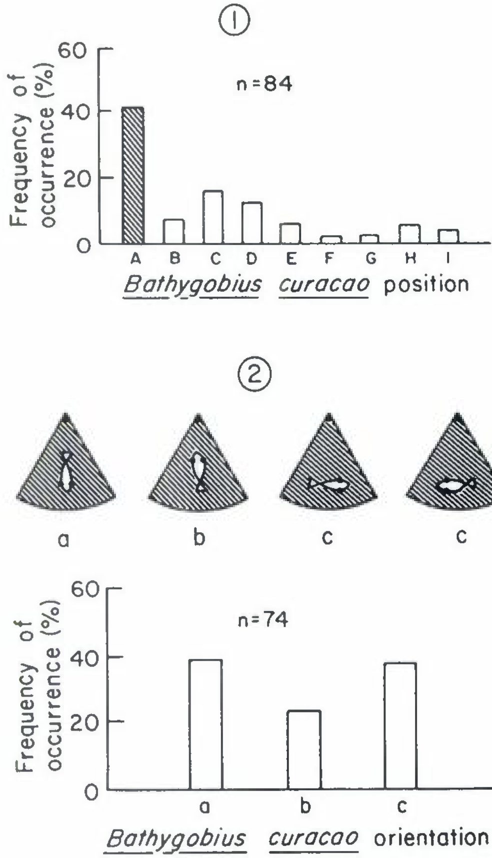

Figure 3. 1. Position of *Bathygobius curacao* at the burrow entrance of *Alpheus floridanus*. The goby spent at least 1 min in each location. (See Fig. 2 for definitions of position zones).
2. Orientation of *Bathygobius curacao* to the burrow opening while in the shrimp activity zone. The goby spent at least 1 min in each position. (Fish in an intermediate orientation were assigned to the closest defined category).

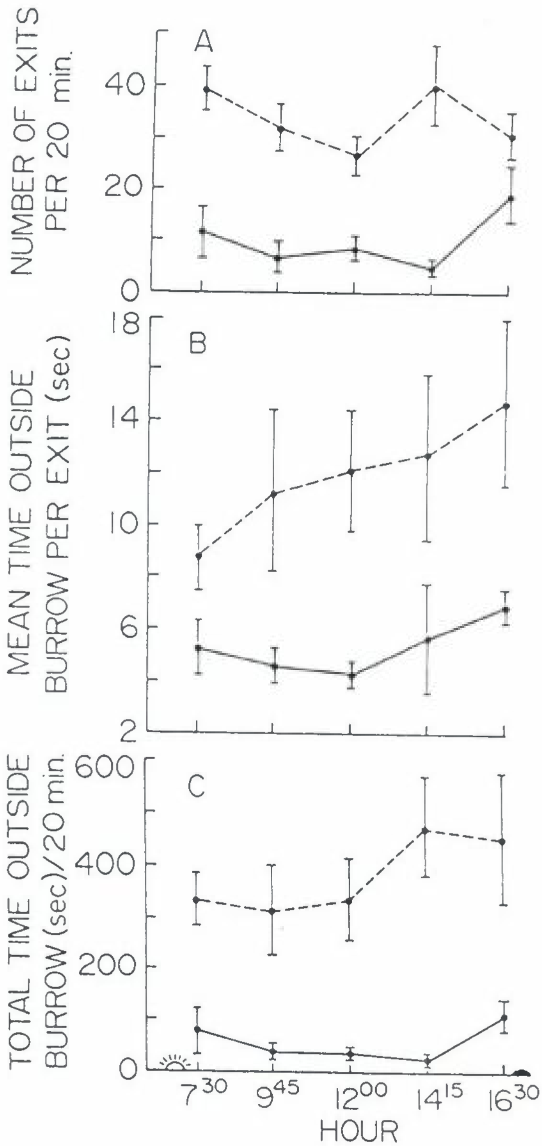

Figure 4. Activity of *Alpheus floridanus* outside its burrow when associated with the *Nes longus* (broken line) and *Bathygobius curacao* (continuous line).

Table 2. Results of ANOVA (F values) of number of exits, mean time outside burrow per exit and total time outside burrow of *Alpheus floridanus* in association with *Nes longus* and *Bathygobius curacao*.

Effect	d.f.	Variable		
		No. of exits	Mean duration of exit	Total time outside burrow
Fish	1, 65	79.48^{***}	30.96^{***}	91.28^{***}
Time	4, 65	$0.95^{N.S.}$	$0.39^{N.S.}$	$0.73^{N.S.}$
Interaction	4, 65	$1.95^{N.S.}$	$0.29^{N.S.}$	$0.63^{N.S.}$

N.S. = Not significant
*** = $P < 0.001$

of these variables:
Exit number = T_i - 0.22 Depth, where $T_1 = 27.8$, $T_2 = 18.8$, $T_3 = 21.6$, $T_4 = 18.6$, $T_5 = 36.3$.

The majority of exits of *A. floridanus* from its burrow during the daily cycle were performed with its chelae loaded with sediment, irrespective of the species of associated goby. Few exits were carried out with empty chelae or while transporting plant material.

The mean time spent by the shrimp outside its burrow while associated with *N. longus* and *B. curacao* is presented in Fig. 4B. There was a highly significant difference in the mean duration of an exit dependent on the fish partner, lack of effect of time of day and lack of interaction between fish species and time (Table 2). Exits when associated with *N. longus* lasted more than twice as long as when associated with *B. curacao.* There was no effect of tested environmental variables on the mean duration of exit when the shrimp is associated with *B. curacao*, but a significant effect of cloud coverage and current speed on mean exit duration when associated with *N. longus.* The following equation ($r^2 = 0.28$) relates exit duration to cloud coverage and current speed: Exit duration (sec) = 10.1 + 1.4 cloud coverage - 0.34 current speed.

The major activities of *A. floridanus* outside the burrow are dumping of sediment, digging in sediment and picking at plants (Fig. 5). The most common activity irrespective of fish partner species or hour of day was dumping of sediment transported from within the burrow. This activity is practiced more often when *A. floridanus* is associated with *B. curacao* than when associated with *N. longus.* There was no effect of time of day on dumping sediment nor an interaction of fish species and time (Table 3). Digging in the sediment and picking at plants are both practiced significantly more often when *A. floridanus* is associated with *N. longus* than when associated with

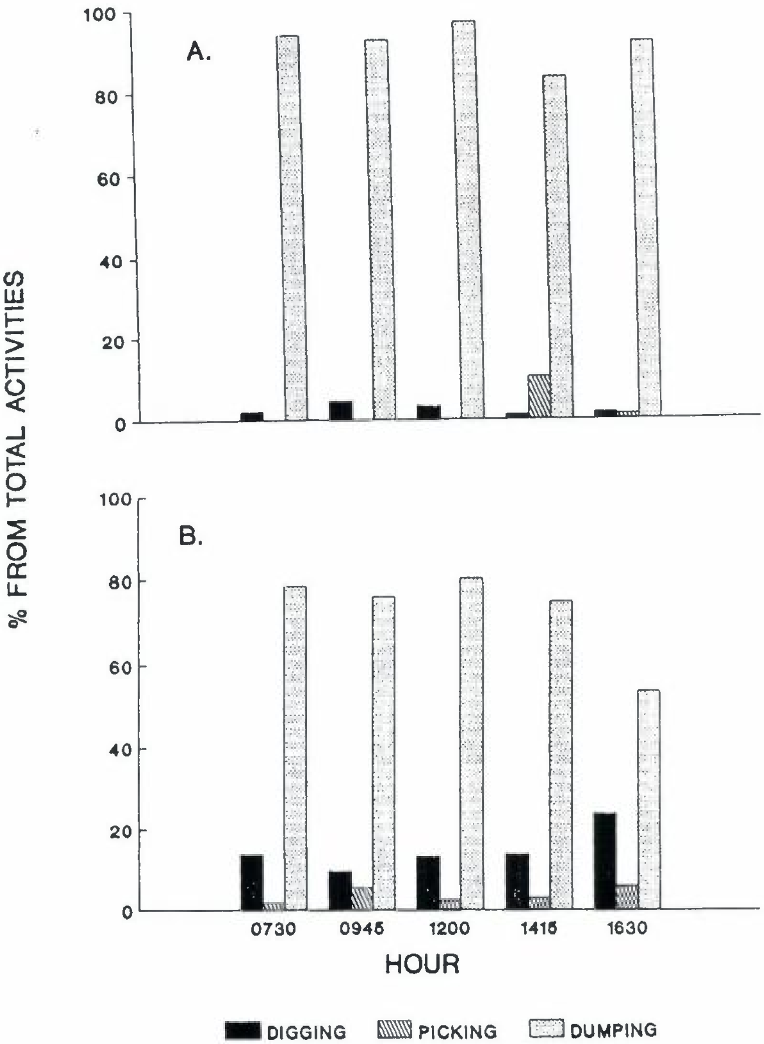

Figure 5. Main activities of *Alpheus floridanus* outside its burrow when associated with (A) *Bathygobius curacao* and (B) *Nes longus*.

B. curacao. There was no effect of time of the day on these activities nor an interaction between fish species and time (Table 3). Mean time dumping sediment was 5.2±2.2 sec, picking at plants 19.8±20.1 sec and digging in sediment 27.9±16.1 sec. Significant differences in the time the shrimps spent carrying out these activities were found (Table 4). They tended to spend less time outside their burrows while carrying out these activities when associated with *B. curacao* than when associated with *N. longus* (Table 4).

Table 3. Results of ANOVA (F values) of frequency of digging in sediment, picking at plants and dumping sediment by *Alpheus floridanus* in association with *Nes longus* and *Bathygobius curacao*

Effect	d.f.	Variable		
		Digging	Picking	Dumping
Fish	1, 63	25.87***	4.66*	22.62***
Time	4, 63	0.42N.S.	1.16N.S.	0.81N.S.
Interaction	4, 63	0.59N.S.	0.76N.S.	0.55N.S.

N.S. = Not significant
* = $P < 0.05$
*** = $P < 0.001$

Table 4. Results of ANOVA (F values) of duration of *Alpheus floridanus* activities outside the burrow (i.e. digging in sediment, picking at plants and dumping sediment) in association with *Nes longus* and *Bathygobius curacao*

Effect	d.f.	Variable-duration
Fish	1, 125	3.94*
Activity	2, 125	72.08***
Interaction	2, 125	0.73N.S.

N.S. = Not significant
* = $P < 0.05$
*** = $P < 0.001$

The total time spent outside its burrow by *A. floridanus* when associated with *N. longus* and *B. curacao* is presented in Fig. 4C. There was a highly significant difference in the total time spent outside the burrow depending on its fish partner, a lack of effect of time of the day and a lack of interaction between fish species and time (Table 2). On the average, the shrimp spent five-fold more time outside its burrow when associated with *N. longus* than when associated with *B. curacao*. This difference is due to higher frequency of exits and also longer mean exit time, mainly due to a higher frequency of exits involving the lengthy digging and plant picking activity.

A. floridanus entered its burrows with empty chelae irrespective of its fish partner or hour of the day. Very few entrances were carried out while transporting plant material into its burrow.

Interactions between Nes longus *and* Bathygobius curacao

Little information is available on competition between *N. longus* and *B. curacao* over the burrows of *A. floridanus*. Only once was a *N. longus* observed chasing away a *B. curacao* which approached its burrow opening. Long lasting co-habitation of burrows by these two species probably does not occur. *N. longus* tends to enter its burrows at high current speed. At these times *B. curacao* often occupies the entrances of these burrows. As the current speed declines, *N. longus* reappears at the burrow entrance and *B. curacao* moves at first only 20–25 cm away from the opening. Subsequently it leaves the area. *B. curacao*, chased by a diver, occasionally took shelter in a burrow occupied by *N. longus*. These *B. curacao* reappeared rapidly at the burrow entrance probably due to the activity of the resident *N. longus*.

Preference of fish partner by the shrimp

Direct evidence for the preference of a specific fish partner requires controlled laboratory experiments (Karplus et al., 1981). One field observation also suggests a preference. *A. floridanus* in our study area usually had a single opening which leads to its subterranean burrow. It seldom had two openings, but on one such occasion *B. curacao* was positioned at one opening and *N. longus* at the other. The shrimp was active outside the burrow at the entrance occupied by *N. longus*. Several times *N. longus* switched openings with *B. curacao*, and each time the shrimp moved over to the opening occupied by *N. longus*.

Shrimp without fish partners

Shrimp without fish partners spend most of their time subterraneously. However, their burrow openings are kept open. Occasionally the shrimp appears at the burrow opening, sometimes emerging partly. At other times the shrimp emerges completely but usually not moving further than 10 cm from the opening. The activity of three free-living shrimp was monitored for 1 hr. The shrimp left their burrows on the average 8.7 ± 7.9 times per hour. The mean duration of each exit was 6.7 ± 0.2 sec. On two occasions a free-living shrimp was observed to move over a distance of 50–60 cm to an adjacent burrow occupied by another *A. floridanus*. On one occasion it was accepted by the owner while on the second it was rejected or the owner was displaced. A clear snap of the pistol-like propodus was heard, and one shrimp left the burrow and moved to another adjacent burrow.

4. Discussion

The major finding of this study is that facultative and obligatory fish partners differ in the complexity and efficiency of their communication system and as a result, in the time their subterranean shrimp partner spends outside the burrow.

The comparison of the goby-shrimp communication system in Atlantic and Indo-Pacific species is of interest. Head-first entries of the goby into its burrow which consistently causes the retreat of its shrimp partner were performed by both Atlantic and Indo-Pacific gobies. This is the most efficient warning signal produced by gobies at high emergency. The detailed study of this signal requires the application of a frame by frame analysis as applied to warning signals of the Indo-Pacific *Amblyeleotris steinitzi* (Karplus et al., 1979).

The tail flick warning signals were carried out only by *N. longus*, the obligatory partner and not by *B. curacao*, the facultative one. These warning signals described for obligatory partners in several Indo-Pacific species (Karplus et al., 1979; Yanagisawa, 1982, 1984; Magnus, 1967), are superficially similar in the Atlantic and Indo-Pacific species. A reliable comparison of these signals requires the detailed analysis of their structure.

One of the major differences between obligatory and facultative partners was the unawareness of the shrimp of the presence of the facultative partner at the burrow entrance. The obligatory partner would position itself in the activity zone of the shrimp, assuring the shrimp's awareness of its presence. The Indo-Pacific goby *Amblyeleotris japonica* went one step further. This species would perform, after some absence of the shrimp, a wide amplitude tail movement that probably signals the shrimp a kind of guarantee of the safety outside the burrows (Yanagisawa, 1984).

The activity of *A. floridanus* outside its burrow, while associated with fish partners, differed from that described for associated Alpheid from the Indo-Pacific region. *A. purpurilenticularis*, *A. rapax* and *A. djiboutensis* were all reported to follow a pronounced daily activity cycle. The shrimp left their burrows in the morning for short periods of time, mainly dumping sediment outside the burrows. In the afternoon they left their burrows with empty chelae for approximately a 5 times longer period feeding actively on the upper undisturbed layer of the sediment. They usually returned to their burrows with their chelae loaded with sediment (Magnus, 1967; Karplus, 1987). *A. floridanus*, on the other hand, carried out the same activities over the entire day, dumping sediment outside the burrow, occasionally digging, but returning to its burrow with empty chelae. The differences in the activities of the Atlantic and Indo-Pacific shrimp outside the burrows reflects their differential feeding habits. The Indo-Pacific species feed largely on sediment outside the burrow while the Atlantic *A. floridanus* seems to rely more on subterranean feeding. This trend fits a facultative partner, at times acquiring food without the protection of a goby. This shift to feeding increasingly on sediment outside the burrow may reflect a further step taken by the Indo-Pacific species during co-evolution of goby-shrimp partnerships.

The Atlantic facultative shrimp partner differs from the obligatory Indo-Pacific species in its behaviour in the absence of a fish partner. All activity outside their burrows ceases in the absence of the goby. They gradually block the opening, leaving open only a very small crevice to enable a potential fish partner to insert its tail. The presence of the goby triggers the clearance of the opening and renewal of the shrimp activity outside the burrow (Karplus, 1981, 1987). In contrast, *A. floridanus* in the absence of a fish partner keeps its burrows open, occasionally dumping sediment outside.

Little information is available on the reproductive behaviour of alpheid shrimp associated with gobies. Several species of these shrimp have been reported to live in pairs sharing the same burrow (Karplus, 1987). The reproductive behaviour has been studied in detail in a single obligatory species *A. bellulus* off Japan (Yanagisawa, 1984). Shrimp of this species have never been observed to move between burrows. They are thought to acquire a mate following the subterranean fusion of their burrows. *A. floridanus* have been observed to move between adjacent burrows occasionally. In this facultative shrimp species, pair formation may be achieved in this way.

Obligatory shrimp partners such as *A. purpurilenticularis* were disoriented when isolated from their fish partners and walked straight into a glass jar (pers. observ.). The facultative *A. floridanus* when moving between burrows, would avoid being captured by moving rapidly into the nearest burrow. These differences in the evasive behaviour of the shrimp may be due to the structure of their eyes. The eyes of the obligatory shrimp partner *A. djiboutensis* were described as having little pigmentation, suggesting poor vision (Luther, 1958).

Partnerships between *A. floridanus* and *B. curacao* are less advantageous for the shrimp as compared to its partnerships with *N. longus*. Partnerships between the shrimp and *B. curacao* may occur because of a surplus of shrimp relative to the number of *N. longus* in the study area. *A. floridanus* in association with *B. curacao* are better off than free-living shrimps, spending more time outside their burrows while being protected by a crude warning system.

In Key Biscayne, within a very small area, the same species of shrimp *A. floridanus* was found free-living, in association with a facultative fish partner and an obligatory one. This unique situation can provide us with some insight into the possible evolutionary process underlying the formation of complex associations between shrimp and goby. The free-living shrimp spends very little time outside its burrow and depends for its nutrition mainly on food located subterraneously. This phase may be represented by the free-living

A. floridanus. Facultative partnerships provide the goby with shelter when it retreats into the shrimp's burrows. The shrimp obtains the advantage of a primitive warning system. At these initial phases of the association, the head-first entries of the goby provides the main warning signal to the shrimp. In the next phase, the shrimp positions its antenna on the goby's body, thus becoming aware of any rapid movement of the goby which causes it to retreat into its burrow. At this phase the shrimp spends more time outside the burrow. The association between *A. floridanus* and *B. curacao* may represent this phase. As the relationship becomes obligatory, specific tail flick warning signals evolved allowing the goby to warn the shrimp while remaining outside the burrow. Concomitantly evolved the orientational behaviour of the goby, which positions itself in the activity zone of the shrimp with its tail directed towards the opening. This assures the shrimp meeting the goby while emerging from its burrow. The association between *A. floridanus* and *N. longus* may represent this advanced phase. The reconstruction of the evolutionary pathway in the formation of the complex partnership between gobies and shrimp is still very speculative but the occurrence of intermediate phases provides some missing links.

Acknowledgements

I am grateful to Prof. A.A. Myrberg of the Rosenstiel School of Marine and Atmospheric Sciences of the University of Miami for his advice, encouragement and support while carrying out this study. I wish to thank Prof. C.R. Robins for his advice and for the identification of the gobies and Mr. J. Garcia-Gomez for the identification of *Alpheus floridanus*. I also wish to thank Prof. J.E. Randall from the Bernice Bishop Museum for the photo of *Bathygobius curacao*. I am grateful to Drs. G.W. Wohlfarth, S. Harpaz, A. Milstein and Mr. A. Barki for their critical comments on the manuscript. This study was made possible through the receipt of a G. Meirbaum fellowship from the Hebrew University of Jerusalem.

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