

Ethology **111**, 255–269 (2005)
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Ontogeny of Acoustic and Feeding Behaviour in the Grey Gurnard, *Eutrigla gurnardus*

M. Clara P. Amorim & Anthony D. Hawkins

FRS Marine Laboratory, Victoria Road, Aberdeen, UK

Abstract

Although sound production in teleost fish is often associated with territorial behaviour, little is known of fish acoustic behaviour in other agonistic contexts such as competitive feeding and how it changes during ontogeny. The grey gurnard, *Eutrigla gurnardus*, frequently emits knock and grunt sounds during competitive feeding and seems to adopt both contest and scramble tactics under defensible resource conditions. Here we examine, for the first time, the effect of fish size on sound production and agonistic behaviour during competitive feeding. We have made sound (alone) and video (synchronized image and sound) recordings of grey gurnards during competitive feeding interactions. Experimental fish ranged from small juveniles to large adults and were grouped in four size classes: 10–15, 15–20, 25–30 and 30–40 cm in total length. We show that, in this species, both sound production and feeding behaviour change with fish size. Sound production rate decreased in larger fish. Sound duration, pulse duration and the number of pulses increased whereas the peak frequency decreased with fish size, in both sound types (knocks and grunts). Interaction rate and the frequency of agonistic behaviour decreased with increasing fish size during competitive feeding sessions. The proportion of feeding interactions accompanied by sound production was similar in all size classes. However, the proportion of interactions accompanied by knocks (less aggressive sounds) and by grunts (more aggressive) increased and decreased with fish size, respectively. Taken together, these results suggest that smaller grey gurnards compete for food by contest tactics whereas larger specimens predominantly scramble for food, probably because body size gives an advantage in locating, capturing and handling prey. We further suggest that sounds emitted during feeding may potentially give information on the motivation and ability of the individual to compete for food resources.

Correspondence: M. Clara P. Amorim, Unidade de Investigação em Eco-Etologia, ISPA, Rua Jardim do Tabaco 34, 1149-041 Lisboa, Portugal. E-mail: amorim@ispa.pt

Introduction

Aggression is often observed in animals while competing for limited and unevenly distributed resources like food (Archer 1988). Feeding success may reflect the individual's ability to either compete or to scramble for food items, depending on the patterns of resource distribution in space and time. If food is presented in a way that enables one or few animals in a group to monopolize the resource (contest competition), feeding success should be proportional to the individual's fighting ability (Grant 1993; McCarthy et al. 1999). However, when resources are indefensible, the proportion of food obtained by an individual in a foraging group may reflect its capacity to be faster or more efficient in finding and exploiting food under conditions of scramble competition (Grant 1993; Weir & Grant 2004). Animals may show behavioural plasticity and switch between scramble and contest tactics depending on the opportunity to monopolize the resource (e.g. Goldberg et al. 2001; Grant et al. 2002). Hence, resource defence theory (sensu Brown 1964) predicts that when animals forage in groups, aggressiveness should increase as resources become more defensible, i.e. more clumped in space, less clumped in time and more predictable in both space and time (Grant 1993; Goldberg et al. 2001).

Acoustic signalling is known to play an important role in agonistic contexts in fish (reviewed in Ladich 1997), and may influence the outcome of contests (Valinski & Rigley 1981; Ladich et al. 1992a). Acoustic cues from sounds emitted during confrontations may provide information on the individual's relative fighting ability and may mediate decisions to quit or escalate fights (Clutton-Brock & Albon 1979; Myrberg 1997). For example, the dominant frequency of sounds may give indication of body size in fish and in other animals (Davies & Halliday 1978; Clutton-Brock & Albon 1979; Myrberg et al. 1993). Little is known about agonistic sound production outside territorial defence (Ladich 1997), but sound production has been observed in competitive feeding contests in triglids and other fishes, and may signal feeding arousal and different levels of aggression (Hawkins 1993; Amorim & Hawkins 2000; Amorim et al. 2004).

The characteristics of sounds may change throughout the life span of fishes (Henglmüller & Ladich 1999; Wysocki & Ladich 2001). For example, the dominant frequency of sounds decreases with increasing body size in a number of fish species (e.g. Ladich et al. 1992b; Myrberg et al. 1993; Amorim et al. 2003). The frequency and intensity of agonistic behaviour associated with competitive feeding may also change with fish ontogeny (Ryer & Olla 1991). However, ontogenetic changes of sound production and agonistic behaviour during competitive feeding have never been studied so far. Our aim was to investigate the effect of fish size on sound production and feeding interactions in the grey gurnard, *Eutrigla gurnardus*, and to find out variations in the characteristics of the emitted sounds during ontogeny, from small juveniles [10 cm in total length (TL)] to large adult fish (40 cm in TL).

Methods

The Study Species

The grey gurnard is a marine demersal fish commonly found in coastal waters of the eastern North Atlantic at depths from approx. 20 m down to 140 m (Wheeler 1969), in small (Protasov 1965) to occasionally extremely large shoals (Heesen & Daan 1994). A previous study has shown that the grey gurnard seems to both scramble and contest for food under defensible conditions (Amorim et al. 2004). Whether grey gurnards scramble or contest for food, their production of sounds increases substantially compared with non-feeding situations (Amorim et al. 2004). Competing fish emit knocks predominantly while grasping food and during non-agonist behaviour, and they emit grunts mainly while performing frontal displays to opponents, suggesting that knocks and grunts are associated with different levels of aggression. A third sound type, the growl, is heard typically at the end of grunt sequences but is emitted only rarely (Amorim et al. 2004). In the absence of conspecifics, this species rarely emits sounds during feeding bouts indicating that sound emission is part of the social/agonistic behavioural repertoire of this species (Amorim 1996). Typically, knocks are composed of 12 pulses, grunts of 48 and growls of more than 10 pulses, and also differ in their duration and pulse repetition rate (Fig. 1; Amorim et al. 2004).

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 (UK). We grouped fish into the following size classes: 10–15 cm (small, S), 15–20 cm (medium, M), 25–30 cm (large, L), and 30–40 cm (extra-large, XL) in total length. According to length–age data found in the literature, S, M, L and XL fish were probably $\leq 1, 2,$

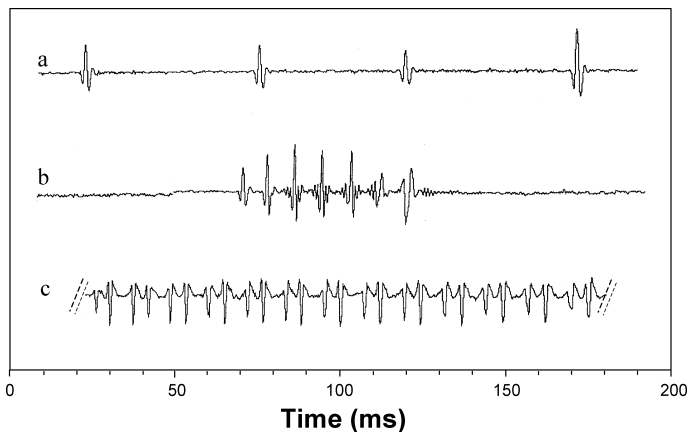


Fig. 1. Oscillograms of a sequence of knocks (a), a grunt (b), and part of a growl (c), emitted by the grey gurnards during competitive feeding

4–5, and > 6 yr old, respectively (Damn 1987). Two sets were used for the ‘sound recording’ and for the ‘feeding interactions’ experiments. The established groups were composed of three to eight individuals of both sexes and were sexually inactive, although L and XL individuals had reached the size of maturity (Papaconstantinou 1983). We maintained small and medium specimens in 1.5- and 3-m-diameter fibreglass tanks, respectively, and larger specimens in a swimming pool of 7.0 m × 3.5 m × 1.5 m (length × breadth × depth). Experimental tanks were provided with a sand substrate and with filtered and sterilized re-circulated seawater, with temperatures ranging from 7°C (winter) to 12°C (summer). The light : dark illumination cycle resembled the natural photoperiod. We fed fish three times a week, with fish or shrimp.

Recording and Analysis of Sounds

Sounds were recorded two to three times a week in 5-min feeding sessions in all groups, with a hydrophone (Plessey, MS83; Plessey Company Ltd, London, UK), a low-noise amplifier (Brookdeal, model 450; Brookdeal Electronics Ltd, London, UK) and a DAT recorder (Casio, model DA1; Casio Electronics Co. Ltd, London, UK), as described in Amorim et al. (2004). We dropped food every minute through a feeding tube throughout the recording session. The amount of food was scarce and the presentation of food (clumped in space and predictable in time) was in such a way as to promote competitive feeding (Grant 1993; Weir & Grant 2004). A total of 11, 20, 10, 11 sound recording sessions were obtained for S, M, L and XL sized fish respectively. These recordings were obtained during different periods of the year according to the availability of fish: Jun.–Jul. (water temperature: 11.8°C) for S, May–Dec. (9.4–12.4°C) for M, Mar.–Apr. (11.3–11.6°C) for L, and Oct.–Nov. (10–11.6°C) for XL fish. Recordings for medium fish covered water temperatures and seasons of the year similar to the other fish size classes, to allow fish size comparisons. Fish group sizes used for sound recordings varied: four to five, three to four, three to four and eight individuals for S, M, L and XL fish respectively.

We measured sound production rate (number of sounds emitted per minute) from each recording session. We analysed knocks and grunts (described in Amorim et al. 2004) with the Loughborough Sound Images software (version 2.0; 1986 Metagraphics Software Corporation[®]) for: 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 a maximum of 10 pulses, ms; number of pulses: total number of pulses within a sound; pulse period: mean time elapsed between the peak amplitude of two consecutive pulses within a sound, ms; and peak frequency: the frequency component with the highest energy in the entire sound, measured for each pulse of sound, Hz.

Feeding Interactions

We studied feeding interactions in S, M, XL size classes using synchronized image and sound recordings obtained with a Sony video 8 camcorder (CCD-

FX500E Pal 8; Sony Video 8, Sony, London, UK) as described by Amorim et al. (2004). Recordings of approx. 15 min were obtained for each fish group three times a week. Video recordings for each size class were performed at different times of the year because of fish availability but feeding activity and behaviour did not show any noticeable seasonal variation (M. C. P. Amorim & A. D. Hawkins unpubl. data). Six video sessions were obtained for small and medium fish and nine sessions for extra-large fish. We fed fish with few items of food (fewer than the number of fish) every minute throughout the filming session (from minute 0 to minute 14) to promote competitive feeding, as explained above. Fish group sizes used for this part of the study were six, four and eight individuals for S, M, and XL fish respectively.

We considered fish to be interacting with one another when they were in close proximity and altered one another's behaviour. We registered the succession of behavioural acts for each fish participating in each interaction and considered the following behavioural categories: dash, circle, grasp, orient, approach + chase, frontal display and flee, as described by Amorim et al. (2004). We measured interaction duration (s) in 50 interactions taken at random from the three size classes considered. We also took the following measurements for size class comparisons: number of behavioural acts per interaction (per fish): measured for each sequence of behaviours observed for each fish in an interaction; frequency of a behaviour act in interactions (per fish): number of occurrences of a particular behaviour per minute observed for each fish in an interaction; interaction rate: number of interactions per min observed per session; number of fish involved in an interaction: averaged per session; proportion of interactions accompanied by sound production: averaged per session.

Data Analysis

As sound emissions could not always be attributed to individual fish (Amorim et al. 2004) we tested the effect of fish size on the different sound and feeding interactions variables with fish size classes as the grouping variable. Parametric statistics were generally used, but the effect of fish size on sound characteristics was tested with the nonparametric Kruskal–Wallis statistics since none of the commonly used transformations managed to meet the normality and homoscedasticity assumptions of the ANOVA. We used Dunn tests as *a posteriori* tests to examine differences between groups.

For the analysis of sound production rate, we tested the effect of fish length on normalized data for the effect of group size by dividing the number of sounds produced by minute by the number of fish in each group. For the analysis of feeding interactions a different approach was used, given that competitor density (defined as the number of competitors on a patch), and not group size, is considered an important variable during competitive feeding (Goldberg et al. 2001). In this case, we tested the effect of fish size with ANCOVA, where the mean number of fish involved per interaction and session (i.e. the mean number of competitors per session) was used as an explanatory covariate. When the mean number of fish involved per interaction was not significantly correlated

(Spearman correlation) with the dependent variable, we performed one-way ANOVA instead. We used 95% confidence intervals as *a posteriori* tests to examine differences between groups.

Results

Sound Production

Fish emitted sounds frequently during feeding sessions. Fish from S, M, L, and XL groups produced on average 5.8 (4.6/0.8), 4.3 (3.0/1.2), 2.9 (1.8/1.1), 1.1 (0.6/0.5) sounds (knocks/grunts) per fish per minute respectively (Fig. 2). Smaller individuals emitted significantly more sounds per minute than larger ones (group level: one-way ANOVA: $F_{3,48} = 7.74$, $p = 0.0003$; fish level: one-way ANOVA: $F_{3,48} = 10.10$, $p = 0.00003$; Fig. 2). Individual size also had an effect on the characteristics of the emitted sounds. Sound duration, pulse duration and the number of pulses increased with fish size whereas the peak frequency decreased with fish size, for both knocks and grunts (Kruskal–Wallis test: all differences were significant at $p < 0.01$; Fig. 3). Sound duration increased by a magnitude of 7 ms in knocks and in 34 ms (median values) in grunts with increasing body size. Median pulse duration increased from S to XL fish by 1.3 ms for knocks and by 1.7 ms for grunts. Knocks and grunts of XL grey gurnards had one or two pulses more than their smaller counterparts. Knock peak frequency decreased 265 Hz from S to XL fish and grunt peak frequency decreased by 31 Hz (median values).

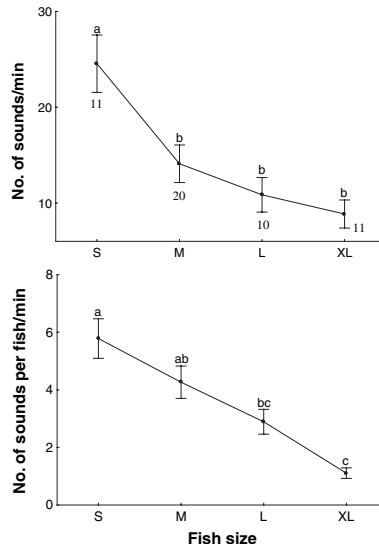


Fig. 2: Sound production rate (mean \pm SE) observed at the group and at the individual level for small (S), medium (M), large (L) and extra-large (XL) size classes of fish during feeding sessions. Numbers are sample sizes and are the same for both graphs. Groups that are significantly different ($\alpha = 0.05$) are indicated by different letters (results from 95% confidence intervals)

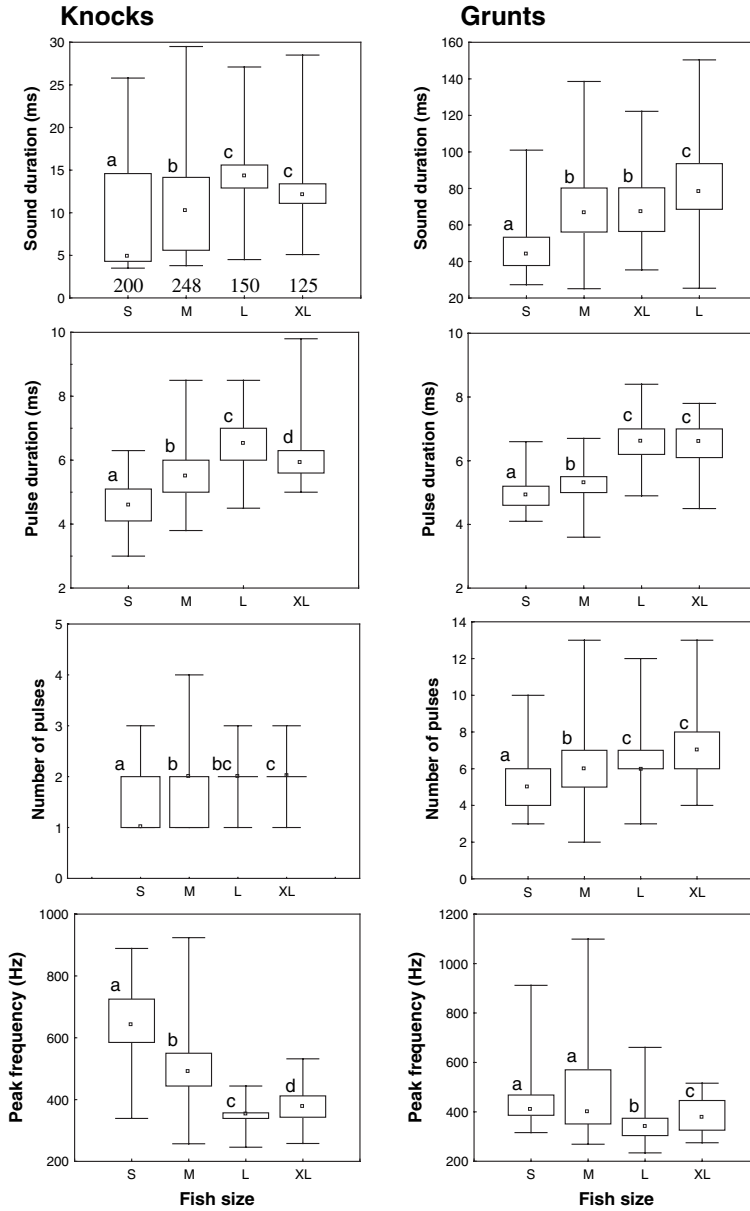


Fig. 3: Comparison of sound and pulse durations, number of pulses and peak frequency of knocks and grunts observed for small (S), medium (M), large (L) and extra-large (XL) size classes of individuals during feeding sessions. Small squares represent the median, the open rectangles show the 25 and 75 quartiles and bars indicate range. Numbers are sample sizes and are the same for all graphs. Groups that are significantly different ($\alpha = 0.05$) are indicated by different letters (results from Dunn tests)

Feeding Interactions

At the sight of food, most fish swam rapidly towards the feeding area and started interacting with one another often producing sounds, as described in Amorim et al. (2004). The mean number of competitors per interaction was significantly higher in M than in S or XL fish (ANOVA: $F_{2,18} = 8.58$, $p = 0.002$; Fig. 4), although biological differences were probably negligible as the mean number of interacting fish varied between 2.3 for S and XL, and 2.7 for M fish.

Feeding interactions had a mean duration of 4.2 s (± 0.28 SE). The number of behavioural categories per interaction increased with the number of fish per interaction (for all size classes together – Spearman correlation: $r_s = 0.23$, $n = 698$, $p < 0.001$; Fig. 5) and differed significantly between size classes (ANCOVA: $F_{2,694} = 10.90$, $p < 0.001$, data transformed by $1/x$), although there was no trend with fish size, i.e., there was no increase or decrease (of no. of behaviours) with increasing fish size. The mean number of behavioural categories observed per interaction (\pm SE) were 2.9 (± 0.07), 3.4 (± 0.10) and 2.7 (± 0.07) for S, M and XL grey gurnards, respectively.

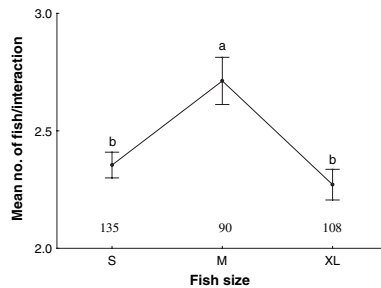


Fig. 4: Number of fish (mean \pm SE) involved per interaction for small (S), medium (M) and extra-large (XL) individuals. Numbers are sample sizes. Groups that are significantly different ($\alpha = 0.05$) are indicated by different letters (results from 95% confidence intervals)

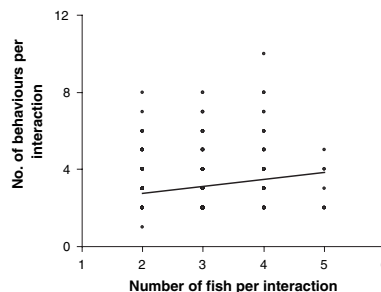


Fig. 5: Relation between the number of fish and the number of behavioural categories observed per interaction

All behaviours except circle, orient and approach + chase (for all size classes together – Spearman correlation: $r_s = 0.07-0.40$, $n = 21$, $p > 0.05$), increased with the mean number of competitors per interaction (for all size classes together – Spearman correlation: $r_s = 0.60-0.81$, $n = 21$, $p < 0.01$). All agonistic behaviours and dash decreased in frequency with fish size, although orient showed only a marginal non-significant difference between size classes (Table 1; Fig. 6).

Interaction rate increased with the mean number of fish involved in interactions per session (for all size classes together Spearman correlation: $r_s = 0.66$, $n = 21$, $p < 0.01$).

Controlling for the number of competitors involved in interactions, interaction rate decreased significantly with fish size (ANCOVA: $F_{2,17} = 7.53$, $p = 0.005$; Fig. 7), from an average of 3.0 interactions per minute for S to 1.7 for XL fish.

Feeding interactions were frequently accompanied by bursts of knocks and grunts [n (recording sessions) = 21; $\bar{x} \pm SE$ for all fish sizes: $87.9 \pm 0.02\%$). The average number of competitors per interaction did not have any effect on the proportion of interactions accompanied by sound, or specifically by knocks or grunts (for all size classes together Spearman's correlation: $r_s = 0.10-0.39$, $n = 21$, $p > 0.08$). Overall, fish size had no significant effect on the proportion of feeding interactions accompanied by sound production (one-way ANOVA: $F_{2,18} = 0.09$, $p = 0.91$; Fig. 8). However, the trends observed for knocks and grunts were opposite and cancelled each other out. The proportion of interactions accompanied by knocks were smaller in S than in larger fish (one-way ANOVA: $F_{2,18} = 4.28$, $p = 0.03$; Fig. 8), but the reverse was observed for the proportion of interactions accompanied by grunts, which decreased with fish size (one-way ANOVA: $F_{2,18} = 6.58$, $p = 0.007$; Fig. 8).

Table 1: Effect of fish size on the frequency of behaviours observed during feeding interactions

Behaviour	Test	df	F-value	p-value
Orient	ANOVA	2, 18	10.90	0.097
Approach + chase	ANOVA	2, 18	7.18	0.005
Frontal display	ANCOVA	2, 17	7.39	0.005
No. of fish		1	8.53	0.010
Flee	ANCOVA	2, 17	11.88	0.0006
No. of fish		1	26.62	0.00008
Dash	ANCOVA	2, 17	6.88	0.006
No. of fish		1	10.17	0.005
Circle	ANOVA	2, 18	0.91	0.42
Grasp	ANCOVA	2, 17	2.09	0.15
No. of fish		1	18.34	0.0005

When the mean number of fish involved per interaction had a significant effect on the dependent variable it was used as an explanatory covariate.

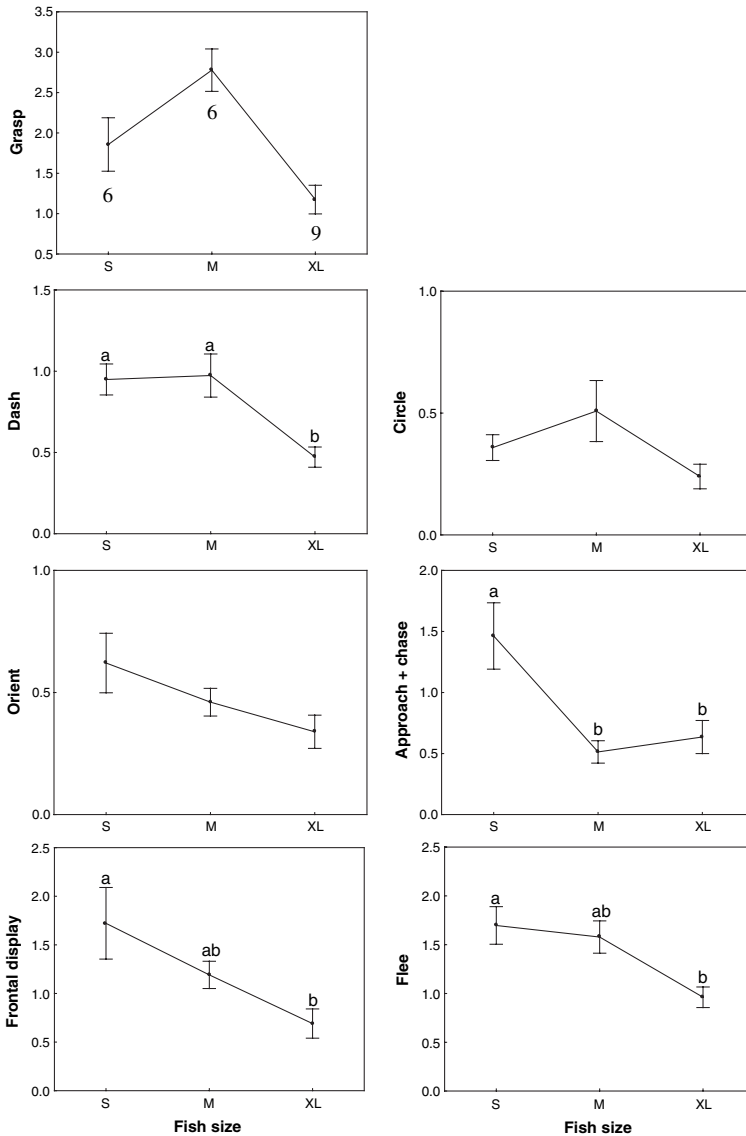


Fig. 6: Frequencies (mean \pm SE) for the behavioural acts observed for small (S), medium (M) and extra-large (XL) size classes of grey gurnards during feeding interactions. Numbers are sample sizes and are the same for all graphs. Groups that are significantly different ($\alpha = 0.05$) are indicated by different letters (results from 95% confidence intervals)

Discussion

In this study, we have shown that both sound production and associated feeding interactions changed with fish size in the grey gurnard. Smaller fish were

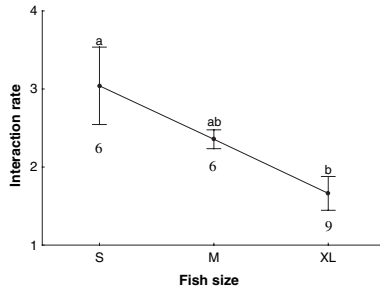


Fig. 7: Interaction rate (mean \pm SE) observed for small (S), medium (M) and extra-large (XL) grey gurnards during feeding interactions. Numbers are sample sizes and are the same for all graphs. Groups that are significantly different ($\alpha = 0.05$) are indicated by different letters (results from 95% confidence intervals)

more active sound producers than larger ones as they produced more sounds per minute during feeding sessions. The acoustic features of knocks and grunts, the most commonly emitted sounds, also changed with fish size. Sound duration, pulse duration and the number of pulses increased with fish size whereas the peak frequency decreased with fish size, for both knocks and grunts. The change in the predominant frequency of the sounds during ontogeny was almost certainly the result of the increase in body size.

Sounds from different size classes of grey gurnards were recorded at different time of the year because of their availability and therefore at different temperatures. Water temperature is known to influence different parameters of sounds such as sound duration and pulse period (e.g. Connaughton et al. 2000) and may have influenced our results. We suggest, however, that the detected differences between fish groups were because of fish size. S fish were recorded at very similar temperatures to L gurnards. Moreover, temperatures for M gurnards covered the range of all groups, thus covering all variability caused by any temperature effect. Thus, any variability in sound features caused by temperature would have decreased the probability of finding a size effect rather than creating a spurious size effect.

Interaction rate decreased significantly with fish size during competitive feeding sessions. Moreover, agonistic behaviour including frontal displays decreased in frequency with fish size. These results suggest that smaller fish interact more often and are more aggressive during competitive feeding than larger ones. We do not believe that differences in group size among size classes influenced these results as variability in the mean number of interacting fish was small among size classes and was accounted for as a covariate in ANCOVA. Differences in fish density were also unlikely to have affected fish interactions because tank space was plentiful and, when feeding occurred, fish concentrated around the feeding area where social interactions took place.

There were no differences between the proportion of feeding interactions accompanied by sound production between fish size classes. However, the percentage of interactions accompanied by knocks and by grunts increased and

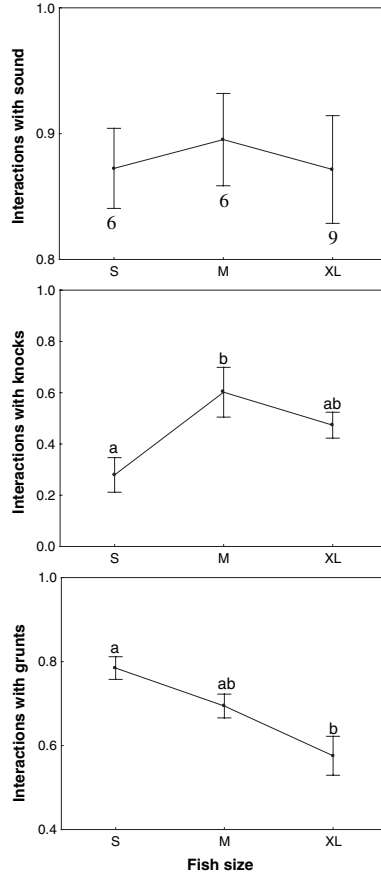


Fig. 8: Proportion of feeding interactions (mean \pm SE) accompanied with sounds (a), and specifically with knocks (b) and grunts (c) for small (S), medium (M) and extra-large (XL) grey gurnards. Numbers are sample sizes and are the same for all graphs. Groups that are significantly different ($\alpha = 0.05$) are indicated by different letters (results from 95% confidence intervals)

decreased with fish size respectively. Smaller fish performed more agonistic acts including frontal displays, which are associated with the emission of grunts (Amorim et al. 2004). Conversely, the emission of knocks is associated with grasping food and nonagonistic acts (Amorim et al. 2004) and was frequent in larger, less aggressive grey gurnards.

The fact that smaller fish emitted sounds at a higher rate, interacted more frequently during feeding, performed more agonistic acts, and showed a lower and higher proportion of interactions accompanied by knocks and grunts than larger animals, respectively, suggest that smaller grey gurnards competed for food by contest tactics whereas larger specimens predominantly scrambled for food. According to the resource defence theory (Brown 1964), animals will only defend resources and adopt aggressive tactics when the net benefits of defence are greater

than those of alternative tactics such as scrambling for the resource. As fish with larger bodies are more efficient in locating (e.g. Browman & O'Brien 1992), capturing (e.g. Wanzenböck 1992) and handling prey (e.g. Mittelbach 1981), it is probably more economically advantageous for larger grey gurnards to scramble than to compete aggressively for food than it is for smaller ones, under similar patterns of food availability.

Grey gurnards make sounds by contracting sonic muscles attached to the gas-filled swimbladder. The vocal apparatus increases with fish size but does not show evident macroscopic structural changes (Amorim 1996). The peak frequency of sounds produced by a swimbladder mechanism is expected to decrease with fish size as the resonance frequency of the swimbladder reduces with size (e.g. Myrberg et al. 1993; Amorim et al. 2003). Lower peak frequencies and longer pulse durations may also result from muscle-scaling effects (Wainwright & Barton 1995), as larger fish with larger sound-producing muscles would take longer to complete a muscle twitch, resulting in longer pulse durations and lower peak frequencies (Connaughton et al. 2000, 2002). The ability of larger fish to make longer sounds with a higher number of pulses (i.e. higher number of contractions of the sonic muscle), could reflect the fact that they had reached the size of sexual maturity (Papaconstantinou 1983) and thus may have suffered physiological changes associated with the increase of sonic muscle fatigue resistance for the production of courtship sounds (Fine et al. 1990; Brantley et al. 1993; Connaughton & Taylor 1995; Modesto & Canário 2003). Fish courtship sounds are typically longer and with a faster pulse repetition rate than agonistic sounds (Gray & Winn 1961; Hawkins 1993; Brantley & Bass 1994). Another species of fish that has been studied for ontogenetic changes in sound production (the croaking gourami, *Trichopsis vittata*) also showed an increase of the temporal characteristics (total duration, number of pulses, pulse interval) and a decrease of dominant frequencies of the agonistic croaking sounds (Henglmüller & Ladich 1999; Wysocki & Ladich 2001).

This study shows that sound production in fish in agonistic contexts is not limited to territorial defence and that sound-producing behaviour shows plasticity with fish ontogeny and with the feeding strategy adopted. In the grey gurnard, the rate of sound production, the sound type emitted, and the temporal and frequency characteristics of knocks and grunts are potentially able to give information on the level of individual motivation and ability to contest food resources.

Our study also adds to the literature on sound production in juvenile fish. Data on acoustic behaviour of juvenile poikilothermic vertebrates is scarce and has been only mentioned for juvenile fish in four species other than the grey gurnard (reviewed in Henglmüller & Ladich 1999 and Wysocki & Ladich 2001). The ontogeny of sound production from hatching to maturation has only been investigated in the croaking gourami (Henglmüller & Ladich 1999; Wysocki & Ladich 2001) and in the cichlid fish, *Tramitichromis intermedius* (Ripley & Lobel 2004), although 40 families of fish are known to vocalize during agonistic interactions (Ladich 1997) suggesting that many fishes are likely to emit sounds when immature.

Acknowledgements

This research was financially supported by a grant (BD/2346/92-IG, Programa Ciência) and by the pluriannual programme (UI&D 331/94) of FCT, Portugal. We thank D. Urquhart and M. Burns for their technical support, V. Almada for valuable suggestions for the behavioural analysis, Y. Stratoudakis for comments on this manuscript. We are also thankful to M. Fine and another anonymous referee for their comments.

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Received: April 14, 2004

Initial acceptance: June 8, 2004

Final acceptance: October 22, 2004 (L. Sundström)