

Unusual synchronization of Red Sea fish energy expenditures

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Abstract

The highly gregarious goat fish *Parupeneus forskalii* found in the Red Sea at Eilat, Israel exhibit highly synchronous swimming and feeding activity. Five fish were studied under controlled conditions and highly resolved time-series of their energy expenditures were measured. All fish demonstrated strong phase synchronization in that their activity levels, although erratic in time and intensity, were collectively coordinated and peaked simultaneously together. The synchronization of these wildly varying, and possibly chaotic signals of energy expenditures, were quantified using phase analysis. We suggest that, ecologically, this collective synchronization is a strategy that increases food-catch.

Keywords

Chaos, collective behaviour, energy expenditure, fish, metabolic rate, synchronization.

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Organisms that collectively synchronize their behaviour give rise to some of the most magnificent sights to be seen in the natural world. In the Great Barrier Reef, on a single day each year after the November full-moon, corals synchronize by collectively releasing millions of gametes in an extraordinary large-scale mass-spawning event (Harrison *et al.* 1984). Similarly, certain Asian firefly species are famous for their ability to gather in dense swarms, where they rhythmically flash on and off in perfect unison, in a spectacular synchronized display of courtship (Loyd 1981). Theoretical population biologists and ecologists have now attained a good mathematical understanding of the manner in which populations might synchronize with such precision, through the study of coupled periodic oscillators. Much work, in this area has focused around the synchronization of epidemics (e.g. Keeling & Rohani 2002; He & Stone unpubl. ms.). In recent years, the theory (Pecora & Carroll 1990; Pikovsky *et al.* 2001) has taken on a whole new dimension with the realization that coupled oscillators do not have to be periodic to synchronize – they can also be erratic and chaotic. Such synchronization phenomena are often more subtle and possibly even hidden to the eye. Despite the enormous literature that deals with this form of complex synchronization, there have been few, if any, clear-cut biological or ecological examples. Here we report a particularly transparent example.

We studied the highly gregarious goat fish *Parupeneus forskalii* caught in the Red Sea at Eilat, Israel. These fish live in groups swimming and feeding in unison, as also observed by Ormond & Edwards (1987). Figure 1(a–c) shows a time series of energy expenditure for three of five individual goat fish for 24 h of the 48 h experiment. The fish were caught and kept for 24 h in holding tanks to become acclimatized before beginning the experiment, and then transferred to transparent plexiglass respiration chambers where oxygen consumption (a proxy of energy expenditure) was measured every 10 min (Focken *et al.* 1994) for 48 h. The fish were not fed during the measurements, water temperature was kept constant (24 °C) and daylight was 12 h per day with faint background light at night.

The ‘wild’ variations (Fig. 1a–c) arise because the main activity of the fish, continued digging for invertebrates in bottom sediments, is strenuous and energetically demanding. The fish appear to ‘dig’ around the clock instead of stopping during the night. Upon analysis, the irregular fluctuations in energy expenditure show the key signatures of chaos, in particular, having a positive Lyapunov exponent ($\chi = 0.36$; see Appendix). However, as the time series are of limited lengths ($N = 281$) and the influence of noise must be present, the fluctuations are likely to be a mixture of both deterministic and stochastic dynamics.

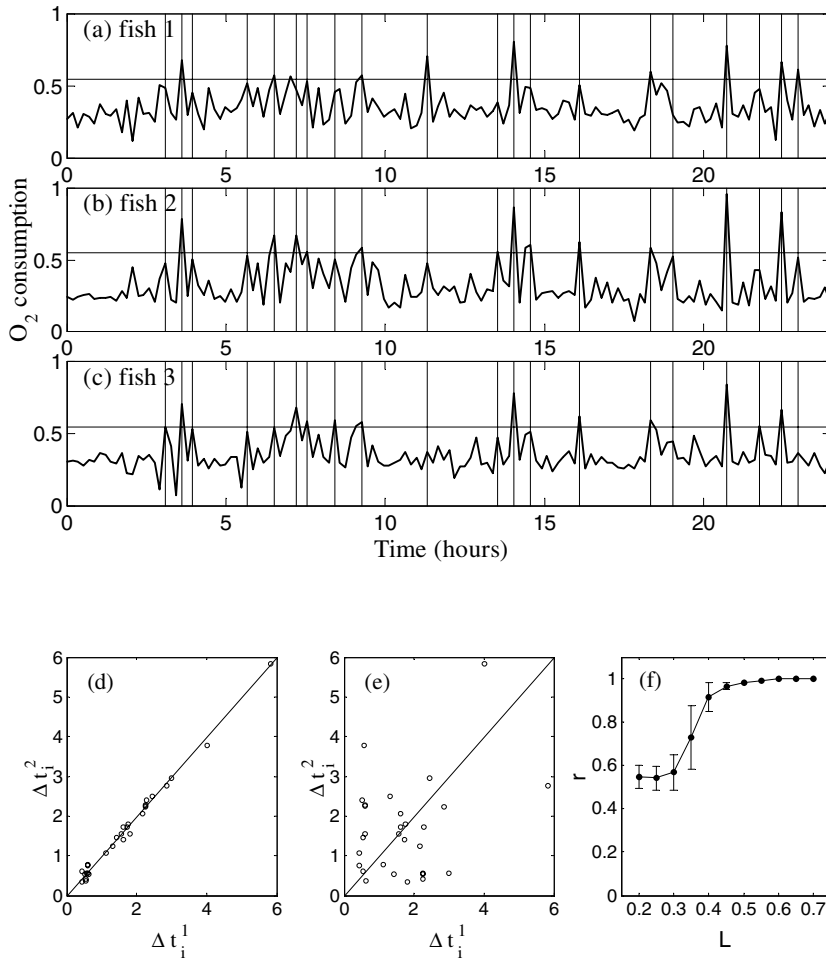


Figure 1 (a-c) Fluctuations in oxygen (O₂) consumption, a proxy of energy expenditure, for three of five individual fish in neighbouring tanks for 24 of the 48-h experiment. Dotted horizontal line indicates preset threshold level ($L = 0.55$) for peak detection. Dotted vertical lines are drawn when at least one of the five fish had a supra-threshold activity peak. (d) A plot of Δt_i^1 vs. Δt_i^2 ($L = 0.55$). The points sit almost on the 45° line reflecting strong phase synchronization. (e) The same as in (d) but after shuffling inter-peak intervals Δt_i^2 thereby removing any ordering correlations. (f) The mean correlation of inter-peak intervals between all 10 pairs of fish, i.e. $\langle r(\Delta t_i^j, \Delta t_i^k) \rangle$, plotted as a function of the threshold level L . The vertical bars represent standard deviations of the 10 sample correlations.

There is an obvious synchronicity in the erratic activity of the five fish, with high correlation between all 10 pairs. For example, the time series of fish 1 & 2 (Figs 1a,b) have correlation $r = 0.75$ ($N = 281$, $P < 0.001$). The synchronous behaviour is a result of visual cues between the neighbouring goat fish, and continues even at night when light levels are low, but disappears in the absence of visual contact. (Similar spontaneous synchronized behaviour was noted for other gregarious species, e.g. *Acanthourus nigrofasciatus*). This is all the more unusual, since it is not periodic activity levels that are synchronized, but wild and possibly chaotic fluctuations; something which is rarely observed in nature. Note that despite numerous observations, it was impossible to deduce whether there was any specific fish that initiated a dive for hunting earlier than the others. In short we found no evidence for a ‘pace-maker’ in the five fish. Individuals did not appear to take their cues from a fixed leader.

In order to study the synchronization, we extracted the peak times at which the energy expenditure reached a local maximum in the time series, and the corresponding peak

amplitudes. A threshold criterion was imposed to suppress the effects of noise, although results turn out to be largely insensitive to the threshold level (Fig. 1f; legend). Let t_i^j be the peak times of fish j , with inter-peak intervals $\Delta t_i^j = t_{i+1}^j - t_i^j$. Figure 1(e) presents a plot of the inter-peak intervals for fish 1 and 2 and reveals a remarkably straight line, with almost perfect correlation $r(\Delta t_i^1, \Delta t_i^2) = 0.997$ ($N = 29$, $P < 0.01$). In fact, for all pairs of fish $r(\Delta t_i^j, \Delta t_i^k) > 0.99$, for the same threshold level. Figure 1(f) is designed to give a guide of the correlation coefficients over all pairs of the five fish.

This strong *phase synchronization* (Blasius *et al.* 1999; Pikovsky *et al.* 2001) proves to be statistically significant (see Fig. 1e and legend). Upon randomization, the data generate a correlation $r(\Delta t_i^1, \Delta t_i^2 + i) = 0.08$. Ten thousand such randomized data sets gave similar results, and could not reproduce the correlations levels in the raw data. Analysis showed that the observed values of statistics of $S = \sum (t_i^1 - t_i^2)^2$ and $S_\Delta = \sum (\Delta t_i^1 - \Delta t_i^2)^2$ were always less than any of the respective shuffled statistics. Hence the observed signs of synchronization are extremely unlikely to occur by chance alone.

Correspondingly, the peak amplitudes of pairs of fish are only weakly correlated, e.g. for fish 1 and 2, $r_A = 0.224$ ($N = 29$, $L = 0.55$, $P < 0.01$). These observations fit in well with the current theoretical ideas on chaotic and stochastic synchronization, whereby phase-locking is the first step in the transition to complete synchronization, and amplitudes only fully synchronize when levels of coupling or feedback between oscillators are sufficiently strong.

Curiously, the fish appear to find advantage in synchronizing their digging behaviour as they search for prey. The diet of these goat fish includes small crustaceans and polychaets, which are patchily distributed and buried in the upper 3–4 cm of the sediment. As the goat fish move across the sediment their dives for food, and thus their activity levels, seem to be erratic due to the patchy distribution of their prey. These prey organisms become aware of fish predators and attempt to escape only when the fish begin to dig in the sediment. This occurs precisely when the chain barbs and mouth of the fish hit the bottom sediment in the process of digging (Fishelson, personal observation). Here is the payoff of synchronization. Compared to a single foraging fish, a synchronized group can (a) monitor and control larger areas of the sediment making it very much harder for any prey to escape; and (b) is potentially more effective in locating patchily distributed prey. Thus by synchronizing, these fish have the ability to increase their food catch. In addition, by sharing the ‘catch’ all members of a ‘pack’ need less energy for exploration, and so all profit. Note that the synchronization is observed in adult goat fish whose size is large enough that they need not be concerned about predation from other fish. (This turns out to be an important factor, since hunting predators could otherwise be potentially advantaged by the ease of locating and preying on groups of synchronized goat fish.) Interestingly, goat fish in Eilat smaller than 100 mm (total length) do not show such precise synchronized grouping. Their uncorrelated activity should be viewed more as anti-predator behaviour.

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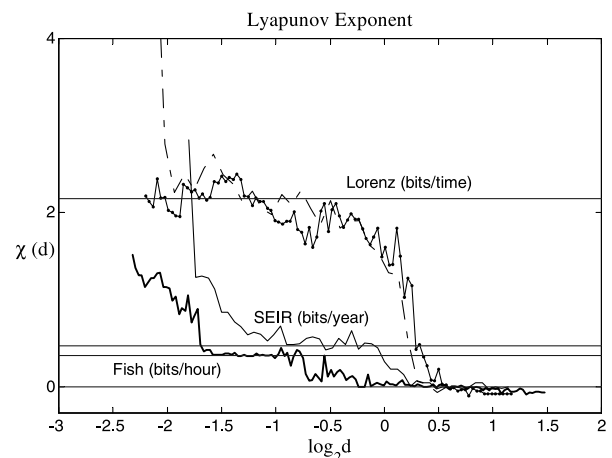
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APPENDIX

The most direct way to detect deterministic chaos in real systems is to show the existence of the sensitive dependence as measured by the Lyapunov exponents (LE). These quantify the different long-time exponential rates at which nearby orbits diverge or converge. The presence of chaos implies a positive largest LE, χ . Wilson & Rand (1993) proposed a method for detecting low-dimensional chaos in short time series when there is dynamical noise present. They estimate the function $\chi(d)$ at different spatial scales d ,



$\chi(d)$ is approximately constant for intermediate values of d (beyond noise level) where it converges to the largest LE and is seen as a plateau in the above figure.

For purposes of comparison and as a reference we estimated the Lyapunov Exponent for several standard models often seen in the nonlinear dynamics and ecological literature. For the standard Lorenz model with parameters: $\sigma = 16.0$, $\rho = 45.92$, $b = 4.0$ for $N = 300$ and $N = 1000$ data points, the theoretical LE value is 2.17. We also estimated the LE of the SEIR model with measles

parameter values, $m = 0.02$, $a = 35.84$, $g = 1000$, $b_0 = 1800$, $b_1 = 0.28$. The LE value from the literature is 0.46. We adopted the same scheme on the time series of Fish Energy Expenditure; the estimated LE value was 0.36 ($N = 281$; embedding dimension $E = 6$). As the time series is relatively short and noise is non-trivial, we must be cautious in concluding that chaos is present, although the signs (the striking horizontal plateau in the above figure) are encouraging.