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Sound production during competitive feeding in the grey gurnard

M. C. P. AMORIM*†, Y. STRATOUDAKIS‡
AND A. D. HAWKINS*§

*FRS Marine Laboratory, P. O. Box 101, Victoria Road, Aberdeen, AB11 9DB, U.K.,

‡Instituto de Investigação das Pescas e do Mar (IPIMAR), 1449-006 Lisboa,

Portugal and §Department of Land Economy, University of Aberdeen, St Mary's
King's College, Aberdeen, AB 24 3UF, U.K.

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The acoustic repertoire of captive grey gurnard *Eutrigla gurnardus* during competitive feeding consisted of three types of sound: knocks, grunts and growls. Knocks were audible as a single sound, whereas grunts and growls were perceived as longer, pulsed sounds to the human ear. Typically, knocks were composed of 1–2 pulses, grunts of 4–8 pulses and growls >10 pulses. Growls were longer and had shorter pulse periods than grunts. All sound types had peak frequencies of *c.* 500 Hz. The sequences of behaviours observed during feeding interactions suggest that grey gurnard obtain food both by scramble and contest tactics. Competing fish emitted knocks mainly while grasping a food item and also during other non-agonistic behaviour, suggesting that knock production may reflect a state of feeding arousal but could also serve as a warning of the forager's presence to nearby competitors. Grunts were mainly emitted during frontal displays, which were the most frequent behavioural act preceding grasps, suggesting that they may play a role in deterring other fish from gaining access to disputed food items.

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Key words: agonistic behaviour; bioacoustics; calling; scramble and contest competition; teleosts.

INTRODUCTION

Fish produce sounds that are usually made up of short repeated low frequency pulses with a large variation in their temporal characteristics (Hawkins, 1993; Ladich, 2003). Sound production during agonistic behaviour is widespread in fishes (Ladich, 1997) and may give an advantage in territory defense (Rigley & Muir, 1979; Myrberg, 1997), the outcome of contests (Valinski & Rigley, 1981; Ladich *et al.*, 1992) and in regulating the opponent's aggressive behaviour (Schwarz, 1974; Rigley & Muir, 1979). Most accounts of acoustic emissions by fishes in agonistic contexts are related to territorial defense, often associated with reproduction (Hawkins, 1993; Ladich, 1997). Few are associated with competitive aggression at smaller temporal and spatial scales, as, for example, during brief contests over ephemeral resources such as food patches.

†Author to whom correspondence should be addressed at present address: Unidade de Investigação em Eco-Etologia, ISPA, Rua Jardim do Tabaco 34, 1149-041 Lisboa, Portugal. Tel.: +351 218811700; fax: +351 218860954; email: amorim@ispa.pt

Competition for limited food resources may be resolved by scramble or contest tactics (Milinsky & Parker, 1991). When food resources are too costly to monopolize and defend from other competitors, it becomes more advantageous for an individual to simply be faster and more efficient than others in acquiring food without dispute (scramble competition; Grant, 1993). As resources become more clumped in space, less clumped in time and more predictable in both space and time, they become more economically defensible, and hence an animal's aggressiveness is predicted to increase (contest competition; Grant, 1993; Robb & Grant, 1998; Goldberg *et al.*, 2001). Animals often resolve such contests with displays, during which acoustic communication can co-occur with visual or other types of signals (Huntingford & Turner, 1987).

Sound production is widespread amongst species of the family Triglidae and the sound producing ability of these fishes was already known to fishermen in Aristotle's time (Moulton, 1963). Sound production and associated behaviour, however, has been poorly studied in this family (Amorim & Hawkins, 2000), perhaps because field work is greatly limited by the depths at which triglids live (Wheeler, 1969; Papaconstantinou, 1983). The grey gurnard *Eutrigla gurnardus* (L.), is a common benthic gregarious species in coastal waters of the eastern North Atlantic, typically found at depths down to 140 m (Wheeler, 1969), in small (Protasov, 1965) to occasionally extremely large shoals (H.J.L. Heesen & N. Daan, pers. comm.). This species has a pair of strongly developed intrinsic sonic muscles embedded laterally on each side of the swim bladder wall and produces typical swim bladder sounds composed of brief low frequency pulses repeated at different rates, which are easily heard under laboratory conditions during staged feeding (Amorim, 1996). In this study, the sounds produced by captive grey gurnards during competitive feeding interactions were investigated. The sequences of behaviour occurring during feeding interactions were studied to identify the types of strategies used during competitive feeding. Finally, the association of emissions of different sound types with accompanying behaviour was determined.

MATERIALS AND METHODS

FISH COLLECTION AND MAINTENANCE

Fish were trawled at depths of 15–40 m in the North Sea and taken to the aquarium facilities of the FRS Marine Laboratory, Aberdeen (U.K.). Subject fish were kept indoors under a computer-controlled day-night schedule, set to simulate the natural photoperiod (57°08' N). Experimental tanks were provided with treated re-circulated sea water (filtered and sterilized), with temperatures ranging from 7° C (winter) to 12° C (summer). For experiments, fish were kept in four groups of four to eight individuals of similar size. Smaller specimens (10–20 cm total length, L_T) were kept in 1.5 and 3 m diameter fibreglass tanks, and larger specimens (25–40 cm L_T) in a swimming-pool of 7.0 × 3.5 × 1.5 m, length × width × depth, with a sand bottom. Fish were fed three times a week, with dead fishes or shrimp. Fish were of both sexes, but were sexually inactive.

ACOUSTIC REPERTOIRE

Sounds were recorded from the four fish groups during 5 min feeding sessions two to three times a week, throughout 1 year. The sound recording equipment consisted of a

hydrophone (Plessey, MS83), with a sensitivity of -170 dB re 1 V for $1 \mu\text{Pa}$ and with a flat frequency response from 10 to 40 kHz, a low-noise amplifier (Brookdeal, model 450) and a DAT recorder (Casio, model DA-1). Sounds were analysed using a Loughborough Sound Images Workstation (version 2.0; 1986 Metagraphics Software Corporation[®]).

Grey gurnard sounds were classified aurally into three types: knocks, grunts and growls. All consisted of repeated low frequency pulses when viewed as oscillograms of sound pressure against time. Knocks were audible to the human ear as a single pulse of sound, whereas grunts and growls were heard as longer pulsed sounds. The following features of sounds were measured: sound duration (time elapsed from the start of the first to the end of the last pulse in a sound, ms); pulse duration (time elapsed between the start and the end of a pulse, averaged for all or at least 10 pulses in long sounds, ms); number of pulses (total number of pulses in a sound); pulse period (mean time elapsed between the peak amplitude of two consecutive pulses, ms); peak frequency (the frequency component with the highest energy in the entire sound, measured for each pulse of sound, Hz). Sounds (knocks, grunts and growls) were emitted alone or in sequences of two to several sounds, here referred as bursts of sounds. The following acoustic features were measured for bursts of sounds: burst duration (time elapsed between the start of the first sound and the end of the last sound within a burst, s); number of sounds (total number of sounds in a burst); interval between sounds (time elapsed between the end and the start of different sounds, ms).

A linear discriminant analysis based on all sound features (Statistica 6.0) was used to validate the adequacy of the aural classification of the three sound types.

BEHAVIOUR

Video recordings

Feeding interactions and the association of sound production with behaviour were studied in three of the experimental fish groups by means of video recording and analysis. Video recordings were taken with a Sony video 8 camcorder (CCD-FX500E Pal 8) placed above the tanks and connected to the sound recording system so that the images could be synchronized with the sounds. Ten sessions of video recording lasting *c.* 15 min each were obtained for each fish group. Fish were recorded three times a week. Food was dropped every minute through a feeding tube throughout the filming session (from minute 0 to minute 14). Feeding was considered competitive since the food was scarce and it did not exceed demand (Milinsky & Parker, 1991). The system of feeding chosen was intended to promote maximum competition for food, since food items were clumped in space and were spatially and temporally predictable (Grant, 1993; Goldberg *et al.*, 2001).

Feeding interactions

Fish were considered to participate in a feeding interaction when they were in close proximity and altered the conspecifics' behaviour. Feeding interactions were characterized by registering the succession of behavioural acts for each fish participating in the interaction. The following behavioural categories were considered: (1) dash, swimming rapidly towards a food item and suddenly stopping just before reaching it and without attempting to grasp it, typically with conspecifics in close vicinity; (2) circle, circling the feeding area without attempting to grasp any food item; (3) grasp, taking a food item into the mouth; (4) orient, turning the head towards a conspecific; (5) approach, slowly swimming or moving on the substratum towards a conspecific, decreasing the distance between the performer and the recipient; (6) chase, similar to approach but in a fast motion; (7) frontal display, spreading out the paired and dorsal fins with the head directed towards the opponent's head; (8) flee, swimming rapidly away from a conspecific.

These behavioural categories were established during preliminary observations carried out during the study of the species' acoustic repertoire. The typical sequences of behavioural acts during feeding interactions were examined by determining which sequences of behaviours were more frequently observed than if they had occurred at random, using a first-order Markov chain analysis that tests for dependence of one act on the previous

one. A simulation analysis for tests of independence of contingency tables that follows the rationale of a χ^2 (programme ACTUS; Estabrook & Estabrook, 1989) was used to test the dependence of one behavioural act on the previous one (Amorim & Hawkins, 2000).

Association of sound production with behaviour

As grey gurnards do not perform specific body movements when emitting sounds and compete for food very actively (several fish can be seen together, all moving and displaying very quickly), it was very difficult to attribute sound production to an individual fish. Hence, the association of sound production with behaviour was studied at the group level. The association of behaviour and sound production was analysed with a one-zero sampling (time sampling) recording technique (Martin & Bateson, 1993): each video session was divided into 5 s intervals, and at the end of each sample interval it was noted whether each behavioural category had occurred. The number of grunt and knock bursts emitted were also noted per 5 s interval. The duration of the sample interval, 5 s, was chosen to optimize the accuracy of the time-sample record and to compromise as little as possible the reliability of recording several categories of behaviour at once (Martin & Bateson, 1993). Data were pooled at the minute level for analysis by summing the number of 5 s intervals in which a behavioural category occurred. The number of knock and grunt bursts scored at the 5 s level were also pooled for each min.

Generalized linear models (GLM, McCullough & Nelder, 1989) were used to associate the number of knock and grunt bursts produced per minute to the number of grasps, agonistic (orient, approach and chase, frontal display and flee) and non-agonistic (circle and dash) behaviours. The number of sound bursts (grunts or knocks) produced per minute of recording was assumed to follow a Poisson distribution and its expected value was linked to the explanatory variables (time within recording session and number of 5 s intervals at which each of the three behavioural classes occurred per minute) by a logarithmic link function. GLM were fitted using the open source software R (Venables & Ripley, 2002) and the resulting models were checked using standard residual inspection plots. The significance of each explanatory variable was tested using *t*-tests which were based on an estimate of the variance obtained by the use of the quasi-Poisson family distribution.

RESULTS

THE SOUND REPERTOIRE

Grey gurnards emitted three sound types during competitive feeding: knocks, grunts and growls (Figs 1–3). A discriminant analysis based on the measured acoustic features supported the adequacy of this classification ($n=1080$, Wilks' $\lambda=0.139$, $P<0.001$). Single-pulse knocks were not considered in this analysis since these do not have values for the variable pulse period. More than 90% of the knocks and grunts, and 73% of the growls were correctly classified (Table I). The variables that mainly contributed to the discriminant functions were the pulse duration, the number of pulses and the pulse period (Table II).

Pulse duration was shorter in growls than in knocks or grunts, probably due to a shorter pulse period (Table III). Sound duration and number of pulses increased from knock to grunt to growl. Most knocks had one or two pulses (85%), typical grunts had four to eight pulses (87%) and typical growls 10 to 40 pulses (59%). The peak frequency of all sound types was *c.* 500 Hz (Table III). Knock and grunt bursts typically lasted for a little over a second and usually consisted of five consecutive sounds (Table III). Knocks were the most frequent

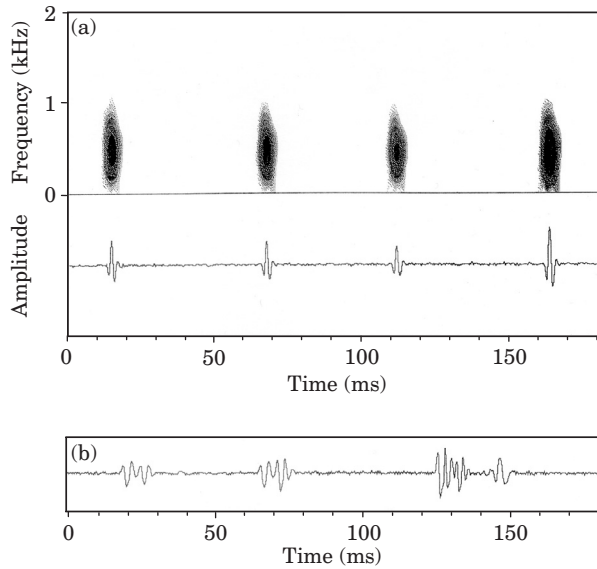


FIG. 1. (a) Sonogram and oscillogram of a burst of single pulsed knocks. (b) A burst of knocks made up of two and three pulses. The filter bandwidth of the sonogram is 125 Hz.

sound type [mean \pm s.d. (range): 9.8 ± 8.6 (0–32.8) knocks min^{-1}] during the 5 min feeding bouts ($n = 64$). Growls occurred rarely [0.3 ± 0.7 (0–3.8) growls min^{-1}], usually within or at the end of grunt bursts [4.6 ± 4.6 (0–21.6) grunts min^{-1}]. Only 64 growls were recorded during this study.

BEHAVIOUR

Outside feeding periods fish usually stayed on the bottom of the tank, resting or moving with the help of the pectoral fin rays in a small loose shoal, interacting and emitting sounds infrequently (Amorim, 1996). When food was presented, however, most fish swam rapidly towards the feeding area and attempted to

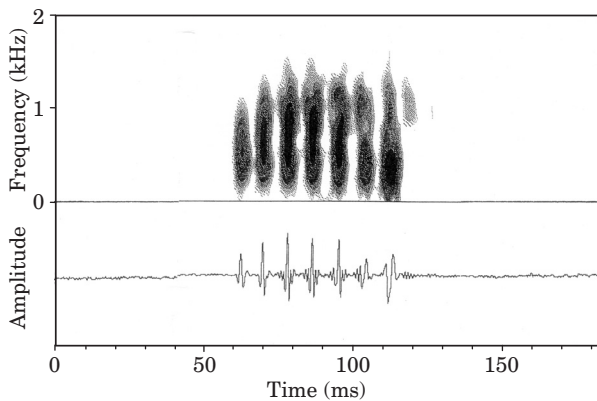


FIG. 2. Sonogram and oscillogram of a grunt with seven pulses (filter bandwidth of 125 Hz).

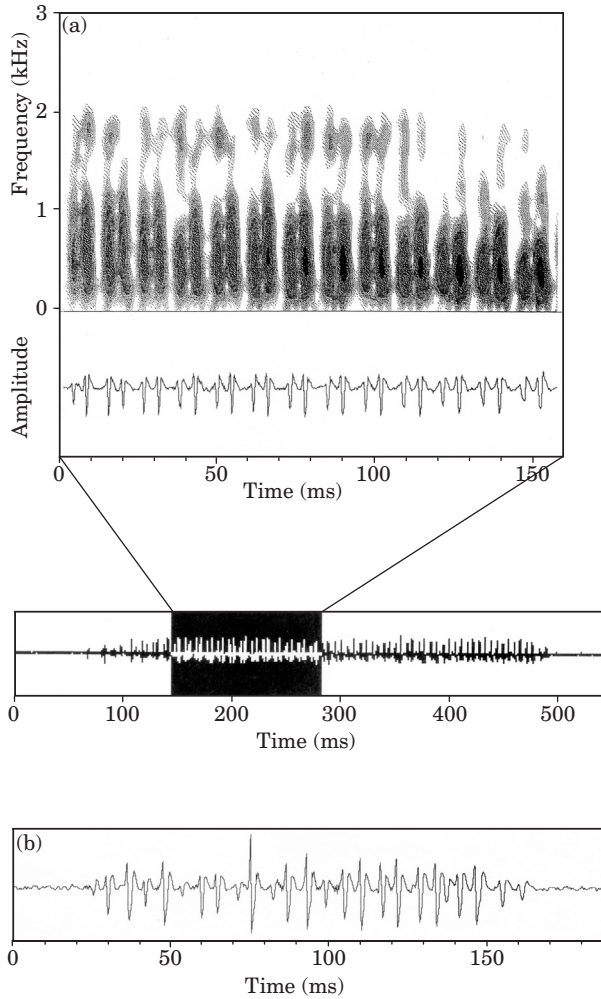


FIG. 3. (a) Sonogram and oscillogram of a section of a growl and the envelope of the complete growl showing its 78 pulses. The filter bandwidth of the sonogram is 125 Hz. Note pulses occur in pairs. (b) Oscillogram of a shorter growl with 24 pulses in which a double-pulse structure is not clear.

grasp the food, resulting in a marked increase in the frequency of social interactions and sound production. Grasp was the behaviour that most frequently started a sequence of behaviour in an interaction ($n = 698$, 38.5%), followed by dash (29.8%) and approach (19.2%). Interactions typically involved two to three fish [2.67 ± 0.74 (2–5)]. It was rare (15.3%), however, that more than one of the interacting fish started an interaction by grasping food and in 26.1% of the cases none of the interacting fish initiated a behavioural sequence with a grasp. This suggests that when food is presented, fish rush to the feeding area with only one usually immediately grasping a piece of food and deterring competitors from grasping simultaneously. The other fish dash or approach the successful conspecific. Interacting fish then start a sequence of behaviours (Fig. 4) that eventually leads to one or more grasps by all interacting individuals.

TABLE I. Summary of sound type classification given by linear discriminant analysis. Columns show the reallocation of sounds in each group (sound type). Knocks with only one pulse were not used in the analysis

Sound type	True group		
	Knock	Grunt	Growl
Knock	297	41	10
Grunt	28	649	7
Growl	0	1	47
Total n^1	325	691	64
Proportion correct (%)	91.4	93.9	73.4

¹Total number of each sound type analysed.

The sequences of behavioural acts observed during feeding interactions that occurred more frequently than expected by chance are depicted in Fig. 4. Typically food was either obtained directly by grasping or by waiting for an opportunity to grasp (circle and grasp), or by means of aggressive behaviour. The behavioural act that most frequently preceded grasp was frontal display (40.5%; any other act had values <17%) suggesting that the frontal display was an effective means of gaining access to food. Fleeing mostly ended feeding interactions for the fish concerned.

Bursts of knocks were significantly associated with grasps and also with non-agonistic behaviour (dash and circle; Fig. 5 and Table IV), while the relation with agonistic behaviour was non-significant. On the contrary, bursts of grunts were mostly associated with agonistic behaviour (Fig. 5 and Table IV), while there was a marginally significant relation with grasp and a non-significant relation with non-agonistic behaviour. Repeating the analysis on grunts separately for each type of agonistic behaviour showed that the most significant relation was obtained for the behaviour frontal display. Both knock and grunt emissions decreased with time (Fig. 5).

DISCUSSION

The grey gurnard produced three types of sound during competitive feeding (knocks, grunts and growls), which were associated with different behavioural

TABLE II. Linear discriminant functions for the validation of sound type classification

Variables	Discriminant functions		
	1	2	3
Constant	-48.51	-48.46	-55.58
Number of pulses	0.93	0.24	1.68
Sound duration	-0.14	-0.01	-0.12
Pulse duration	12.48	10.72	10.08
Pulse period	0.67	1.47	0.73
Peak frequency	0.04	0.04	0.04

TABLE III. Acoustic features measured in knocks, grunts, growls and bursts of sounds. Values are means \pm s.d. and range is given in parentheses

Parameters		Knock	Grunt	Growl
Sounds	<i>n</i>	968	693	64
	Sound duration (ms)	11.8 \pm 6.8 (2.6–30.8)	70.1 \pm 24.3 (18.3–297.5)	263.6 \pm 167.3 (50.8–846.5)
	Pulse duration (ms)	5.6 \pm 0.9 (2.6–9.8)	5.6 \pm 0.8 (3.6–8.4)	4.6 \pm 0.4 (3.9–5.5)
	Number of pulses	1.8 \pm 0.8 (1–4)	6.2 \pm 2.3 (2–37)	41.1 \pm 26.5 (9–140)
	Pulse period (ms)	7.8 \pm 2.3 (3.4–19.6)	11.0 \pm 1.9 (5.7–18.6)	6.2 \pm 0.9 (4.6–8.7)
	Peak frequency (Hz)	510 \pm 160 (246–1064)	478 \pm 202 (229–1170)	499 \pm 159 (304–1018)
	Bursts of sounds	<i>n</i>	130	85
Burst duration (s)		1.4 \pm 2.1 (<0.1–9.2)	1.1 \pm 2.0 (<0.1–12.7)	–
Number of sounds in a burst		5.3 \pm 5.1 (1–30)	4.6 \pm 6.5 (1–52)	–
Interval between sounds (ms)		324.0 \pm 368.1 (5.6–2172.0)	253.0 \pm 287.7 (6.4–1858.0)	–

patterns. Other triglids, such as the streaked gurnard *Trigloporus lastoviza* (Bonnaterre) and the American searobins *Prionotus* spp., are also known to increase the rate of sound production during competitive feeding (Fish, 1954; Amorim & Hawkins, 2000) but they seem to have a smaller repertoire of agonistic sounds than the grey gurnard. The streaked gurnard emits only one sound type (very long growls) during competitive feeding (Amorim & Hawkins, 2000), while the northern searobin *Prionotus carolinus* (L.) and the striped searobin *Prionotus evolans* (L.) emit at least one sound type, squawks and grunts respectively, when fed alone or competitively (Fish, 1954). The terminology used to label the sounds produced by the searobins is however confusing (Fish, 1954; Moulton, 1956; Fish & Mowbray, 1970), not permitting a clear identification of the total number of distinct sound types produced by these species.

All sounds emitted by the grey gurnard were made up of repeated, short, low frequency pulses and were readily distinguishable by the human ear, and statistically discriminated by their pulse duration, number of pulses and pulse period. Knocks, grunts and growls differed considerably in their number of pulses and therefore in sound duration. Typical number of pulses for knocks, grunts and growls were 1–2, 4–8 and 10–40 respectively, and average sound durations were 12, 70 and 264 ms, respectively. Average pulse period also differed *c.* 3 ms between knocks and grunts and *c.* 5 ms between grunts and growls. Sounds, or at least grunts, are generated in this species by synchronous contractions of the left and right sonic muscles, as proven by simultaneous electromyograms and sound recordings registered during spontaneous sound production (Amorim, 1996). This suggests that the basic unit of sound production is a

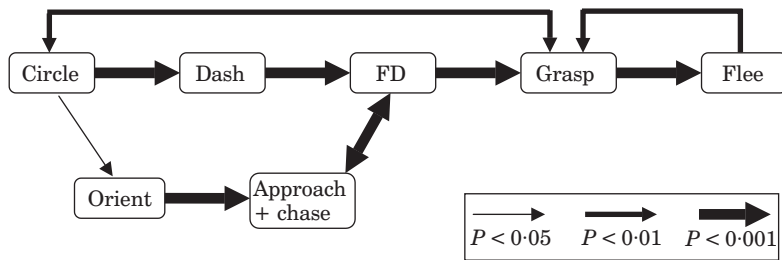


FIG. 4. Behavioural sequences observed during competitive feeding interactions occurring more frequently than expected by chance alone. Sequential dependence of behavioural acts was tested by comparing observed frequencies with those expected if the observations were independent. The probabilities were determined by the programme ACTUS, a simulation analysis for tests of independence of contingency tables ($n = 1372$). FD, frontal display.

single pulse. Some knocks and growls, however, show a double-pulse structure suggesting that perhaps in some occasions the sonic muscles may contract non-simultaneously as observed in the northern searobin (Bass & Baker, 1991).

Although knocks, grunts and growls can be discriminated into three different sound types, it is not clear whether hearing generalists such as the grey gurnard, are able to discriminate sounds with such differences in the temporal characteristics of sounds (Fay & Simmons, 1999; Wysocki & Ladich, 2003). The plainfin midshipman *Porichthys notatus* Girard, seems capable of fine temporal resolution (Bodnar & Bass, 1997; McKibben & Bass, 2001), and the pumpkinseed, *Lepomis gibbosus* (L.) seems to be able to process the pulses of conspecific sounds, each contributing to a compound brainwave recorded at the brainstem (Wysocki & Ladich, 2003). In general, the temporal patterning of sounds is believed to be the most important feature in acoustic communication by fishes (Winn, 1964; Myrberg *et al.*, 1978). Amorim (1996) has performed behavioural playback tests to ascertain whether grey gurnards can differentiate between knocks, grunts and growls, but the experiments elicited no responses. Playback experiments with teleosts often fail to elicit a response unless the sounds are accompanied by visual stimuli (Hawkins & Myrberg, 1983; Ladich, 1997).

Knocks and grunts emitted by the grey gurnard are likely to differ in their biological significance since knocks were mainly associated with grasping food and other non-agonistic behaviour, while grunts were mainly associated with frontal displays. Growls were emitted typically at the end of a grunt sequence. The main difference between grunts and growls is the higher pulse number and repetition rate. These features are thought to increase as the fish's motivational state becomes more intense (Myrberg *et al.*, 1978; Hawkins & Amorim, 2000). As the presence of a fish grasping food usually made competitors circle or dash, however, the emission of knocks, grunts and growls could perhaps be seen as a continuum in aggressive motivation.

The sequences of behavioural acts observed during feeding interactions suggest that grey gurnards used both scramble and contest competition tactics (Milinsky & Parker, 1991), as foraging fish succeeded in grasping a piece of food either by being the fastest to snap a food item and by circling the feeding area until they had an opportunity to grasp without being aggressive, or by

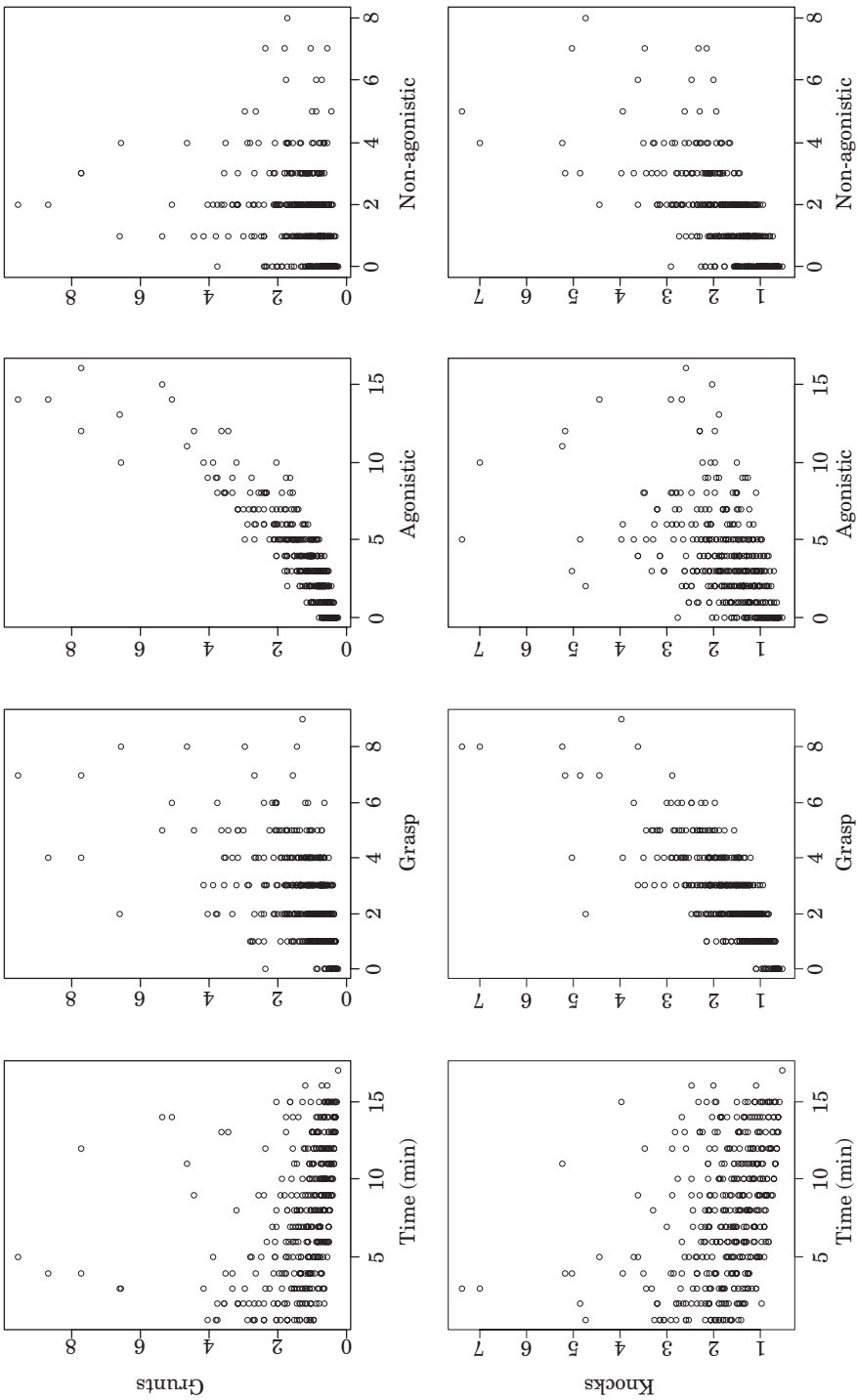


Fig. 5. Fitted values of the number of grunt and knock bursts (from GLM with Poisson distribution) produced per minute in relation to time and the associated behaviours.

TABLE IV. Results of GLM with Poisson distribution fitted to the number of grunt and knock bursts produced per minute in relation to time and the associated behaviours

Sound	Variable	Parameter	S.E.	<i>t</i> -value	<i>P</i>
Grunt	Time	-0.064	0.010	-6.18	<0.001
	Grasp	0.055	0.028	1.98	0.048
	Agonistic	0.171	0.013	13.26	<0.001
	Non-agonistic	0.059	0.033	1.78	0.076
Knock	Time	-0.039	0.010	-3.75	<0.001
	Grasp	0.154	0.028	5.47	<0.001
	Agonistic	0.020	0.016	1.24	0.216
	Non-agonistic	0.152	0.029	5.23	<0.001

performing agonistic behaviour such as approaches and frontal displays. The emission of sounds may confer advantages to a foraging fish. Knock production associated with grasp, circle and dash, may reflect a state of feeding arousal caused by the sight of food, although it could also serve as a warning to potential competitors. Grunts were mainly emitted during frontal displays suggesting that they are aggressive signals. The spread-out of fins in a frontal display, in particular of the large pectorals, may be enhanced by grunting, and seemed an effective behaviour in deterring other fish from getting closer to the sound emitter and the food items, as this was the behaviour that most frequently preceded grasps.

The role of sound production in feeding interactions has been rarely mentioned in the literature but is probably widespread. Sound production outside the reproductive season by croakers (*Sciaenidae*), longspine squirrelfish *Holocentrus rufus* (Walbaum), gurnards (*Triglidae*) and haddock *Melanogrammus aeglefinus* (L.) has been related to feeding activity (Fish, 1954; Moulton, 1958; Protasov, 1965; Hawkins, 1993; Amorim & Hawkins, 2000). The present work provides one of the few detailed studies on the use of acoustic emissions during competitive feeding in fishes (Amorim & Hawkins, 2000), demonstrating the significance of acoustical signals in non-territorial fish species. Although the association of knocks and grunts with particular behavioural displays is not sufficient to validate their function, it is an easy and a non-intrusive method that gives valuable cues of the role of different sound types emitted by fishes (Torricelli *et al.*, 1986; Amorim & Hawkins, 2000; Amorim *et al.*, 2003). Given that the social significance of sound emissions is unknown in many fish species because experimental studies demonstrating the function of fish sounds are difficult to achieve or intrusive (Bass & McKibben, 2003; Ladich, 2003), it is suggested that this method could be more widely applied in fish sound production studies.

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