

BRIEF COMMUNICATION**Effects of seawater temperature on sound characteristics
in *Ophidion rochei* (Ophidiidae)**

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Although the sound production mechanisms of male and female *Ophidion rochei* (Ophidiidae) differ significantly, temperature affects them in the same manner. In both sexes, temperature correlated negatively with pulse period and positively with sound frequencies but had no, or weak effects on other sound characteristics.

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The suborder Ophidioidei (Ophidiidae and Carapidae) contains more than 200 species (Nielsen *et al.*, 1999). All species investigated in this taxon show distinctive and complex sonic apparatuses based on extrinsic sonic muscles that insert directly or indirectly on the swimbladder wall (Rose, 1961; Courtenay & McKittrick, 1970; Courtenay, 1971; Parmentier *et al.*, 2003; Fine *et al.*, 2007). Unfortunately, studies describing sound characteristics in Ophidioidei are limited to two ophidiids (Mann *et al.*, 1997; Kéver *et al.*, 2012) and five carapids (Parmentier *et al.*, 2003, 2006) mainly because the majority of species are quite inaccessible. The way environmental factors affect these sounds is even less documented and is limited to three studies. The first suggested that seawater temperature affects sounds recorded in the field attributed to *Ophidion marginatum* Dekay 1842 (Sprague & Luczkovich, 2001), the second showed that the sounds of carapids are negligibly affected by the tegument of their sea cucumber hosts (Parmentier *et al.*, 2006) and the third reported sound amplification by the host (pearl oyster) cavity in the carapid *Onuxodon fowleri* (Smith 1955) (Kéver *et al.*, 2014a).

Because fishes are poikilotherms, the activity of the neuromotor system depends on temperature (Walker, 1975). Generally, higher water temperatures increase the contraction rate of sound production muscles (Demski *et al.*, 1973; Feher *et al.*, 1998). Effects of this relationship on sounds were described in a few species (Fine, 1978;

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Connaughton *et al.*, 2000; Sprague & Luczkovich, 2001; Papes & Ladich, 2011). In weakfish *Cynoscion regalis* (Bloch & Schneider 1801), higher temperatures increase pulse rate, call intensity and dominant frequency of sounds (Connaughton *et al.*, 2002). Similar effects were observed for sounds of *Opsanus tau* (L. 1766) (Fine, 1978), *O. marginatum* (Sprague & Luczkovich, 2001) and *Platydoras armatulus* (Valenciennes 1840) (Papes & Ladich, 2011).

During the puberty of *Ophidion rochei* Müller 1845, the sonic apparatus becomes highly modified in males but not in females (Kéver *et al.*, 2012). Adult males but not females have a mineralized structure called the rocker bone at the anterior end of their swimbladder. They also have larger sonic muscles and swimbladder plates (modified epineurals in association with the swimbladder) than females. Modifications of the male sonic apparatus during sexual maturation are related to important modifications in sound characteristics (Kéver *et al.*, 2014b) and the sexual dimorphism in the sound production mechanism of *O. rochei* has been associated with completely distinct sound types (Kéver *et al.*, 2012): long and pulsed sounds in males, and short and more tonal sounds in females (Fig. 1). Male calls show a unique pattern: the pulse period increases through the first several pulses, then it alternates between long and short durations in successive pulses (Parmentier *et al.*, 2010; Kéver *et al.*, 2012). The aim of this study was to describe the effects of seawater temperature on the different *O. rochei* sound characteristics.

In *O. rochei*, the reproductive period lasts from June to September (Jardas, 1996). Sounds were recorded at night in May 2010, July 2010 (Kéver *et al.*, 2012), September 2008 (Parmentier *et al.*, 2010) and September 2011 in Duće-Glava (Croatia) at 2 m depth. The water temperatures were 13.5, 21.5, 23.5 and 25° C, respectively. A few additional male calls were recorded from 9 to 10 August 2010 in Banyuls-sur-mer (France) at 27 m depth with the temperature 17.5° C. Recordings were made with a digital spectrogram long-term acoustic recorder (DSG, Loggerhead Instruments; www.loggerhead.com). This hydrophone (−186 dB *re* 1 V μPa^{-1}) was programmed to record 10 min per half hour during night-time at a sample rate of 20 000 Hz.

Sounds were analysed in Avisoft SAS-Lab Pro 4.5 using the semi-automatic method described and used in previous studies (Kéver *et al.*, 2012, 2014b). Sounds were recorded from both sexes but it was not possible to identify the sound producer because the fish were active in the dark (Matallanas & Riba, 1980). For female sounds, pulse number, pulse duration (duration from beginning to the end of a pulse, ms), pulse period (duration from the beginning of a pulse to the beginning of the next one, ms), fundamental frequency (Hz) and the first two harmonics were measured. The following variables were collected from male sounds: pulse number, pulse duration, alternation start (the pulse number when the pulse period alternation pattern was initiated), short pulse period (short pulse periods after the alternation start, ms), long pulse period (long pulse periods after the alternation start, ms) and the two peak frequencies (Hz). Because sounds contained many pulses, variables such as pulse duration and pulse periods (short and long pulse periods in males) were measured whenever possible. Then, data were averaged in order to obtain one value per sound.

Linear regressions were chosen to describe the effects of temperature on sound characteristics because they provided a better fit to observations than non-linear regressions. Regression lines were produced with Graphpad Prism 5 (Graphpad Software, Inc.; www.graphpad.com). The data of all variables were \log_{10} transformed and the normal distribution of data and regression residuals was verified.

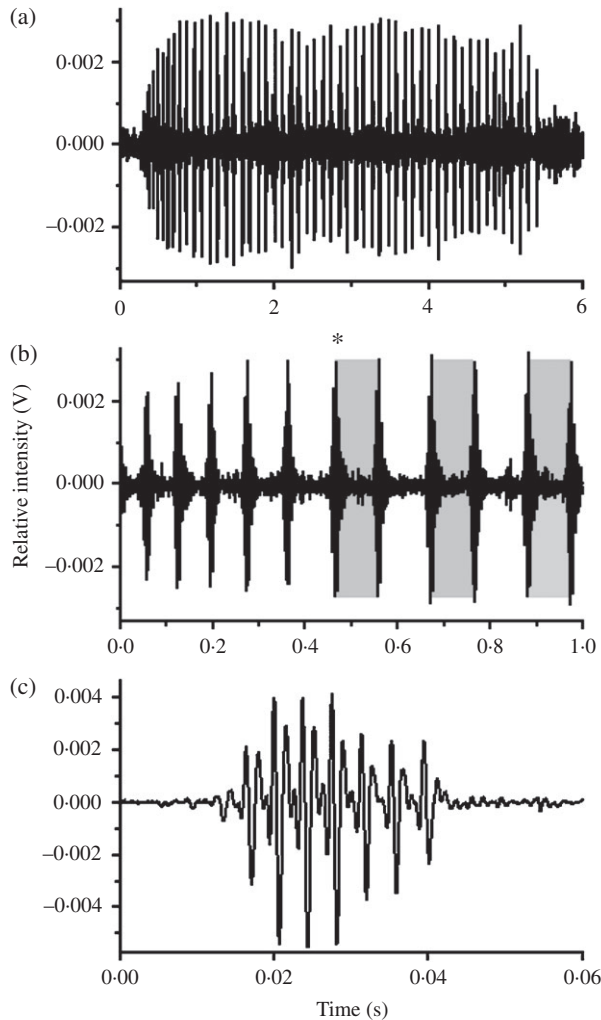


FIG. 1. Waveforms of two *Ophidion rochei* calls recorded in July 2010 in Duće-Glava (Croatia). (a) Waveform of a multiple-pulsed sound of a male *O. rochei*. (b) Zoom in (pulses 6–16) on the waveform of the call shown in (a). (c) Waveform of a sound of a female *O. rochei*. *, alternation start; ■, first three short pulse periods of the male call.

In females, the slopes for pulse duration and pulse number against temperature did not differ from zero [Fig. 2(a), (b)]. On the other hand, pulse period and sound frequencies were strongly correlated with temperature ($r^2 > 0.8$): pulse period correlated negatively with temperature, whereas the fundamental frequency and related harmonics were positively correlated with this factor [Fig. 2(c), (d)].

In males, alternation start and pulse number [Fig. 3(a), (b)] were negatively (although weakly) correlated with temperature: the alternation start happened later in the call and pulse number was higher at lower temperatures [Fig. 3(a), (b)]. Short and long pulse periods decreased with seawater temperature ($r^2 \geq 0.83$) [Fig. 3(c), (d)] while the first and second peak frequency increased ($r^2 \geq 0.73$) with temperature [Fig. 3(e), (f)]. Note,

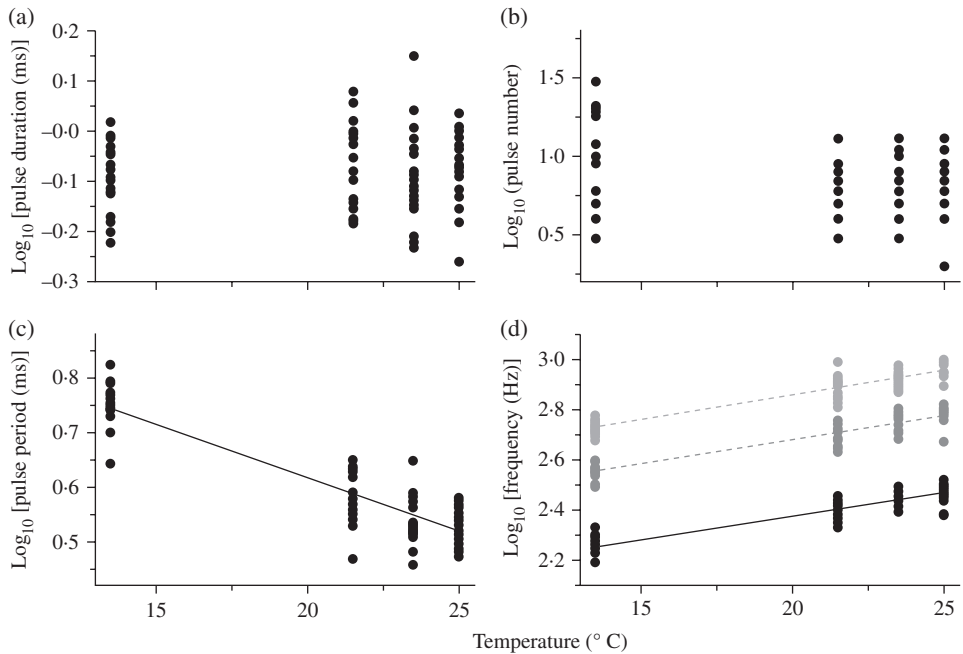


FIG. 2. Influence of temperature on acoustic variables in female *Ophidion rochei*. (a) Pulse duration (number of sounds, $n = 81$, $r^2 < 0.01$, $P > 0.05$), (b) pulse number ($n = 81$, $r^2 = 0.04$, $P > 0.05$), (c) pulse period ($n = 81$, $r^2 = 0.86$, $P < 0.01$) and (d) fundamental frequency ($n = 74$, $r^2 = 0.84$, $P < 0.01$) and first two harmonics (first harmonic: $n = 77$ and second harmonic: $n = 76$) and seawater temperature. Results are expressed as mean value for each sound. The curves were fitted by: (c) $y = -0.020x + 1.008$ and (d) $y = 0.019x + 1.997$ for fundamental frequency, $y = 0.019x + 2.297$ for the first harmonic and $y = 0.020x + 2.467$ for the second harmonic. The three frequencies in (d) are displayed on the same graph but harmonics were represented by ● to facilitate visualization.

however, that the results for second peak frequency should be considered with caution. Although the slope significantly differed from zero, it was the only variable for which residuals of the linear regression did not show a normal distribution (D'agostino & Pearson, $P > 0.05$). In this particular case, the linear regression is not appropriate to describe the variations in the data. It could result not only from obstacles in sample analysis (*e.g.* background noise in the field probably impairs the analysis in some frequency bands) but also from the contribution of factors other than temperature to the variability [*e.g.* second peak frequency is highly affected by fish morphology (Kéver *et al.*, 2014b)]. Despite the difference in the recording depth, second peak frequency of fishes from Banyuls-sur-mer fit relatively well with the regression line based on fish from Duće while the first peak frequency was higher [Fig. 3(e), (f)]. The pulse period was also longer in Banyuls-sur-mer [Fig. 3(c), (d)].

In both sexes, temperature increases were associated with shorter pulse periods and higher frequencies. The significant effect of temperature on sound pulse period and frequency has been shown in other teleosts (Fine, 1978; Connaughton *et al.*, 2000; Papes & Ladich, 2011). In poikilotherms, higher temperatures increase rates of sonic muscle contractions (Rome & Lindstedt, 1998) and neural motor activity (Walker, 1975). Walker (1975) showed also that the results from linear regressions fit better than Q_{10}

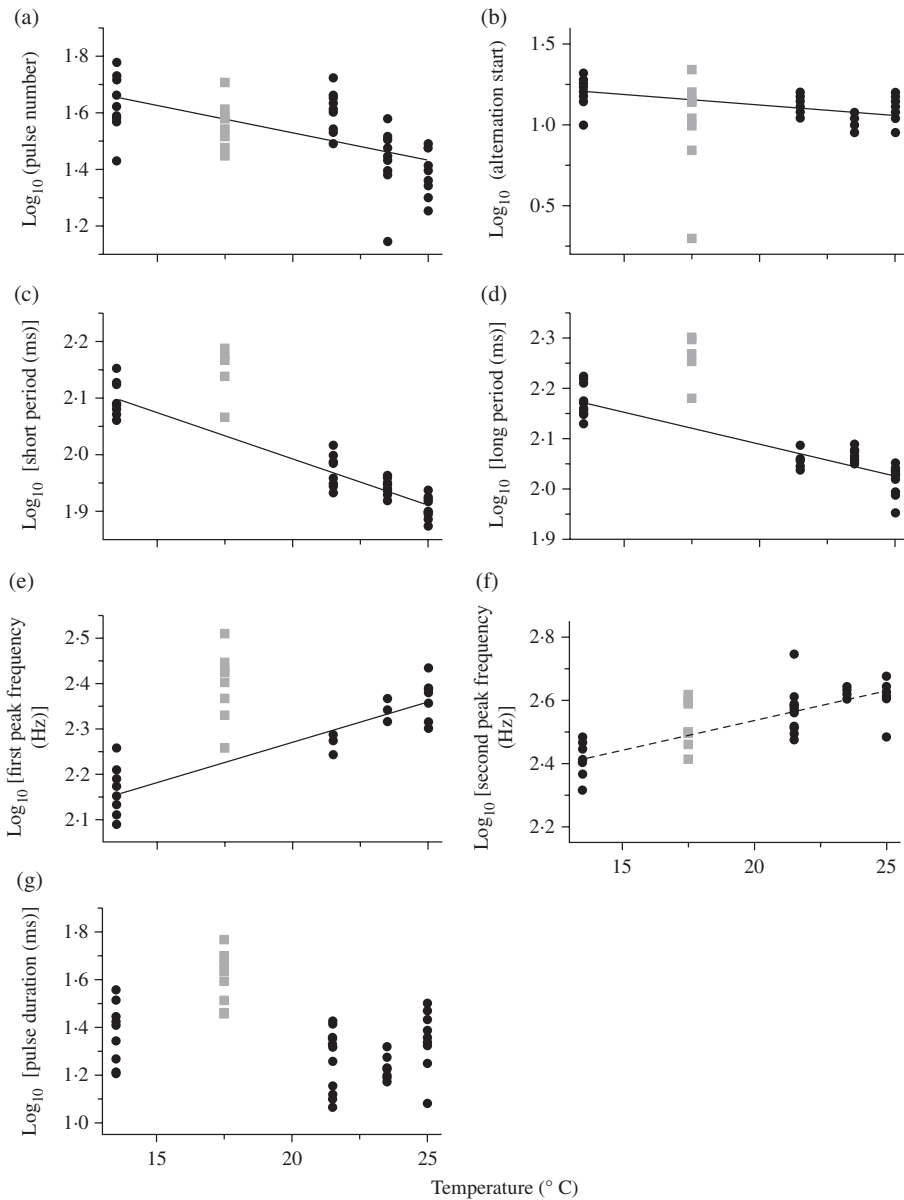


FIG. 3. Influence of temperature on acoustic variables in male *Ophidion rochei*. (a) Pulse number (number of sounds, $n = 44$, $r^2 = 0.38$, $P < 0.01$), (b) number of the alternation start pulse ($n = 44$, $r^2 = 0.38$, $P < 0.01$), (c) short pulse period ($n = 44$, $r^2 = 0.90$, $P < 0.01$), (d) long pulse period ($n = 44$, $r^2 = 0.83$, $P < 0.01$), (e) first peak frequency ($n = 44$, $r^2 = 0.84$, $P < 0.01$), (f) second peak frequency ($n = 40$, $r^2 = 0.73$, $P < 0.01$) and (g) pulse duration ($n = 44$, $r^2 = 0.07$, $P > 0.05$) and seawater temperature. Field data are from Duće-Glava (Croatia; ●) and Banyuls-sur-mer (France; ■). Results are expressed as mean value for each sound. The regression line for the second peak frequency is dashed (---) because the distribution of the residuals was not normal (D'agostino & Pearson, $P > 0.05$). The curves were fitted by: (a) $y = -0.019x + 1.913$, (b) $y = -0.013x + 1.391$, (c) $y = -0.016x + 2.315$, (d) $y = -0.013x + 2.243$, (e) $y = 0.018x + 1.914$ and (f) $y = 0.019x + 2.157$.

values to describe a variety of temperature functions. The present results are in full agreement with these previous observations.

According to anatomical and physiological data (Kéver *et al.*, 2012, 2014c), female sounds are produced by fast successive contractions of sonic muscles as in toadfishes (Fine *et al.*, 2001) or piranhas (Millot *et al.*, 2011). In this case, muscle contraction rate corresponds to pulse period and determines the frequency of swimbladder wall vibration, fixing the fundamental frequency of the sound (Fine *et al.*, 2001; Millot *et al.*, 2011). Higher temperature increases activation rate and muscle contraction speed in female *O. rochei*, shortening pulse period and increasing sound dominant frequency.

In males, pulse period also decreased with increasing temperature, meaning the muscle contraction rate increased. Although peak frequency increased with temperature, sound frequency is independent from contraction rate in male calls for at least two reasons: the fundamental frequency (*c.* 250 Hz) does not match with the pulse period (*c.* 100 ms) and dominant frequency is constant throughout the call despite differences in pulse period within a call (Parmentier *et al.*, 2010). Sonic muscle hypertrophy during the spawning period has been reported in different fish species such as *C. regalis* (Connaughton & Taylor, 1994; Connaughton *et al.*, 1997), haddock *Melanogrammus aeglefinus* (L. 1758) (Templeman & Hodder, 1958) and cod *Gadus morhua* L. 1758 (Rowe & Hutchings, 2004). This kind of modification has not yet been shown in *O. rochei* but it was the case in the related ophidiid *Lepophidium profundorum* (Gill 1863) (Nguyen *et al.*, 2008), which has a slightly different sound-producing mechanism (Fine *et al.*, 2007). Thus, the increase in peak frequency of male sounds is more likely related to contraction speed (*i.e.* duration of a contraction–relaxation cycle) and force (*i.e.* sonic muscle hypertrophy) rather than the contraction rate (*i.e.* pulse period of the call) of the sonic muscle. The increase in peak frequency could also be due to the dilation of the gas: more tension in the swimbladder tissues could result in shorter-amplitude movements (Parmentier *et al.*, 2003).

Finally, male and female sounds recorded at each temperature are impressively variable with many measurements varying over several folds. The variability in the calls recorded may reflect interindividual differences in which case they can potentially be used by the listening fish to differentiate nearby individuals. The variability in some sound characteristics could also be due to differences in caller motivation. Mann & Lobel (1998) argued that changes in motivation likely explain why *Dascyllus albisella* Gill 1862 emits sounds composed of fewer pulses against heterospecifics than conspecifics. Because pulse number was shown to vary among calls emitted by a single male *O. rochei* (Kéver *et al.*, 2014b), it is more likely affected by punctual changes in motivation.

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