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Spawning aggregations and mass movements in subtidal *Onchidoris bilamellata* (Mollusca: Opisthobranchia)

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Little is known about spawning aggregations in subtidal populations of the nudibranch Onchidoris bilamellata. *We provide photographic evidence of the spawning aggregations and associated spawning migrations or mass movements whose occurrence was debated.*

Keywords: nudibranch, mass movements, spawning aggregations, reproduction

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The nudibranch mollusc *Onchidoris bilamellata* (L., 1767) is distributed around the British Isles, the Atlantic coast of France, Iceland, Greenland, North America and various locations in the North Pacific (Sea Slug Forum, 2007). It has a primarily intertidal distribution matching that of its major prey species, the barnacle *Semibalanus balanoides* (L., 1767) (Todd, 1979). Spawning occurs between December and April with planktonic settlement, which is induced by *S. balanoides* presence (Todd, 1979), starting in June (Todd, 1981). An additional spawning period is sometimes observed mid-summer which has been attributed to rapidly growing June settlers which underwent precocious maturation, spawning and death within around three months of settling (Todd, 1981). After spawning, individuals die; this species having a sub-annual life history (Todd, 1979).

Onchidoris bilamellata and *O. muricata* (Müller, 1776) are known to aggregate with the onset of reproduction (Pelseneer, 1922). Other evidence of aggregation is anecdotal including several occurrences of *O. bilamellata* in Scotland, Ireland and California and *Stylocheilus striatus* (Quoy & Gaimard, 1832) in the Caribbean (Sea Slug Forum, 2007). Disappearance of nudibranch aggregations after spawning has been attributed to post-spawning death rather than offshore migrations (Costello, 1938; Miller, 1961; Nybakken, 1978; Sea Slug Forum, 2007).

There are suggestions in the literature that nudibranchs undertake migrations. Nearly all reports address intertidal populations where migrations have been inferred from the sudden appearance and disappearance of littoral populations. These have been attributed to spawning migrations and subsequent adult death (Pelseneer, 1922). However, sudden appearances have also been attributed to colonization by new settlers (Miller, 1961), tidal/current/wave aggregation (Costello, 1938), the emergence of individuals from under rocks onto their upper surfaces, possibly to breed (Nybakken, 1978) and shoreward movements in response to climate factors including light (Crozier, 1917). Reviews such as that by Nybakken (1978) have considered the possibility of migrations but conclude no such migrations occur. A review by Todd (1981), however, does not exclude the possibility of reproductive migration.

Observations on subtidal migrations of nudibranchs are limited. Crozier (1917) attributed shoreward movements in response to physical conditions, e.g. light. More recently, anecdotal evidence of mass movements has emerged for *O. bilamellata* both in Ireland and California (Sea Slug Forum, 2007).

We observed subtidal aggregations and mass movements of the nudibranch *O. bilamellata* on a boulder substratum near Millport, Scotland (055°44.79′N 004°55.49′W) using SCUBA divers during July 2006 (−14 m Chart Datum, temperature 12°C). Initially (5 July 2006), we observed *O. bilamellata* aggregated on rocks and boulders. Aggregations were associated with small numbers of egg masses (Figure 1). In addition, large numbers of *O. bilamellata* were observed moving between and within boulders in a uni-directional belt, i.e. all moving in the same direction in belts ~50–100 individuals wide. Also, a small number of individuals were observed moving in single to triple-file lines (similar to Figure 3). Two days later these aggregations had dispersed with some individuals remaining associated with very dense egg masses (Figure 2). The belt movements had also dispersed but individuals were still observed moving in single to triple-file lines (Figure 3) which were heading in a westerly direction towards shallower water. Ten days after the initial observation few individuals were observed. Some were associated with the egg masses while others moved individually on rocky substrata but no mass movements or aggregations were observed. No dead *O. bilamellata* were observed on any of these occasions. No *S. balanoides* were observed on any rocks at these (subtidal) depths.

Our observations provide photographic evidence of mass movements of *O. bilamellata* associated with spawning aggregations in a subtidal population. The timing of these aggregations suggest that they are composed of precocious

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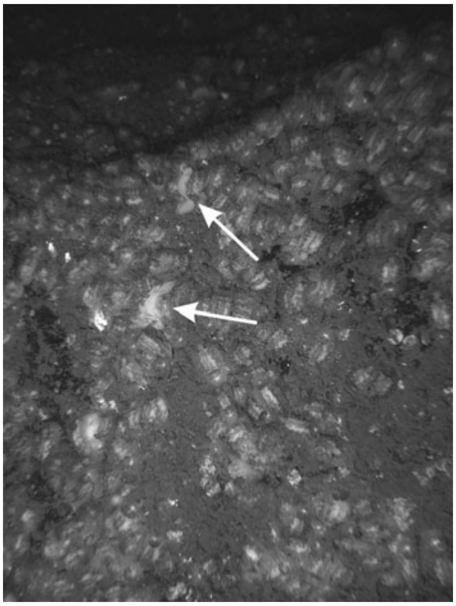

Fig. 1. Aggregated *Onchidoris bilamellata* associated with a few egg masses (indicated by arrows).

juveniles which settled during June of the same year (see Todd, 1981).

We suggest that these mass movements are spawning migrations as: (1) *O. bilamellata* is a specialist feeder on *S. balanoides* (Todd, 1979) which we did not observe to occur subtidally at this locale, so feeding *O. bilamellata* populations are likely to be restricted to intertidal areas (Todd, 1979); (2) aggregations of nudibranchs have often been accounted for by settlement from the plankton directly onto their food supply followed by rapid growth and appearance as aggregations rather than migrating to a site specifically to

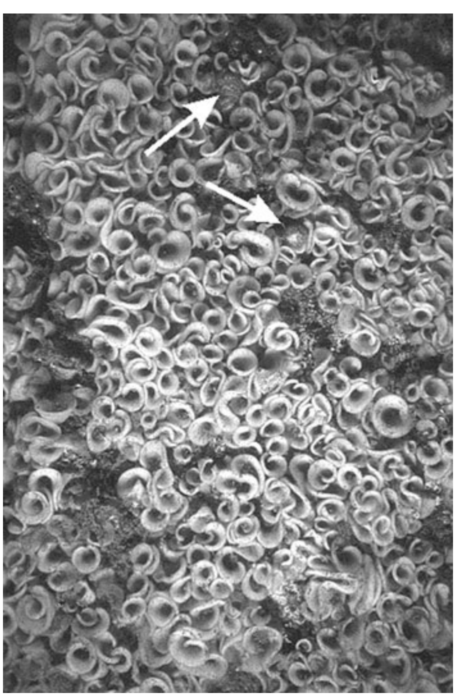

Fig. 2. Dense egg masses of *Onchidoris bilamellata* associated with a few spawning individuals (indicated by arrows).

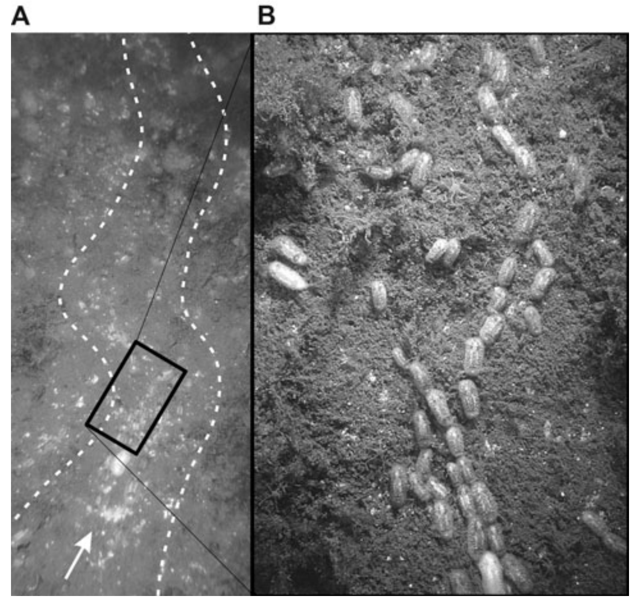

Fig. 3. (A) Mass movements undertaken by *Onchidoris bilamellata* are indicated by the dashed lines within which individuals are visible. The direction of movement is indicated by the arrow; and (B) close-up of black box in (A) indicating *O. bilamellata* moving in single to triple-file.

spawn (Sea Slug Forum, 2007). However, the absence of *S. balanoides* in this locale excludes that settlement theory; and (3) the absence of any dead *O. bilamellata* suggests that these individuals may have migrated back into shallower water following spawning as suggested by the post-spawning westward mass movements. Behaviourally, these mass movements may be explained by mucus 'trail-following' (Todd, 1979) and/or possible responses to magnetic fields as suggested for *Tritonia diomedea* (Bergh, 1894) (Lohmann *et al.*, 1991). However, we acknowledge the possibility that subtidal populations of *O. bilamellata* may occur and they may be dependent on a food source other than *S. balanoides*, thus these movements can be attributable to mass movements within a spawning area.

This photographic evidence reveals large spawning aggregations and possible associated spawning migrations of *O. bilamellata* described by Pelseneer (1922). Pelseneer's (1922) observations were strongly refuted by Thompson (1984) after a visit to the site 61 years later. However, our observations corroborate the spawning migrations described by Pelseneer (1922) for *O. bilamellata*, which clearly occupy a very brief period and may not be as pronounced every year.

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