Oecologia (Berlin) (1985) 67:255–259

Oecologia

The recolonization potential of *Metridium senile* in an area previously depopulated by oxygen deficiency

Martin Wahl*
Abteilung Mar. Ökol. Syst., Universität Kiel, D-2300 Kiel, Federal Republic of Germany

Summary. Every summer the deepest parts of the inner Flensburg fjord are subject to O_2-deficiency lasting from a few weeks to several months. In spring, however, populations of *Metridium senile* can be found in these areas, in spite of the fact that frequently the local anoxic period of the previous summer has been 2–3 times longer than their anoxia LD_{50}-value (3 wks).

Responsible for this phenomenon is an intensive recolonization by adult *Metridium* during autumn and winter. This process has been investigated in an 8 months monitoring from May to December 1981. Results on the recolonization mechanism, the population structure of immigrating anemones and recolonization rate as a function of available hard substratum are presented.

Every summer, the particular topography of the Flensburg fjord (54°50′N, 9–10°E), the wind-caused bottom-near inflow of colder North Sea water and the warming of low-salinity surface water induce the formation of an extremely stable thermocline (Kändler 1963; Gemeinsames Komitee Flensburger Förde 1974). Eutrophication phenomena cause a continuous sedimentation of organic matter through the thermocline into the now hydrographically isolated waterbody causing O_2-deficiency as a result of amplified heterotrophical metabolism (Sasaki et al. 1977; Jørgensen 1980; Dehtlefsen and Westernhagen 1982; Rachor and Albrecht 1983).

The extension in space and time of this oxygen deficiency situation depends principally on meteorological factors (temperature, winds, etc.) which influence the plankton primary production and the stability of the thermocline. As oxygen depletion always starts in the deepest parts of the Fjord which are also the last to return to oxic conditions, the length of summer anoxia increases with depth (see Fig. 1B for the summer 1981). In the deepest water layers of the inner Fjord O_2 may be lacking for several months without interruption.

The LD_{50}-value for *Metridium senile* is about 3 weeks (Fig. 2; Wahl 1982, 1984). As not a single *Metridium* survives more than 6 weeks under the given circumstances (total anoxia, 6–9° C; Wahl op. cit.) a single summer should suffice to rid large portions of the inner Fjord of its *M. senile* populations. All the same, I frequently found anemone populations in good condition in these critical depths.

The only plausible answer to this apparent inconsistancy must be an intensive recolonization during winter by *Metridium senile*, a species considered to be sessile or hemisessile. (Larval settlement seems not to occur in the Fjord.) Recolonization strategies of other macrofauna species between periodic defaunations due to hypoxia have been investigated by Dauer and Simon (1976), Simon and Dauer (1977) and Santos and Simon (1980a, b).

In the following I describe an 8 months survey of a Flensburg fjord summer anoxia and the subsequent recolonization by *M. senile* of the depopulated areas.

Methods

The SCUBA-diving monitoring of the O_2-deficiency and the recolonization process has been carried out near Kollund (Dk) in the depth range between 10 and 15 m. It started in May 1981 and was brought to an end in January 1982 by a long lasting freezeover of the Fjord that made SCUBA-diving impossible.

1) Every 5 to 10 days I visited the survey area to determine the oxygen concentration at different depths (Fig. 1B), and to note the exact position of the thermocline and the habitus, behavior and strategies of immigrating sea anemones.

2a) For the numerical monitoring of the recolonization a survey area was marked out. Parallel nylon lines with numbered brass tags at one meter intervals were used to demarkate four 50 cm wide sediment strips of different lengths: Two bands ran along the 10 m and 12 m isobaths (lenghts 40 m and 20 m respectively), connected at right angles by a strip of 20 m length. A second 'vertical' strip stretched from the 12 m band well into the 15 m zone (length 56 m). During one monitoring dive each month the number of anemones in every 0.5 m^2 field was counted. (Due to technical difficulties, on December 19 the abundance values between 11 m and 14 m had to be estimated.)

2b) Whenever a section of a monitoring strip was covered by detached, wandering mats of *Zostera marina* leaves or red algae the above described way of counting was complemented by another method on the nearest free sediment patch at the same depth: A 0.25 m^2 PVC-frame was placed on the sediment surface and the anemones within the frame

* *Present address:* Laboratoire Arago, F-66650 Banyuls/Mer

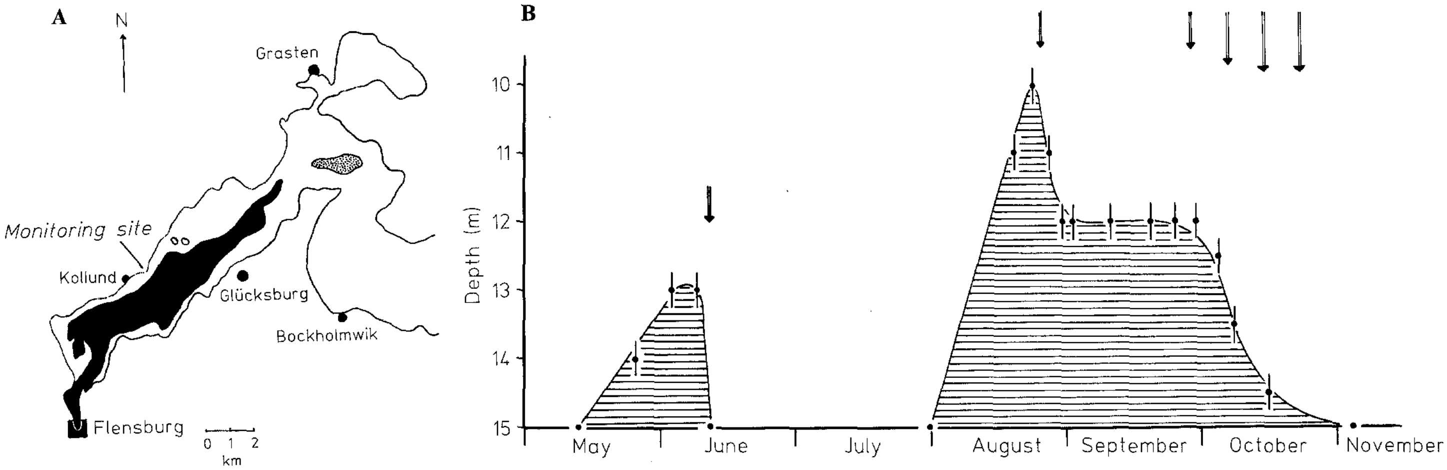

Fig. 1A, B. Oxygen deficiency in the Flensburg fjord (summer 1981) **A** Areas of the inner fjord where oxygen was absent for more than three weeks without interruption; ■ monitored, ▣ presumed. **B** Vertical extension of anoxic waterbody and length of anoxia at different depths at the Kollund monitoring site. Examples for reading: 11 m, ca 1 wk; 14 m, 1.5 wks and 9 wks; ● upper limit of anoxic waterbody, ↓ = storms

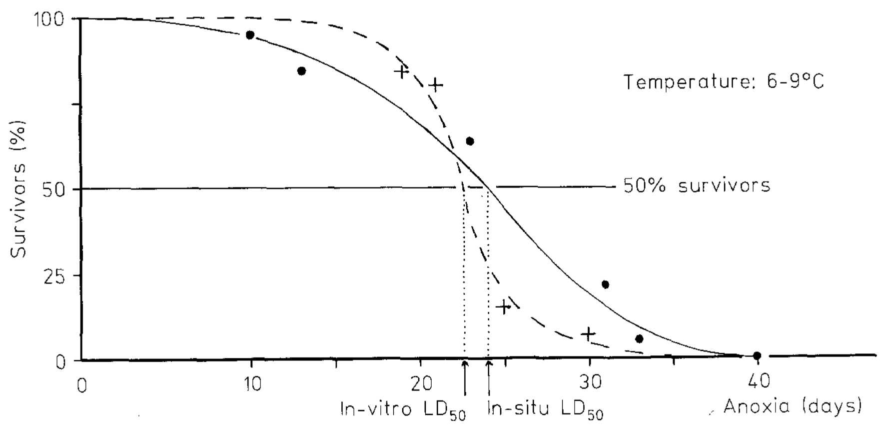

Fig. 2. O_2-deficiency resistance of *Metridium senile* as tested by laboratory (+) and in-situ (●) experiments (Wahl 1984). After 22 and 24 days of anoxia, respectively, half of the test organisms do not recover when returned to oxic conditions

were counted. Then the frame was turned over its frontal edge and the next counting done, etc., thus proceeding in a straight line until 20 to 100 counts were made.

3) On December 19 anemones were collected at random between 12 m and 15 m depth for a characterization of the immigrating *Metridium* population by dry weight (DW) determination (72 h at 80° C) as compared with the mean values of the average *Metridium* fauna of the Flensburg fjord (26 stations with 15 to 80 anemones per station, 3 to 24 m depth; Wahl 1982).

Results

1a) The anoxic situation. In the inner Fjord, the summer of 1981 was characterized by two periods of oxygen deficiency (Fig. 1B). The first lasted four weeks (May to June) and reached the 13 m level, the second started at the end of July and ended during the second week of November (ca. 12 weeks). Both periods were brought to an end by stormy weather.

At maximum expansion (August) the uppermost O_2-free water level swept over the 10 m mark. The duration of O_2-depletion increased with depth: a few days at 10 m; one week at 11 m; 6 weeks at 12 m; 1 week, then 8 weeks at 13 m; 2.5 weeks, then 9 weeks at 14 m; 4 weeks, then 12–13 weeks at 15 m. Below 12 m ($\geq$6 weeks of anoxia) all anemones had disappeared when oxygen returned in autumn. But even between 11.5 m and 12 m with O_2 lacking for only two weeks, not a single anemone survived this summer's O_2-deficiency.

This may seem surprising considering the fact that the LD_{50}-value for *M. senile* oxygen deficiency resistance is 3 weeks, and the toughest individuals even survive nearly 6 weeks of oxygen depletion (Fig. 2). However, other factors acting in synchrony with O_2-deficiency aggrevate its effects: Extreme rates of plankton sedimentation (up to 10 cm/wk, pers. obs.) and the death of living hard substratum (sponges, molluscs, etc.) by O_2-starvation. Furthermore, *Metridium* detaches from its substratum during the first weeks of O_2-depletion and may drift away. A detailed describtion of the behavior of *M. senile* under anoxic conditions has been given elsewhere (Wahl 1984).

1b) Reoxygenation. If the development of an anoxic situation was made possible by water stagnation below a stable thermocline, reoxygenation, on the other hand, was generated by an ever more intensive mixing of the water column due to stormy weather. It started in the shallow depths and eventually reached the deepest parts of the Fjord. A first step was taken in August, when the upper limit of the anoxic waterbody fell from 10 m to 12 m (Fig. 1B). There it stabilized for over one month. Heavy storms in October progressively pushed the anoxic frontier below the

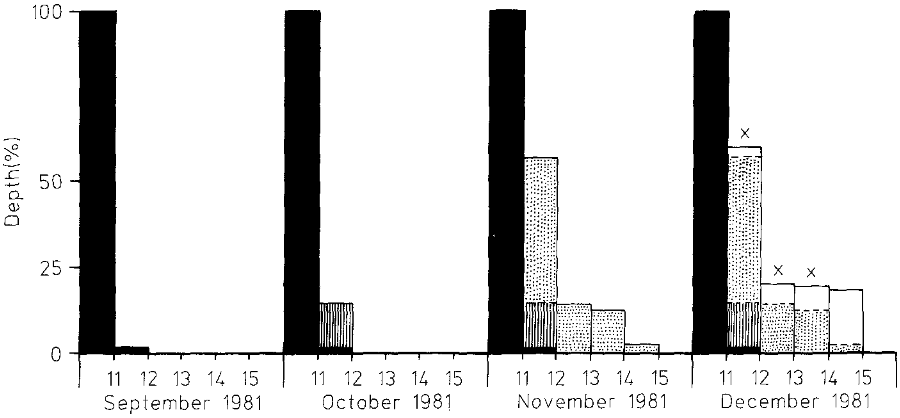

Fig. 3. Metridium recolonization of areas previously depopulated by anoxia. For every month, 100% is the actual Metridium abundance in the 10–11 m range, that had remained unharmed by anoxia (≤1 wk in August)
■ = reference abundance (10–11 m) and survivors of the summer anoxia (10–11 m, 11–12 m)
▥ = immigration September–October
▩ = immigration October–November
□ = immigration November–December
× = the abundance increase in December for the depths 11–14 m had to be estimated

13 and 14 m marks, and during the first week of November the deepest range (15 m) had finally been reoxygenated.

2) The recolonization process. When oxic conditions returned, the *Metridium* situation to a certain extend reflected the length of previous anoxia at the different depths: unharmed and dense populations between 2 m and 11 m, a numerically reduced population between 11 m and 11.5 m, total absence of *M. senile* below 11.5 m. Soon after reoxygenation the first adult *Metridium* immigrants appeared in the survey area.

2a) Origin of the immigrating metridium. In healthy biotopes the sight of a detached, living *Metridium* is a very rare thing, even after heavy storms. Therefore the large numbers of drifting anemones in autumn must come from nearby areas where O_2 has been lacking long enough to trigger the detachment reaction of the anemones (2–4 wks, Wahl 1984) and they must have found oxic conditions before they were killed by O_2-starvation (within 3–5 wks). Transported by currents they may reach areas just returned to oxic conditions where they readily settle if they contact some piece of hard substratum.

2b) Aspect and behavior of the immigrating anemones. At the latest one week after the return to oxic conditions the first living specimens of *M. senile* appeared in the survey area. All of these were adult individuals. Many were without substratum and had their naked pedal discs blown up to a nearly hemispherical form. This behavior may increase the probability of contact with a new substratum. Other anemones were attached to *Zostera* leaves or the thalli of red algae. Neither is a typical *Metridium* substratum in the Flensburg fjord and must have been accepted during the 'drifting phase' for the lack of anything better, the readiness for re-attachment of detached (see 2a) but healthy *Metridium* being extremely high. Within the survey area those immigrants that contacted a suitable substratum attached, others pushed their pedal disc and lower column into loose sediment, and the majority were drifted away – to be replaced by the next immigration wave.

2c) The settlement rate. The exact evaluation of the colonization rates was made difficult by the continuous coming and going of drifting anemones that did not settle definitively within the survey area. In order to neutralize these fluctuations (which were of similar amplitude in the different depths), in every histogram of Fig. 3 the *actual* abundance value in the 10–11 m range (that had remained unharmed by the few days of anoxia) was equated to 100%. Then

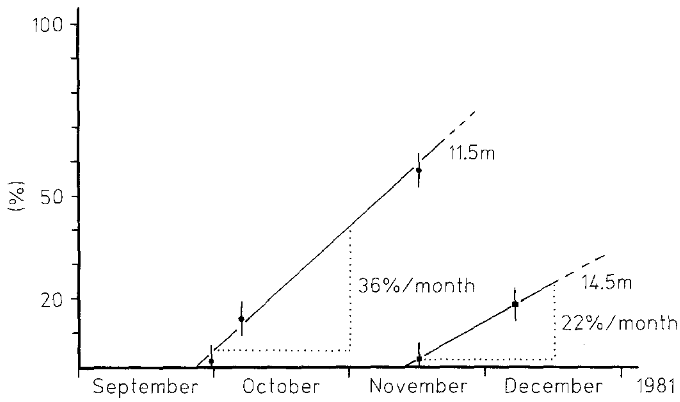

Fig. 4. Recolonization rate in 11.5 and 14.5 m as a percentage of the unharmed 10–11 m abundance: as, during the reoxygenation phase, the upper limit of the O_2-free layers slowly retreats to the deeper parts (see Fig. 1 B) immigration at 14.5 m starts 1.5 months later than at 11.5 m. Recolonization is slower at 14.5 m (22% per month, as compared with 36% per month at 11.5 m) because of the lack of suitable substratum

the counts for the other depths were transformed accordingly. By this method an increase in local abundance-% in Figs. 3 and 4 is essentially due to newly *settled Metridium.*

Figure 3 shows clearly that recolonization begins in the 11–12 m range, which is the first to return to oxic conditions, and eventually reaches the deepest parts (14–15 m), which were not reoxygenated before the first two weeks of November (Fig. 1 B). In mid-December the *Metridium* abundances in the three deeper regions level at approximately 20% of the 10–11 m abundance, while the 11–12 m data have increased only slightly during the last four weeks: The rate of settlement is apparently slowing down. At this stage the limiting influence of limited substratum becomes obvious. The principal obstacle for a 'definite' (that means: until the following summer) colonization by *Metridium* is the lack of hard substratum. In the absence of rocks or boulders in the inner Fjord the only suitable and durable substratum are the shells of living or dead molluscs (*Mytilus edulis, Cyprina islandica, Astarte borealis, Mya truncata,* etc.). But at the monitoring site below 11 m most macrofauna species had died from O_2-starvation and the shells of dead molluscs are quickly buried by heavy sedimentation. Because of longer anoxic periods and looser sediment, accessible shells become more and more scarce with depth. Consequently, the settlement rate diminishes with depth (Fig. 4), showing a gradient that is inverse and parallel to

Table 1. Size spectrum analysis of recolonizing *Metridium* as compared with the average of "normal" Flensburg fjord populations: only middle-size *Metridium* are responsible for the recolonization. (∅max. and ∅min. are the average values of the 26 pairs of station extrema)

Stations	Mean dry weight	Standard deviation	Max. weight	Min. weight	Δ max-min	$\times = \frac{\max}{\min}$
Kollund 12–15 m	0.1183 g (n=21)	0.0754 g (n=21)	0.2864 g	0.0348 g	0.2561 g	ca. 8
			∅max. weight (n=26)	∅min. weight (n=26)	Δ ∅max-∅min	$\times = \frac{\varnothing \max}{\varnothing \min}$
Flensb. Fjord 26 stat. 3–24 m	0.0919 g (n=1,070)	0.2085 g (n=1,070)	1.0762 g	0.0029 g	1.0733 g	ca. 370

the gradients of sedimentation rates and length of summer anoxia.

By mid-December all visible pieces of hard substratum are occupied by anemones. Also, the number of immigrating *Metridium* begins to fall because, with the whole of the Flensburg fjord reoxygenated since November, the "detachment phase" has come to an end and an ever greater percentage of the drifting anemones have either died or settled. Thus, even without further countings, it seems a likely prognosis that during the next months the abundance of firmly settled *M. senile* between 12 m and 15 m will not change significantly – until the beginning of the next O_2-depletion period in summer with a new depopulation of the deeper anoxic areas.

3) The population structure of the immigrants

The results of the dry weight (DW) analysis listed in Table 1 confirm a diving observation during the recolonization phase: The mean DW of the immigrating *Metridium* is 'normal' as compared with the average value of over 1000 anemones collected throughout the Flensburg fjord (26 stations between 3 m and 24 m, Wahl 1982). The amplitude of size variation, however, is much reduced (Table 1): From a mean factor 370 for Fjord populations it shrinks to a factor 8 for the immigrants. This is due to the fact that the recolonization population lacks the two extreme size groups (>0.3 g and >0.03 g). The absence of the biggest *Metridium* can not be explained here conclusively.

The missing of the smaller individuals may seem less astonishing if the following is taken into account: The smallest specimens of *M. senile* succumb more quickly to O_2-starvation (in-vitro tests 1981, unpubl.), frequently even before detachment. They are more easily buried by sedimenting plankton and they probably possess less energy reserves which are essential for a prolonged drifting with difficult or impossible feeding.

Thus, under the particular conditions of the Flensburg fjord and in the absence of larval settlement which has never been observed here, only a 'middle class' of *Metridium* are responsible for the recolonization of an area previously depopulated by oxygen deficiency.

Conclusion

This study shows that in the Flensburg fjord there is a high recolonization potential, at least for the species *Metridium senile*.

If the input of organic nutrients could progressively be reduced by the construction of purification plants with a chemical stage (recuperation of phosphates, nitrates, etc.) or, even better, by a limited use of products generating organic nutrients in agricultural, industriel and household domains, thus gradually diminishing eutrophication, plankton sedimentation and heterotrophic O_2-consumption, a progressive return to healthy conditions seems possible:

Pioneers of a *definitive* recolonization should be species with a high O_2-deficiency resistance such as *C. islandica, A. borealis, M. arenaria*, etc. (Theede et al. 1969). In this way the amount of available hard substratum would increase significantly. A massive recolonization by *M. senile* (after having detached previously in areas *still subject to summer anoxia*) and other sessile organisms such as ascidians, bryozoans, etc. should take place in the following year already. Gradually such a recolonization could gain the deepest and the innermost regions of the Fjord where actually the summer anoxia last longest.

Paradoxically, in this context (no larvae, adult recolonization) a gradual amelioration of conditions, extending over several years, would seem preferable to an abrupt return to non-eutrophic conditions.

Summary:

1. Eutrophication caused summer anoxia rids vast areas of the inner Flensburg fjord of its *Metridium senile*.
2. *Metridium* that have detached under O_2-stress form 'drifting populations' and recolonize defaunated areas soon after reoxygenation in autumn.
3. DW analysis shows that the immigrants represents a middle-class of the 'normal' Fjord population.
4. The principal limiting factor of recolonization is the lack of (biogenic) substratum, the molluscs having succumbed to anoxia and/or been buried by decaying plankton. Substratum gets rarer with depth and towards the innermost parts of the Fjord.
5. Larval colonization does not seem to occur in the Flensburg fjord.

Acknowledgements. I am grateful to Prof. Dr. W. Noodt for his generous tutorship of this study. The diving assistance of Dr. C. Valentin and S. Schuster were a great help. I want to thank G. Wahl for the critical reading of the manuscript.

References

Dauer DM, Simon JL (1976) Repopulation of the polychaete fauna of an intertidal habitat following natural defaunation: Species equilibrium. Oecologia (Berlin) 22:99–117

Dethlefsen V, Westernhagen HV (1982) Sauerstoffmangel in der Deutschen Bucht und seine Wirkung auf Fische und Bodenfauna. Inf Fischwirtsch 29(4):177–185

Gemeinsames Komitee Flensburger Förde (1974) Untersuchungen der Flensburger Förde. Selbstverlag, Amtshuset, Aabenraa

Jørgensen BB (1980) Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effects on the benthic community. Oikos 34:68–76

Kändler R (1963) Hydrographische Untersuchungen über die Abwasserbelastung der Flensburger Förde. Kieler Meeresforsch 19:142–157

Rachor E, Albrecht H (1983) Sauerstoffmangel im Bodenwasser der Deutschen Bucht. Veröff Inst Meeresforsch Bremerh 19(2):209–227

Santos SL, Simon JL (1980a) Marine soft bottom community establishment following annual defaunation: Larval or adult recruitment? Mar Ecol Prog Ser 2:235–241

Santos SL, Simon JL (1980b) Response of soft bottom benthos to annual catastrophic disturbance in a south Florida estuary. Mar Ecol Prog Ser 3:347–355

Sasaki K, Sato Y, Sugiura K, Matsukawa Y (1977) Mechanisms of formation of an oxygen-deficient watermass in Atsumi Bay. Budget of oxygen below transition layer. Bull Tokai Reg Fish Res Lab 89:43–55

Simon JL, Dauer DM (1977) Reestablishment of a benthic community following natural defaunation. In: Coull BC (ed) Ecology of marine benthos. University of South Carolina Press, Columbia, pp 139–154

Theede H, Ponat A, Hiroki K, Schlieper C (1969) Studies on the resistance of marine bottom invertebrates to oxigen deficiency and hydrogen sulphide. Mar Biol 2(4):325–337

Wahl M (1982) In-situ Versuche zum Vorkommen von *Metridium senile* in der Flensburger Förde. Diplomarbeit, Universität Kiel, FRG

Wahl M (1984) The fluffy sea anemone *Metridium senile* in periodically oxygen-depleted surroundings. Mar Biol 81:81–86

Received January 15, 1985