

Documentation of potential courtship-behaviour in *Periphylla periphylla* (Cnidaria: Scyphozoa)

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The distribution pattern and nocturnal surface behaviour of the deep-sea medusa Periphylla periphylla in a Norwegian fjord was studied. Medusa abundance, size distribution and condition were determined, using surface collections, net tows and ROV-based video profiles. Only larger, mature medusae reached the surface and aggregated into small groups of both sexes, whereas juvenile medusae remained in deeper waters. Observations on the behaviour and cytology of aggregated medusae suggested a mating strategy. We hypothesize that this behaviour is the by-product of a holopelagic life history, developed in a more oceanic deep environment with low species abundance, as surface aggregation increases the chance of encounter and mating.

Keywords: Coronatae, *Periphylla*, courtship-behaviour, surface aggregation, deep-sea

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The coronate scyphomedusa *Periphylla periphylla* (Péron & Lesueur, 1810) is almost cosmopolitan in its distribution in the deep oceans (Haeckel, 1880; Vanhöffen, 1908; Kramp, 1948, 1957, 1968; Russell, 1970; Larson, 1986; Hay *et al.*, 1990; Larson *et al.*, 1991; Dalpadado *et al.*, 1998), but its oceanic abundance is sparse in comparison to some Norwegian Fjords (Larson, 1986; Fosså, 1992; Sørnes *et al.*, 2007). Because of its mass occurrence in Norwegian Fjords it is one of the most studied deep-sea medusae (Snelli, 1984; Fosså, 1992; Jarms *et al.*, 1999; Youngbluth & Båmstedt, 2001). However, its unusual life cycle has only recently been revealed (Jarms *et al.*, 1999) and to date, nothing is known about its reproductive strategy.

Approximately 80–90% of the adult population of *P. periphylla* in Lurefjorden show a diel vertical migratory pattern, avoiding daylight due to the phototoxic effect on its pigment porphyrine (Jarms *et al.*, 2002). *Periphylla periphylla* is found more frequently at the surface than other mesopelagic coronates, mostly in high latitudes of the deep oceans and especially at night (Fewkes, 1882, 1886; Vanhöffen, 1908; Brown, 1910; Kramp, 1913, 1957, 1968; Stiasny, 1934; Thurston, 1977; Lid, 1979; Larson, 1986). This behaviour has also been observed in Norwegian coastal waters and Fjords (Havnø, 1918, 1922, 1926; Kramp, 1947, 1968; Lid, 1979; Fosså, 1992; Flood *et al.*, 1997; Youngbluth & Båmstedt, 2001), although the reason for this has been uncertain. Also unclear at present is how a deep-living medusa

is able to find mating partners in the open oceans due to the wide separation of individuals. It is perhaps because of this fact that *P. periphylla* appears to have a high reproductive potential (Larson, 1986) and why developmental stages of this species may be found throughout the year (Jarms *et al.*, 1999).

The observations of *P. periphylla* reported here were made on board the RV 'Håkon Mosby' between 13 and 15 May 2005 in Lurefjorden (5°10'E 60°41'N; for station details see Sötje *et al.*, 2007), Norway. The observed patchy surface mass occurrences began at dusk (2300 Central European Time summertime), during cloudy and calm weather conditions. The abundance and distribution of animals in the fjord was examined with a remotely operated vehicle (ROV) using red light (Båmstedt & Youngbluth, 2000) while recording their natural behaviour (Youngbluth & Båmstedt, 2001). Behaviour at the surface was observed from the deck.

During daytime observations, *P. periphylla* remained ~ >30 m below the surface. During the first night, 47 specimens were counted at the surface within ten minutes within one patch, 43 of these were drifting with a straight upward tentacle extension (tentacle posture B). The foraging mode of this species (for medusae >5 cm in diameter) alternates between ambush (drifting) and ramming (slowly swimming). While foraging, medusae hold their tentacles straight, extending to the oral–aboral body axis (indicating a non-stressed behavioural state) using tentacle posture A or B. This is in contrast to other tentacle postures (C–H) used during non-foraging behaviours (for details see Sötje *et al.*, 2007).

Individuals kept a distance of ~1 m from each other. During the second night, numerous animals were observed to be in contact (or aggregated) with at least one other

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individual. At times, one specimen was seen to actively move towards another specimen and engage into contact, primarily via entanglement of their tentacles. After this, individuals in contact proceeded towards a closer arrangement of their bells, utilizing their tentacles for leverage. Medusae in physical contact usually had their bells arranged in close proximity, often in the same direction, with one or more tentacles entwined around the tentacles of its neighbour (Figure 1A–E). Occasionally, single tentacles of a specimen were extended to the mouth of another.

Aggregated medusae were hand-caught in groups, measured (CD, coronal furrow diameter), sexed, and the germ cells examined by light microscopy. Statistical comparisons of the size differences were made by Student's *t*-test (Lamprecht, 1999). On the first night, nine single specimens were caught, three males and six females (CD 5.4–9.4 cm, mean 7.7 ± 1.45 cm). On the second night, 13 pairs and three groups (3 specimens each) were collected at the surface. Nine of these pairs and all three groups were composed of both sexes (16 males and 18 females, CD 5.0–11.5 cm, mean 8.1 ± 1.63). These specimens were compared with 40 specimens caught by MIK net (Fraser, 1968) from the entire water column. The difference in mean CD between 8.1 ± 1.63 cm (surface) and 5.8 ± 1.96 cm (whole water column) is significant at the $P = 0.001$ level. Medusae of a medium size between 5 and 10 cm were found throughout the entire water column including the surface, whereas smaller medusae (<5 cm CD) were not observed at the surface and larger medusae (>10 cm CD) were observed exclusively at the surface.

All males were sexually mature and had gonads with mature sperm (fully developed tail, strongly mobile and non-aggregated). Most of the females had gonads with mature eggs (larger than 1.1 mm in diameter, yolk-filled and opaque; Jarms *et al.*, 2002). Free eggs were found in the gastrovascular cavity of two females only. In two other females, only unripe eggs were found. Cleavage stages were not present.

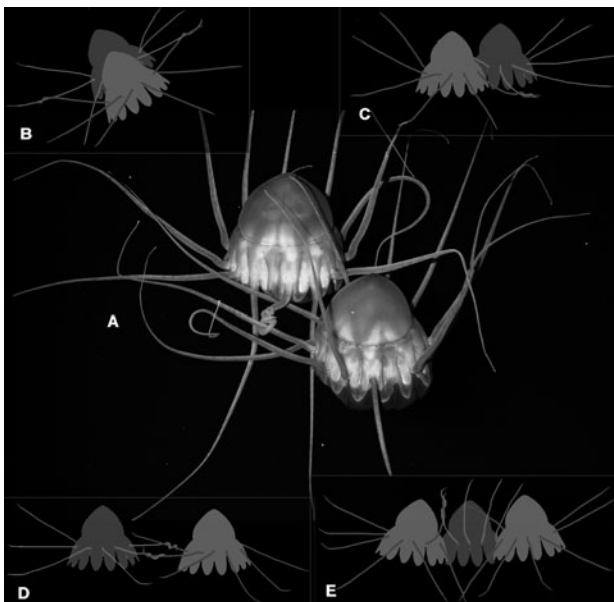


Fig. 1. *Periphylla periphylla*. Courtship-behaviour. (A) Photograph of a pair approaching close contact via tentacle entanglement (photograph P. Flood); (B, C, D, E) different aggregations of pairs, sketches based on live observations.

The abundance of *P. periphylla* medusae at the surface at night was counted in 5 minute transects under a 5 m wide spotlight, while the ship was moving at ≤ 4.9 kn from Station 6 (innermost) to Station 1 (outermost) in Lurefjorden. Medusae were most abundant at the deeper stations and less abundant at the shallower ones (1 and 6, Table 1). These stations were also used in previous studies (Figure 2; Sötje *et al.*, 2007).

Approximately 1% of the entire population (Table 1) reached the surface. All of the animals at the surface were ripe, whereas smaller, unripe medusae (<5 cm CD) were never found there. These results agree with previous observations (Thurston, 1977; Larson, 1986) which note that in the open ocean, the largest-sized specimens of *P. periphylla* (CD >6 cm) occur near the surface. With a year-round reproductive cycle (Jarms *et al.*, 1999), the maturation stage among individual medusae will vary from premature to ripe and spent, thus imposing differential driving forces for surface aggregation on individuals, depending on their reproductive status.

An aggregation of the specimens at the two dimensional surface, in comparison to a three dimensional distribution throughout the water column, will greatly reduce the distance between single individuals, reducing the effort required for direct physical contact between mature individuals and therefore increasing the chances of successful fertilization. This would be especially true in the open ocean. This suggests that the observed surface aggregation may be a behaviour that is inherent in oceanic species. It should be noted that during certain surface events, the patches of medusae appeared to be denser in areas where accumulations of dust and foam were also present, suggesting that surface aggregation could be additionally enforced by the exploitation of physical water movements, as has been reported for several other species (Shanks & Graham, 1987; Kingsford *et al.*, 1991; Larson, 1991; Graham *et al.*, 2001). The differential behaviour of medusae observed on each night could not be correlated to any other measured ecological parameters.

Previous authors note that the cubomedusae *Tripedalia cystophora* and *Carybdea sivickisi* show a similar mating behaviour, in which the animals first make contact with their tentacles after which they swim in direct contact with each other, with the male continuously holding the female, until the spermatozooids are transferred (Werner, 1973; Lewis & Long,

Table 1. *Periphylla periphylla*: size-range (coronal diameter) and abundance of medusae in the whole water column (MIK-net hauls) and surface abundance estimated from ship-based visual counts at night. Sampling was carried out at six sample stations in the Lurefjord between 13 and 15 May 2005.

| Station | Depth [m] | CD [cm] | Abundance [No. medusae/100 m ²] | | |
|---------|-----------|---------|---------------------------------------------|------------|-------------------------|
| | | | At water column | At surface | % population at surface |
| 1 | 143 | 5.0–5.9 | 63.7 | 0.2 | 0.3 |
| 2 | 255 | 2.8–9.4 | 796.2 | 0.5 | 0.1 |
| 3 | 331 | 1.9–9.4 | 732.5 | 7.7 | 1.1 |
| 4 | 441 | 2.1–9.5 | 541.4 | 12.2 | 2.3 |
| 5 | 248 | 2.4–8.6 | 286.6 | 2.8 | 1.0 |
| 6 | 144 | - | 0 | 0 | 0 |

CD, coronal furrow diameter.

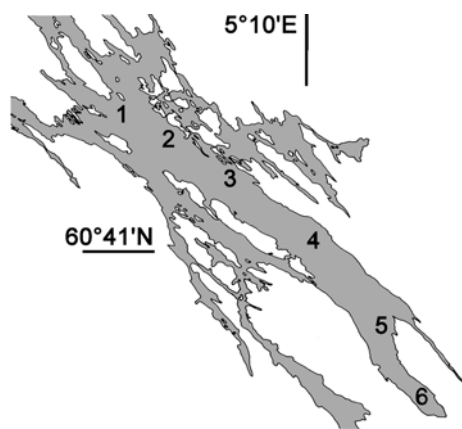


Fig. 2. Map of the sampling sites (Stations 1–6) in Lurefjorden.

2005). A high-density surface aggregation of *Liriope tetraphylla* (hydromedusae) was also assumed to be used for reproduction as most observed animals were ripe and tentacle entanglement also occurred (Ueno & Mitsutani, 1994). Within the coronates, a comparable behaviour has been described in the small medusa *Linuche unguiculata*, which has mass occurrences of ripe specimens for a few days during spawning (Conklin, 1908). The dates of this surface occurrence showed no correlation to the lunar phase, as has been noted in other species (Chung *et al.*, 2001). We attempted to correlate 23 different surface aggregations of *P. periphylla* observed between 1993 and 2005 with a possible lunar-phase connection, but no correlation was found.

In this study, it remains unclear how fertilization specifically takes place in *P. periphylla*, due to the absence of cleavage stages in the sampled females. However, in the absence of any other ecological correlates (i.e. temperature, salinity, season or lunar phase) to the observed surface aggregation of *P. periphylla*, it is difficult to imagine another reason for such large numbers of mature individuals to come into close contact with each other. Therefore, this study provides strong evidence of courtship-behaviour of *P. periphylla*. Further observations of this behaviour, including documented evidence of sperm and egg release and fertilization, will be needed to verify this hypothesis.

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