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Nonlinear time series analysis of food intake in the dab and the rainbow trout

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Abstract

Evidence suggests that dab and rainbow trout are able to quickly adjust their food intake to an appropriate level when offered novel diets. In addition day-to-day and meal-to-meal food intake varies greatly and meal timing is plastic. Why this is the case is not clear: Food intake in fish is influenced by many factors, however the hierarchy and mechanisms by which these interact is not yet fully understood. A model of food intake may be helpful to understand these phenomena; to determine model type it is necessary to understand the qualitative nature of food intake. Food intake can be regarded as an autoregressive (AR) time series, as the amount of food eaten at time t will be influenced by previous meals, and this allows food intake to be considered using time series analyses.

Here, time series data were analysed using nonlinear techniques to obtain qualitative information from which evidence for the hierarchy of mechanisms controlling food intake may be drawn. Time series were obtained for a group of dab and individuals and a group of rainbow trout for analysis. Surrogate data sets were generated to test several null hypotheses describing linear processes and all proved significantly different to the real data, suggesting nonlinear dynamics. Examination of topography and recurrence diagrams suggested that all series were deterministic and non-stationary. The point correlation dimension (PD2i) suggested low-dimensional dynamics. Our findings suggest therefore that any model of appetite should create output that is deterministic, non-stationary, low-dimensional and having nonlinear dynamics.

Keywords: Dab; *Limanda limanda* (L.); Rainbow trout; *Oncorhyncus mykiss* (walbaum); Nonlinear dynamics; Food intake; Nonlinear time series analysis

1. Introduction

In nature, fish face constantly changing food availability, with different prey species having different nutritional values. It is also necessary to adapt to intra-specific nutritional variation, which occurs for a number of reasons. For example seasonal variation, suitability of habitat and availability of their own food. Fish adapt to these changes whilst their systemic need is also continuously changing due to growth, breeding cycle as well as seasonal and environmental influences.

There is a good deal of experimental evidence for the ability of fish to adapt to diets of differing qualities (de la Higuera, 2000). *Limanda limanda* (dab) have long been known to adjust food intake to changes in carbohydrate and lipid (Fletcher, 1982), but not dietary dilution (Gwyther and Grove, 1981). *Oncorhyncus mykiss* (rainbow trout) can also respond to dietary changes (Lee and Putnam, 1973; Bromley and Adkins, 1984; Ruohonen and Grove, 1996; Ruohonen et al., 1997), including compensating for dietary dilutions using up to 67% water, a level comparable to the water content of many natural prey species (Bromley and Smart, 1981).

Day-to-day and meal-to-meal food intake generally exhibits large variation. This has been recorded in almost all studies where fish were allowed to feed to satiation in discrete meals offered at regular time intervals, or are allowed to feed with a demand feeder (e.g. Ruohonen, 1999; Bailey and Alanärä, 2006). The only possible

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exception we have observed are Rainbow trout in Finland eating a linearly increasing amount when they started to feed after the ice melted in the Spring (Ruohonen, unpublished). This could be linear because they are exhibiting strong post-Winter compensatory growth and are therefore feeding to stomach fullness with every meal, and the non-stationarity could be a gastro-intestinal response (Ruohonen and Grove, 1996). Variation is particularly large in flatfish (Pandian, 1970), and is also seen in mammals (Musial et al., 2006) and humans (Weigle et al., 2005).

As well as adaptability and variability, a number of fish species exhibit plasticity of feeding times. *L. limanda* has been observed to be a crepuscular feeder in the Summer months and to take a single midday meal during the Winter (Gwyther and Grove, 1981). Summer feeding time varies with fish size and substrate, and can be nocturnal, diurnal or crepuscular (Carter et al., 1991). *O. mykiss* has also been observed to feed at different times between studies, for example diurnally (Landless, 1976; Boujard and Leatherland, 1992) and nocturnally (Grove et al., 1978). Meal time also varies between individuals when feeding in a group (Alanärä and Brännäs, 1997; Brännäs and Alanärä, 1997). Once a feeding time is established it has been observed to persist (Tabata, 1998). Spontaneous variation in meal timing is observed in a number of other species, for example *Dicentrachus labrax* (Sánchez-Vásquez et al., 1994, 1995a, b, 1997; Madrid et al., 1997; Azzaydi et al., 1998) and *Salmo salar* (Fraser et al., 1993, 1995).

Any model of fish feeding must therefore be able to adapt to a variable and unpredictable diet, result in a day-to-day variation and be able to demonstrate plasticity in meal timing under certain circumstances, as well as having similar statistical properties to real data. Clearly before setting out to create such a model one needs to know as much as possible about the regulatory mechanisms causing these phenomena, and how they interact.

Various reviews have been written concerning endogenous factors controlling appetite, including neuropeptides, hormones and the role of the brain (Le Bail and Boeuf, 1997; de Pedro and Björnsson, 2000; Lin et al., 2000; Volkoff et al., 2005). The endogenous regulation of food intake and satiety in fish clearly involves many factors; how these interact and whether they result in a multi-dimensional control of appetite or are 'parts' of a larger 'machine' resulting in control by one or a few drivers is not yet definitively known.

Exogenous influences, for example environmental variables, position in hierarchy and food availability, provide a further range of potential factors influencing food intake. It has been inferred that endogenous factors such as 'emotions, social factors, time of day, convenience and cost' are the sole reason for variation in food intake in humans (Schwartz et al., 2000). In this scenario exogenous factors alone could result in a multi-factorial explanation for the observed day-to-day variation, however, given that endogenous appetite regulation involves a number of both positive and negative feedback mechanisms (mixed feedback) acting over a range of time scales or time delays (Day et al., 1998; Langhans, 1999; Carter et al., 2000), it is theoretically possible that this variability could arise entirely due to endogenous regulation of food intake (see Glass and Mackey (1988, p. 72) for an example of a mixed feedback system with time delays).

Exogenous and endogenous factors are not necessarily mutually exclusive, increasing the potential number of factors that cause daily variability in food intake.

A useful way of looking at food intake is to regard it as an autoregressive (AR) time series, as the amount of food eaten at time t will be influenced by previous meals. The study of the day-to-day variation per se, considers food intake as a dynamical process (i.e. food intake is changed by a number of 'inputs'). By identifying the type of dynamics that are driving the time series, insights may be gained into the regulation of food intake. Fish are an ideal subject for such a study as they can be fed the same diet over a long period and, once trained, eat all of the food demanded from self-feeders. They can also be kept under constant environmental conditions, so that the focus is on endogenous inputs. This makes them better candidates for this type of study than other groups of vertebrates.

Time series data may arise from linear or nonlinear processes, they might also be due to noise. Linear equations can result in steady states, exponentially growing or periodically oscillating rhythms (Kantz and Schreiber, 1997). Nonlinear equations can produce irregular data and large classes of nonlinear equations exhibit chaos (Cvitanović, 1989). Many nonlinear equations can produce stable and periodic solutions, as well as irregular dynamics, as the functions are varied (May, 1976). From a modelling point of view if a system is driven by multiple deterministic factors (as food intake would be if it was under multi-factorial control) it will be impossible to mathematically distinguish this from multiple chance fluctuations caused by noise. Time series can be due to more than one system and may switch from one generator to another, they can also be due to more than one of the above, for example a linear system with noise superimposed. This paper analyses time series of fish feeding data using nonlinear time series analyses, developed in the study of nonlinear dynamics, in an attempt to determine the qualitative nature of food intake dynamics.

2. Materials and methods

2.1. Data collection

Time series were generated for groups of *L. limanda* (dab) and for both individuals and groups of *O. mykiss* (rainbow trout) using computer-controlled self-feeders (demand feeders). *L. limanda* will not feed when kept singly in captivity. Two types of demand feeder were used; one for groups (King, 2000, modified from Seyhan et al., 1998) the other for individuals (Lyytikäinen and