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Can synchronous spawning be predicted from environmental parameters? A case study of the lugworm Arenicola marina

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Abstract The annual epidemic spawning period of a Scottish population of Arenicola marina (L.) has been recorded over a period of 13 yr. This population spawns between mid-October and mid-November in a discrete spawning event over a period of 4 to 5 d. Endocrine manipulation experiments showed that spawning is induced in females only if sufficient titres of PMH (prostomial maturation hormone) are present in the prostomia. These levels are attained during the 2 to 3 wk prior to the natural spawning date. The East Sands, St. Andrews population always spawns during periods of spring tides regardless of tidal amplitude or whether they are full- or new-moon tides. Meteorological data, including sea-temperature data were collected for each year, and correlation of the environmental data with spawning time was attempted. Correlation of spawning times with weather patterns showed that mean daily air pressures were significantly higher during the spawning period than from September to November as a whole. Evidence also suggests that a reduction in sea temperature is required prior to spawning. A significant moderate negative correlation was found between May to July air temperatures and spawning date, suggesting that higher May to July temperatures may induce early spawning. Daily rainfall and wind speed were also lower during the spawning period, but not significantly so. These results indicate that air pressure (or changes therein) may act as a final spawning cue, and the advantages of this are discussed in relation to fertilization success. A model of the interplay between environmental parameters and the endocrine mechanisms controlling the induction of spawning is proposed. Higher than average summer temperatures may advance gametogenesis to bring the population into a state of maturity (full-size oocytes, well-developed sperm morulae), and may also advance spawning time. Once the population has completed gametogenesis, a drop in sea temperature is then required to trigger an increase in endocrine titres within the prostomium, without which spawning cannot be induced by prostomial injection. The population spawns on spring tides; however a lack of clement weather coinciding with the spring tide will result in population-wide spawning being aborted, as in 1996. Clemet weather (high pressure, low rainfall and wind speed) in conjunction with spring tides permits spawning to proceed to completion.

Introduction

Synchronous spawning has often been defined as a number of individuals spawning in close proximity both temporally and spatially. This definition is now considered too broad, and has recently been subdivided into “mass” and “epidemic” spawning. Mass spawning indicates multispecific spawning at a given locale (Willis et al. 1985), whilst epidemic spawning describes the spawning of a local population of a single species. Several examples of synchronous (mass and epidemic) spawning among broadcast-spawning marine invertebrates and macroalgae have been reported recently (Babcock et al. 1986; Pearse et al. 1988; Clifton 1997; Hay 1997). Mass spawning is typified by the multispecific spawning of coral reef invertebrates and, in particular, the spawning

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events on the Great Barrier Reef, Australia (Harrison et al. 1984; Babcock et al. 1986; Aliño and Coll 1989; Babcock et al. 1992). Mass spawning is also reported to occur among several temperate echinoderm species (McEuen 1988; Pearse et al. 1988).

Some of the best examples of predictable epidemic spawning of an entire population (or large sections thereof) can be found among the marine polychaetes (Caspers 1984; Zeeck et al. 1988; 1990). In many other marine invertebrate species, epidemic spawning strategies and spawning dates have been inferred from gonad indices or even observations of spawning individuals (Minchin 1992). However, these data (particularly single spawning observations) can rarely be reliably extrapolated to the whole population. The authors’ personal observations in the field (Loch Melfort, west coast of Scotland) of single individuals spawning in a large population of the sea urchin *Echinus esculentus* were no indication of the readiness of the whole population to spawn. One of the most striking exceptions to this is the spawning of the stalked crinoid *Comanthus japonica*. Spawning in this species takes place during October, and can be reliably correlated with the time of the solar day, lunar phase (coinciding with the first or last quarter), and maximum declination of the moon (Dan and Kubota 1960; Holland 1981).

Although synchronous spawning events appear to be common, the ability to predict them requires extensive long-term records of the spawning dates and associated environmental conditions. In the examples listed above, epidemic spawning predictions have only been attempted in the Nereidae, the Pacific palolo worm *Comanthus japonica*, and in spawns of corals and associate species on the Great Barrier Reef (mass spawning).

In a number of nereid species, spawning occurs after metamorphosis and the associated swarming of the epitokes in the water column. In *Nereis succinea*, *N. vires* and *N. fucata*, swarming and subsequent spawning occurs when water temperatures reach or exceed a threshold value (Hauenschild 1960; Goerke 1984). In conjunction with temperature, the spawning of many nereid species is also influenced or controlled by the lunar cycle (see “Discussion-Lunar/tidal cycle”).

The literature that has so far been accumulated on predictable synchronous spawning events suggests that no single environmental parameter is wholly responsible for any of the reported spawns. As an example, Caspers (1984) used long-term personal observational data as well as local knowledge of spawning of the Pacific palolo worm (*Eunice viridis*) to generate a set of rules governing the prediction of spawning. However, these rules only related to lunar periodicity and, although they accurately predicted the spawning date, they could not account for temporal differences in the time of solar day at which spawning occurred in populations of worms in different parts of the island chain.

One reason that the precise environmental cues triggering spawning have been so difficult to define for certain species is that in order to induce spawning they must be translated into action by the organisms’ endogenous control mechanisms which initiate the endocrine changes that finally trigger spawning. In visualising this “transduction” the organism is often seen as a “black box”, receiving external inputs and producing a measurable response (spawning) (Olive 1995). Recent research has focused on the mechanism of transduction through endocrine systems that initiates spawning. For example, many experimental studies have shown that environmental manipulation of photoperiod and temperature affects the endocrine systems controlling the gametogenic processes of an organism (for review see Bentley and Pacey 1992). Nevertheless, in many invertebrate groups the links between environmental cues and endocrine systems controlling spawning have yet to be fully described. One notable example, however, of an environmental cue being transduced by an endocrine system to induce spawning is provided by the jellyfish *Spiricodon saltatrix*. Placing ovaries of this species in the dark stimulates the production of a peptide that induces spawning in other ovaries (Ikegami et al. 1978).

In order to elucidate the precise role of environmental parameters in initiating a spawning event and their transduction through an endocrine system, we used the lugworm *Arenicola marina* (L.) as a model species. Exact spawning dates over 13 yr and the corresponding data on a suite of environmental parameters are available for one particular population (e.g. Pacey 1991; Williams et al. 1997). The endocrine manipulation of spawning is also well known (Howie 1959, 1961a; Watson and Bentley 1997, 1998). This paper attempts to correlate spawning with specific environmental parameters and establish an hierarchical system characterising the influence of these parameters on the epidemic spawning of the lugworm population. Not only will this provide information on the environmental factors controlling spawning in an ecologically and commercially important species, but it may also afford insight into the way in which global warming and climate change could act upon the reproductive cycle of a species.

The gonochoristic, annual iteroparous polychaete *Arenicola marina* (L.) (Annelida: Polychaeta: Arenicolidae), commonly known as the lugworm, is an integral part of the fauna of sandy and muddy beaches and outer estuaries of Northern Europe (Thamdrup 1935; Wells 1945; Jacobsen 1967). Gametogenesis in autumn-spawning *A. marina* takes place over a prolonged period, from early spring through to the time of spawning in late autumn (de Wilde and Berghuis 1979).

Most British populations of *Arenicola marina* have an epidemic “spawning crisis” covering a few days in autumn (Newell 1948; Duncan 1960; Howie 1984). However, populations that are geographically quite close can have very different spawning times. These differences manifest themselves not only as differences in the actual spawning period, but also in the nature of the spawning. For example, at the East and West Sands, St Andrews, Scotland, the populations spawn over a few days during