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Induction of swarming of *Nereis succinea*

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Abstract

Nereis succinea (Frey and Leuckart, 1847), collected in 1987 from the Weser estuary, FRG, was exposed to different temperatures in the laboratory. Metamorphosis to heteronereid stages, as well as swarming at a minimum temperature of 12 °C, was induced by raising temperatures around the time of the new moon. Lunar periodicity was illustrated under natural temperature-programs, and at 16 °C. An abrupt increase in temperature caused swarming to occur at different times of the lunar cycle.

Introduction

In marine invertebrates breeding is induced by different factors such as temperature, endogenous and lunar timing (Olive and Garwood 1983), while swarming is controlled by daytime, tide, weather conditions and sex pheromones. Knowledge of these factors is the basis for understanding reproductive biology and studying details of spawning behaviour, i.e., the role of sex pheromones (Zeeck et al. 1988).

Temperature is assumed to be one of the most important external factors synchronizing maturation and spawning in marine invertebrates (Goerke 1984). Many field observations (Bishop 1974, Wu et al. 1984) but few experimental studies (Hauenschild 1956) have been undertaken on the significance of temperature in determining the time of the onset of gametogenesis and spawning in polychaetes. In this paper, experimental investigations and additional field observations on the effect of temperature and a lunar cycle in moonlight, on the swarming of *Nereis succinea* are illustrated.

Olive and Garwood (1983) pointed out the existence of two basic mechanisms for the control of annual reproductive cycles of marine invertebrates – endogenous rhythms, or direct effects of parameters such as temperature and daylength, which were also described by Franke and Pfannenstiel (1984). Using experimental data Hauenschild (1956) showed lunar periodicity, with a 30 d moonlight cycle, in the swarming behaviour of *Platynereis dumerilii.* He described swarming around new moon while Fage and Legendre (1927) reported a semilunar cycle for a population from Concarneau (France). *Nereis zhonghaensis* swarms at full moon, while other nereids of the Chinese coast, like *N. japonica,* swarm at new moon (Wu et al. 1984). A correlation between temperature and additional factors such as moon and weather conditions was reported by Milheikowsky (1958) for *N. virens* from the White Sea. Kristensen (1984) described temperature control in the spawning of *N. diversicolor,* leading to geographical differences in spawning seasons. At Norsminde Fjord, Denmark, (Kristensen 1984) *N. diversicolor* spawn in February and April; in the Severn Estuary, Britain, in May (Mettam et al. 1982); and at Cherbourg, France, (Herpin 1925) throughout the year. In the Danish Isefjord spawning of eight polychaete species is attributed to specific minimum temperatures (Rasmussen 1956).

Both temperature and lunar timing have been indicated in the induction of metamorphosis and swarming behaviour through field observations of *Nereis succinea.* Lillie and Just (1913) and Bishop (1974) reported on swarming around new moon soon after sunset during June to September, while Rasmussen (1973) often observed swarming at full moon and during daytime. Finally, Kinne (1954) reported a direct temperature influence with a positive correlation between the number of heteronereids actively swarming and the seawater temperature. The minimum temperature at which metamorphosis occurs is assumed to be 16 °C (Goerke 1984).

Material and methods

After the period of reproduction (June/July) 1-yr-old *Nereis succinea* (Frey and Leuckart, 1847) were collected in the Weser estuary near Bremerhaven, FRG, and in the Isefjord, Denmark, during September and October 1987. They were maintained in glass tubes in the laboratory, as described by Goerke (1979). Seawater was obtained from the Biologische Anstalt Helgoland, FRG, filtered (charcoal), pasteurized by heating to 80 °C for 30 min, and diluted by distilled water to a salinity of 14‰. Commercially available fish diet and living specimens of *Corophium volutator* were used as food. The initial temperature in the laboratory was identical to that in the field while collecting the specimens. Artificial illumination (50 lx) was used with a daylength of 16 h. According to Franke (1985) moonlight was simulated by glim lamps (0.25 lx), synchronised with the natural lunar phase every 30 d for 4 consecutive nights. Different temperature programs (see Figs. 1 to 6), with a constant daylength of 16 h, were used in experiments. The exception were the control, which had a constant daylength of 8 h and the first experiment (Fig. 1) which had a varied daylength, similar to natural conditions.

The date of metamorphosis, which could be determined rather sharply within 1 or 2 d (at 20 °C), was fixed after observable changes had been completed. As to reproduction, all specimens performed metamorphosis to heteronereids and swarmed. Here "swarming" means the vigorous swimming activities at the water surface. During swarming, both sexes released gametes under the control of sex pheromones and then died after fertilisation. Additional field observations were made at the Isefjord (Denmark) during June 1986, June and July 1987 and June 1988. At the northern part of the Isefjord a population of *Nereis succinea* was observed and plankton samples (100 μm) collected.

Results

Nereis succinea, collected in the Weser estuary in March, were maintained in the laboratory under simulated natural temperature and moonlight (induction of full moon) conditions. The results of this experiment are given in Fig. 1. All surviving specimens underwent metamorphosis from the atokous to the epitokous form and swarmed ($r = 100\%$). Under these simulated natural conditions, metamorphosis commenced at 20 °C in June and July, the main swarming months in the field, and swarming was only observed around new moon. In a control experiment a constant daylength of 8 h was used (temperature program identical to those in Fig. 1) with similar results, i.e., all 17 specimens tested ($n = 17$) underwent metamorphosis and swarmed ($s = 17$). Eleven specimens swarmed around the first new moon phase once the temperature had increased to 20 °C; and the other six during second new moon period, proving that daylength has no influence on metamorphosis and swarming.

To test the possibility that metamorphosis and swarming could be induced outside the normal swarming period by means of temperature manipulation, specimens were collected during September and October (12° and 14 °C) and maintained in the laboratory under different temperature conditions (five parallel experiments). The first temperature program (Fig. 2) showed that it was possible to induce metamorphosis and swarming behaviour in *Nereis succinea* in the winter. Under a winter-summer temperature cycle most specimens swarmed around the new moon at 20 °C. Once the temperature had increased rapidly (from 8° to 20 °C in 4 wk) a few heteronereids appeared outside the new moon phase.

In the second experiment *Nereis succinea* were maintained under a temperature program without previous simulation of winter conditions (Fig. 3). The results were similar to those of the specimens collected in spring (Fig. 1) proving that previous winter conditions were not essential for the initiation of reproduction.

In the next parallel experiment, specimens (collected at 14.7° and heated to 16 °C) were maintained at a constant

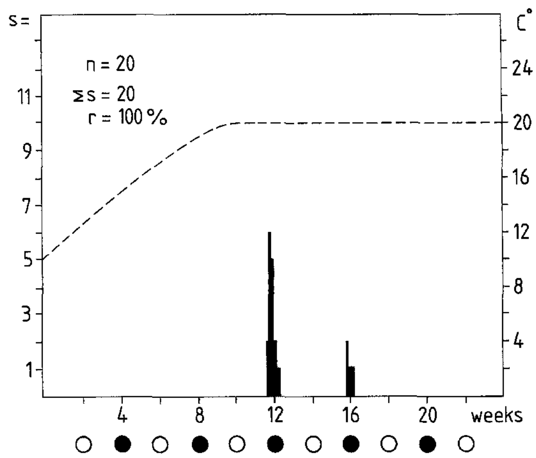

Fig. 1. *Nereis succinea*. Temperature and reproductive behaviour. Natural spring-temperature-program (start = March; swarming = June to July). Natural light-dark cycle: from 12 h light : 12 h dark in March to 15 h light : 9 h dark in August. Bars: number of swarming nereids; – – –: temperature; *n*: number of specimens tested; *s*: number of swarming heteronereids; $\sum s$: total number of swarming heteronereids in experiments; *r*: % of total swarming heteronereids; ●: new moon; ○: full moon

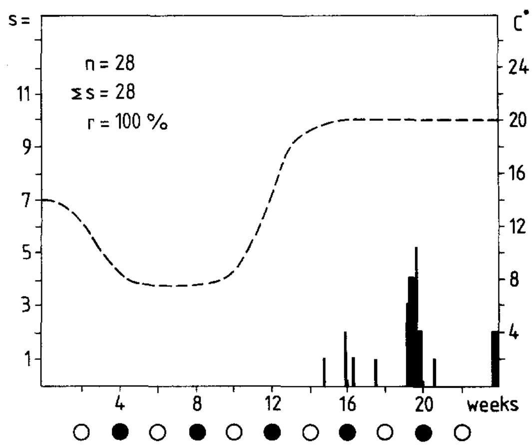

Fig. 2. *Nereis succinea*. Temperature and reproductive behaviour. Induction of reproduction during winter by raising temperatures, (start = September; swarming = February) under a 16 h light : 8 h dark cycle. Symbols as in Fig. 1

temperature of 16 °C (Fig. 4). This is the minimum temperature for swarming and has already been described in the literature (Kinne 1954, Rasmussen 1973). Even under constant conditions (Fig. 4), metamorphosis and swarming could be induced around new moon. In contrast with previous experiments, not all surviving specimens underwent metamorphosis (26 of 56, $r=46\%$).

In two additional control programs specimens were maintained at constant temperatures of 8° and 12 °C. In the first 24 wk, which was the duration of the other experiments (see Figs. 2 to 4), only two metamorphosing nereids could be detected after 4 mo. At a constant temperature of 12 °C, 18% of surviving specimens collected in autumn (October, water temperature 12 °C) and maintained in laboratory for 8 mo (daylength 16 h) metamorphosed and swarmed around new moon, between June and August, while the main swarming months in the field were June or July.

In all experiments, the date at which observable morphological changes were completed was not identical to the start of swarming and reproduction. Fig. 5 shows that ripe heteronereids appeared between 4 and 14 d (average 8 d) before swarming (data from Fig. 3) during the next new moon phase. Swarming outside the new moon phase also occured in three heteronereids. These swarmed in the first weeks after a slow temperature increase.

To compare experimental results with field observations and data from the literature (Kinne 1954, Rasmussen 1973, Bishop 1974), *Nereis succinea* were removed from the Isefjord, Denmark during June 1986. Ripe heteronereids were found 8 d prior to the new moon (water temperature 22 °C, depth 0.8 m) at a time of rising air and water temperatures. The data of swarming was determined by observations on a few heteronereids near the Isefjord Laboratory and by the occurrence of *N. succinea* larvae 5 d prior to the new moon (water temperature increased to 26 °C, depth 0.7 m). In June 1987, ripe heteronereids were removed from the same site, but this time at new moon, no swarming could be observed (water temperature 16 °C, depth 0.6 m). Plankton samples contained a few trochophora larvae during the next days. In the following 3 d, the water temperature rose extremely sharply to 25 °C (depth 0.7 m). However, no ripe heteronereids were found, although many trochophora larvae were seen in plankton samples. Despite the absence of direct swarming observations, the date of mass swarming could be determined as between the 30 June and 2 July, i.e., 4 to 6 d after the new moon. In June 1988, nearly 3000 swarming *N. succinea* were caught in the Isefjord during a 4 d period after the new moon when temperatures rose to 28 °C at 1 m depth (June 18), while at new moon (June 14) at lower water temperatures (17.4 °C) 50 ripe heteronereids were removed from the same site but no swarming specimen was observed.

To test the effect of a sudden rise in temperature on the induction of the swarming behaviour, described above by field observations, *Nereis succinea* was maintained in the laboratory as shown in Fig. 6. According to field observations, swarming occurred at the new moon and also after a period of raised temperatures, mainly outside this lunar phase.

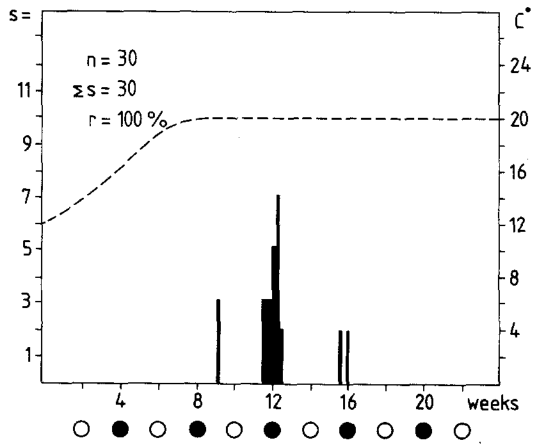

Fig. 3. *Nereis succinea.* Temperature and reproductive behaviour. Induction of swarming without previous winter conditions (start = October; swarming = January) under a 16 h light : 8 h dark cycle. Symbols as in Fig. 1

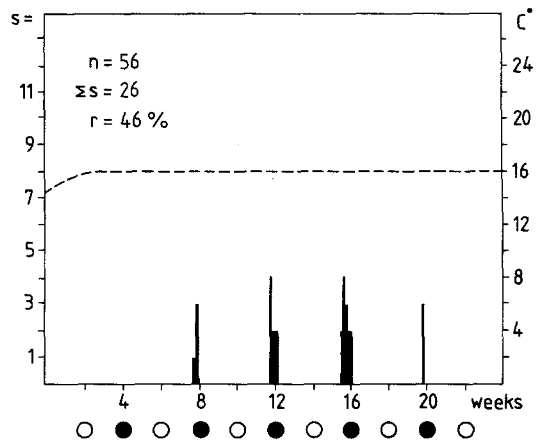

Fig. 4. *Nereis succinea.* Temperature and reproductive behaviour. Reproduction at 16 °C (start = September; swarming = December to March) under a 16 h light : 8 h dark cycle. Symbols as in Fig. 1

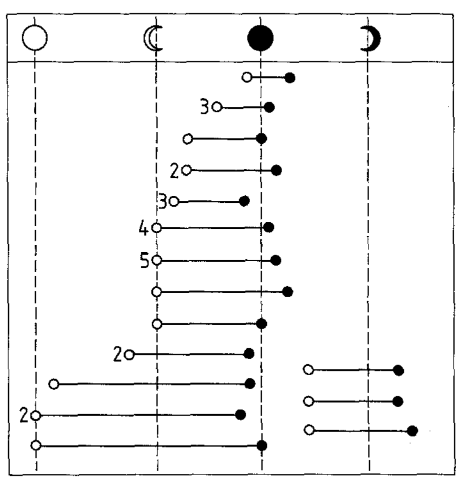

Fig. 5. *Nereis succinea.* Swarming behaviour. Time interval between completion of metamorphosis and beginning of swarming with number of worms represented by 2 o——●; $n=30$; Temperature program: start = October; rising to 20 °C (data from experiment Fig. 3), full moon (o) and new moon (●)

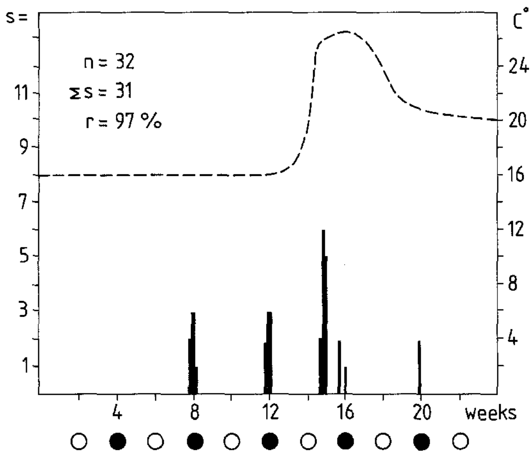

Fig. 6. *Nereis succinea*. Swarming behaviour. Influence of suddenly raised temperatures on lunar timing. Temperature program taken from field observation (start = September; swarming = November to January) under a 16 h light : 8 h dark cycle. Symbols as in Fig. 1

Discussion

Goerke (1984) showed that swarming of different *Nereis* species depends on specific minimum temperatures. The temperature range at which swarming occurs appears to be wider if the characteristic minimum temperature is higher. He concluded that swarming in a temperature range indicates that there are other important environmental factors for breeding e.g. moon, tidal levels etc. Spawning of *N. succinea* occurs at a minimum of 16 °C during June to September (Kinne 1954, Rasmussen 1973, Bishop 1974). In our experiments, swarming heteronereids occurred between 12° and 20 °C. At constant temperatures, up to 16 °C, only 30 to 50% of all surviving worms underwent metamorphosis and swarmed. Ripe heteronereids, at 12 °C (Fig. 4) confirm that not only temperature but also endogenous rhythmus (seasonal timing) influence reproduction, as postulated by Olive and Garwood (1983). Thus, induction of metamorphosis by raising the temperature has been shown by our experiments as a potential zeitgeber.

Temperature programs (see Figs. 2 and 3) allow ripening of heteronereids throughout the year. In their physiological experiments Bass and Brafield (1972) reported an acceleration of gametogenesis in *N. virens* when temperatures were raised. After 10 d at higher temperature (20 °C), brain extracts of *N. diversicolor* contained only 20% as much maturation-inhibiting hormone activity as brains from control nereids maintained at 5 °C (Durchon and Porchet 1971).

The present investigation shows that induction of metamorphosis by temperature is only the first step in the timing of breeding. As seen in Fig. 5, ripe heteronereids can wait for a signal to start swarming behaviour. As described for numerous nereids, the swarming behaviour of *Nereis succinea* has lunar factors as the control synchronizing zeitgeber (Newell 1954, Hauenschild 1956, Rasmussen 1973, Wu et al. 1984). Moonlight-induced swarming behaviour must also have an endogenous component (Schroeder and Hermans 1975). Hauenschild (1956) indicated that *Platynereis dumerilii* synchrony persists for at least one additional moon cycle after cessation of the moonlight stimulus. Thus, swarming rhythms appears to have an endogenous component which maintains synchrony through periods of lunar signal failure.

Sudden temperature raises can influence lunar timing (Fig. 6). This phenomenon has also been described in *Platynereis dumerilii* (Fage and Legendre 1927). A difference in temperature may cause full moon induced swarming at a given date to fall at different times in the lunar cycle, but it will not change the monthly periodicity. An abrupt rise in temperature appears to be a potent force for inducing reproduction in *Nereis diversicolor* (Dales 1950). Clark (1961) pointed out the dangers of assuming, too readily, that spawning is only induced by one stimulus. At this point, it has also to be considered that larval development depends on weather and water temperature conditions (Kinne 1954: optimum at 20° to 22 °C).

This investigation agrees with much of the research on swarming behaviour of *Nereis succinea* by Kinne (1954), but there are also some differences. He observed, in the Kiel Bay, FRG, a positive correlation between the number of actively swarming heteronereids and seawater-surface-temperatures near an illuminated pier. Although swarming occurred around new moon, he reported that swarming was more correlated with temperature than lunar phase. On the other hand, he described the potential elimination of any lunar rhythm by the bright light of a pier, which was used as an observation platform, just as permanent light did in Hauenschild's (1960) experiments with *Platynereis dumerilii*. Therefore, he was not able to explain the swarming control mechanism in more detail. In our investigation, the mechanisms of spawning control could be demonstrated by experiments and additional field observations. The induction of metamorphosis in *N. succinea* is induced by temperatures or endogenous rhythms as supposed by Kinne (1954). An increase in temperature causes metamorphosis to heteronereid stages, and swarming behaviour occurs with lunar periodicity as zeitgeber. Suddenly raised temperatures influence this lunar timing and cause swarming to fall at different times of the lunar cycle with the effect of bigger breeding success at higher water temperatures.

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Literature cited

Bass, N. R., Brafield, A. E. (1972). The life cycle of the polychaete *Nereis virens*. J. mar. biol. Ass. U.K. 52: 701–726

Bishop, J. (1974). Observation on the swarming of a nereid polychaete, *Neanthes succinea* from the northern Gulf of Mexico. Proc. La Acad. Sci. 37: 60–63

Clark, R. B. (1961). The origin and formation of the heteronereis. Biol. Rev. 36: 199–236

Dales, R. P. (1950). Reproduction and larval development of *Nereis diversicolor* O. F. Müller, J. mar. biol. Ass. U.K. 29: 321–360

Durchon, M., Porchet, M. (1971). Premières données quantitatives sur l'activité endocrine du cerveau des Nereidiens au cours de leur cycle sexuel. Gen. comp. Endocr. 16: 555–566

Fage, L., Legendre, R. (1927). Pêches planctoniques à la lumière effectuées à Banjuls-sur-Mer et a Concarneau; Annélides polychaètes. Archs Zool. exp. gén. 67: 23–222

Franke, H. D. (1985). On a clocklike mechanism timing lunar-rhythmic reproduction in *Typosyllis prolifera* (polychaeta). J. comp. physiol. (Sect. A) 156: 553–561

Franke, H. D., Pfannenstiel, H. D. (1984). Some aspects of endocrine control of polychaete reproduction. Fortschr. Zool. 29: 53–72

Goerke, H. (1979). *Nereis virens* (Polychaeta) in marine pollution research: culture methods and oral administration of a polychlorinated biphenyl. Veröff. Inst. Meeresforsch Bremerh. 17: 151–161

Goerke, H. (1984). Temperature-dependence of swarming in north Sea Nereidae. Fortschr. Zool. 29: 29–43

Hauenschild, C. (1956). Neue experimentelle Untersuchungen zum Problem der Lunarperiodizität. Naturwissenschaften 16: 361–363

Hauenschild, C. (1960). Lunar periodicity. In: Cold Spring harbour symposium on quantitative biology, Vol. XXV. Biological clocks. The Biology Laboratory, Cold Spring Harbour, New York

Herpin, R. (1925). Recherches biologiques sur la reproduction et le développement de quelques annélides polychaètes. Bull. Soc. Sci. Nat. l'ouest France (Ser. 4) 5: 1–250

Kinne, O. (1954). Über das Schwärmen und die Larvalentwicklung von *Nereis succinea* Leuckart. Zool. Anz. 153: 114–126

Kristensen, E. (1984). Life cycle, growth and production in estuarine populations of the polychaetous *Nereis virens* and *Nereis diversicolor*. Holarct. Ecol., Copenhagen 7: 249–256

Lillie, F. R., Just, E. F. (1913). Breeding habits of the heteronereis form of *Nereis limbata* at Whitstable, Mass. Biol. Bull. mar. biol. Lab., Woods Hole 24: 147–160

Mettam, C., Santhanam, V., Havard, M. S. C. (1982). The oogenic cycle of *Nereis diversicolor* under natural conditions. J. mar. biol. Ass. U.K. 62: 637–645

Milheikowsky, S. A. (1958). Lunar periodicity in spawning of littoral and upper sublittoral invertebrates of the White Sea and other Seas. Dokl. Biol. Sci. 123: 1006–1009

Newell, E. (1954). The marine fauna of Whitstable. Ann. Mag. nat. Hist. (Ser. 12) 7: 321–350

Olive, P. J. W., Garwood, P. R. (1983). The importance of long term endogenous rhythms in the maintenance of reproductive cycles of marine invertebrates: a reappraisal. Int. J. Invertebrate Reprod. Dev. (Amsterdam) 6: 339–347

Rasmussen, E. (1956). Faunistic and biological notes on marine invertebrates III. The reproduction and larval development of some polychaetes from the Isefjord, with some faunistic notes. Biol. Medd. K. Dan. Vidensk. Selsk. 23: 1–84

Rasmussen, E. (1973). Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia 11: 1–507

Schroeder, P. C., Hermans, C. O. (1975). Annelida: Polychaeta. In: Giese, A. C., Pearse, J. S. (eds.) Reproduction of marine invertebrates, Vol. 3. Academic Press, New York, p. 85–92

Wu, B. L., Sun, R. P., Yang, D. J. (1984). The Nereidae of the Chinese coast. China Ocean Press, Beijing. Springer Verlag, Berlin, Heidelberg, New York, Tokyo

Zeeck, E., Hardege, J., Bartels-Hardege, H., Wesselmann G. (1988). Sex pheromone in a marine polychaete: determination of the chemical structure. J. exp. Zool. 246: 285–292

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