Spawning of the sea cucumber *Cucumaria frondosa* in the St Lawrence Estuary, eastern Canada

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Abstract

Our work presents data on spawning of the commercial sea cucumber *Cucumaria frondosa* from the Lower St Lawrence Estuary, eastern Canada. The rapidly rising concentration of chlorophyll a in early spring 1992 and 1993 appeared as the spawning cue for male and female individuals during the large-scale monitoring. A closer look at the spawning cue on a scale of hours revealed that males spawned first, as the chlorophyll a concentration decreased and as the temperature increased rapidly, during the low tide at sun rise. Spawning in females occurred shortly thereafter and seemed to be triggered by the presence of sperm in the water column. Those results demonstrate that the correlation between spawning and environmental factors is often more complex than that suggested by large-scale monitoring.

Introduction

Cucumaria frondosa, the species chosen for this experiment, is a commonly occurring coastal, large sea cucumber, especially abundant on rocky bottoms along the eastern coast of Canada and the United States. Attaining densities greater than 5ind/m^2 (sometimes reaching 15 kg/m^2), this holothurian is well distributed in both shallow and deep waters.

A somewhat controversial subject, discussed in many studies on holothurians, is the potential trigger of natural spawnings. The temperature (Tanaka, 1958; Conand, 1993), the phytoplanktonic bloom (Cameron & Fankboner, 1986; Hamel et al., 1993), the light intensity (Conand, 1982; Cameron & Fankboner, 1986) and the salinity (Krishnaswamy & Krishnan, 1967) are the most frequent factors identified.

Spawning of *Cucumaria frondosa* has been noted to occur between April and May in Passamaquoddy Bay, New Brunswick (Lacalli, 1981); from February to May in Newfoundland (Coady, 1973); in March in the North Sea; in July farther in Arctic waters (Runnstrôm & Runnstrôm, 1919); and in late March and early April along the coast of Maine (Jordan, 1972). The phytoplanktonic bloom was suggested to be the spawning trigger, especially from the work of Coady (1973) and Jordan (1972).

All those studies deduced spawning or observed it during the course of a long-term sampling, from the occurrence of larvae in the field or following the histologic cycle of the gonad, but the large intervals between each sample allowed only an approximation of the spawning time and cue. In the present study, we carefully monitored the spawning period from beginning to end during two years, collecting samples at close intervals and making correlations with environmental conditions. A more precise observation of the spawning event was made underwater every hour, taking into account the fine-scale variations of the environmental conditions at the study site, in order to increase the resolution of the correlative data.

Materials and methods

Abundance of individuals ready to spawn and having spawned

Just before the spawning event, we determined the number of individuals likely to participate in the spawning in May 1991, 1992 and 1993 at Les Escoumins, eastern Canada (Fig. 1), using SCUBA. The observations were made on 3 samples of 180 – 200 individuals of both sexes, collected randomly at about 15 m depth (where the vast majority of animals were found). Each individual was dissected and the degree of maturity of its gonad determined by the proportion of mature gametes present in the whole gonad. The large tubules were those implicated in the spawning for the current year (Hamel et al., 1993 for *Psolus fabricii*, personal observation during preliminary experiments of this research). We considered that an individual was ready to spawn when the large tubules were fully distended at the maturity stage.

We took equivalent samples of sea cucumbers at the same study site, a few days after the spawning event, and determined the proportion of individuals having released their gametes for the total number of individuals collected at the site. We considered that an individual had spawned when the gonad contained no gonadal tubule at maturity but had an abundance of very small constricted tubules. Because the number of individuals collected at the study site represented a very little proportion of the whole population, the disturbance caused by our collecting effort was minimal.

Seasonal variations of environmental factors in relation to spawning (large-scale)

Samples of 30 sea cucumbers (males and females) were collected monthly or bimonthly to establish the time of spawning and the potential trigger. The chlorophyll a concentration was recorded weekly at the study site by collecting 3 water samples (8 l) at 15 m depth, during high tide.

We made the pigment determination in two sub-samples of 50ml, by filtering them through Whatman GF / C filters, and immediately extracting with 90 per cent acetone for 24 h before evaluating the concentration by the spectrometric method of Yentsch and Menzel (1963).

The temperature at 15 m depth was recorded by 3 Peabody Ryan thermographs. Fresh water run-off data combined those of four rivers: Montmorency, Batiscan, Sainte-Anne and Chaudière, and were provided by Environment Canada (Climatologic Services).

Monitoring of the spawning events (fine-scale)

Gamete release was monitored using SCUBA in summer 1992. At the study site chosen for this experiment (Les Escoumins, St Lawrence Estuary, eastern Canada, see Fig. 1), the population of sea cucumbers attained its maximum density between 10 and 15 m depth, with an almost complete depletion at greater depths. Sea cucumbers were also poorly represented in shallower waters, as the sandy and muddy substrates at those depths discourage colonisation (unpublished data). The sea cucumber population was therefore localised and easier to study during spawning. This experiment was conducted with the help of a team of 24 divers, assisted by boat-skippers.

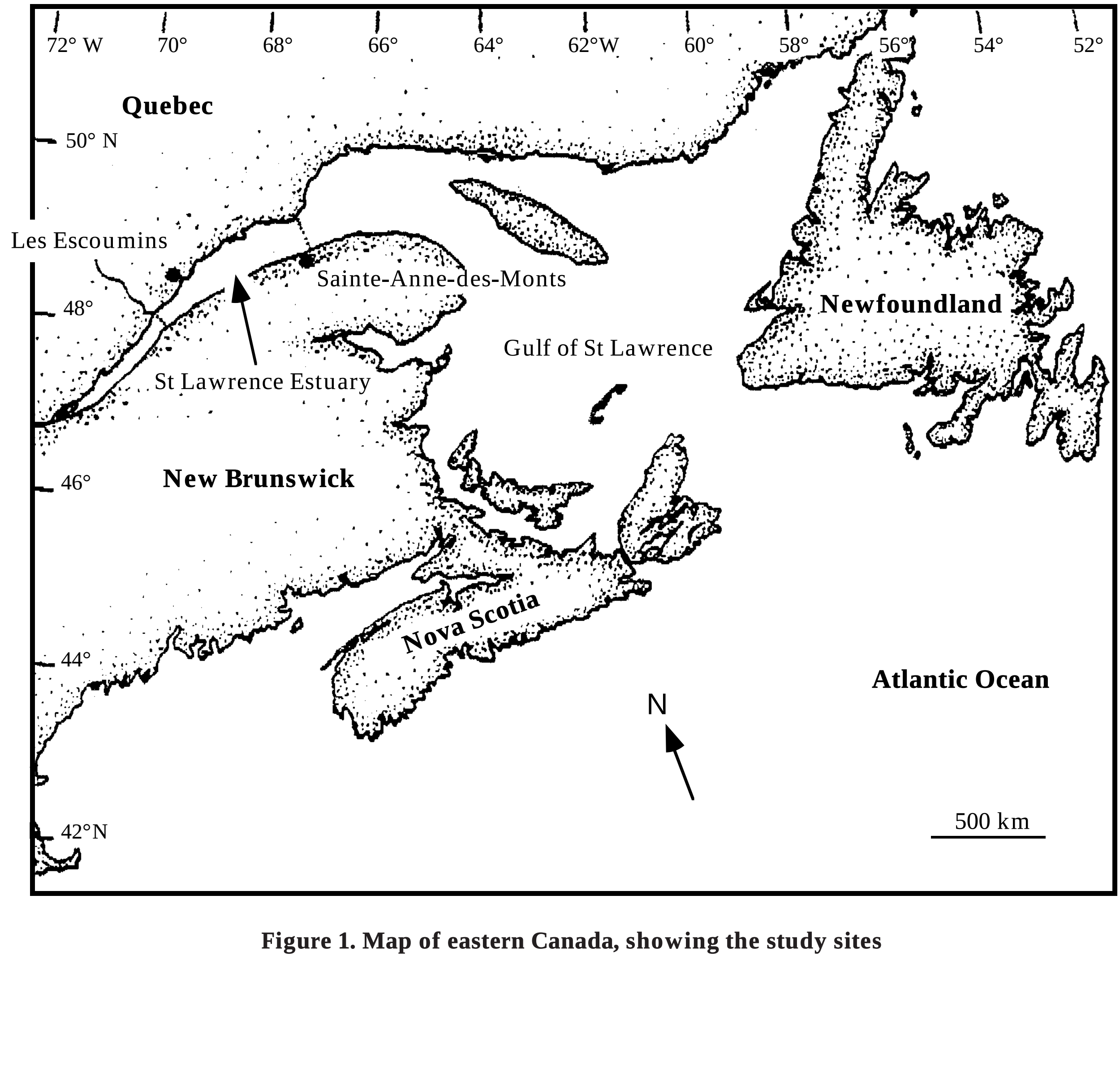


Figure 1. Map of eastern Canada, showing the study sites

After a few days of recognition dives, constant monitoring of the site was initiated in order to detect evidence of spawning events. Beginning on 16 June, alternating pairs of divers maintained a watch, day and night. During these dives, the following parameters were noted hourly: the velocity and direction of the current, with a torpedo currentometer; the direction of the flow in relation to the coast line, by addition of methylene blue to the water column between 10 and 15 m depth; the water temperature close to the sea cucumbers, using an electronic thermometer; the underwater visibility, using a Secchi disc to its total disappearance.

Water samples were also taken from a boat, for later evaluation of the chlorophyll a content. Light power supply was used at night to maintain underwater visibility. The tide level was established from the Canadian tide tables for this area (Canadian Hydrographic Service, Department of Fisheries and Ocean, Canada). Data on wind velocity and direction were obtained from Faune et Environnement Québec (Quebec Government).

At the first signs of spawning, closer monitoring and several types of data collection were initiated, with divers taking turns underwater by groups of up to 10 divers for 50 h until the end of spawning. Each diver spent a maximum of 35 minutes diving at intervals of 3 – 4 h or more. Most of the measures were taken above 10 m (only a few divers needed to descend to 15 m). Routinely, during each dive, we noted the proportion of males and females spawning, between 10 and 15 m depth, along a 100m long transect parallel to the coastline.

The results are presented for males and females as the proportion of spawning individuals (number ind / m^2) in a sample of 350 sea cucumbers observed every hour.

Results

Large-scale environmental fluctuations in relation to spawning

In early summer 1993 (June), the temperature oscillated regularly around 7°C and a few higher peaks between 8° and 10.5°C were observed. This period also corresponded to the spawning time observed between mid-May and mid-June 1993.

Chlorophyll a concentrations at the beginning of the experiment (May 1992) fluctuated around 0.5 and 1 mg / m^3. A strong increase in chlorophyll a occurred in mid-June 1992, with a peak attaining 6mg / m ^{3}, indicating an important phytoplanktonic biomass. Spawning occurred abruptly at this time. This high production persisted until August, although the pigment concentrations were not constant and sometimes fluctuated from the highest values (7 mg / m^3) to less than 1 – 2.2 mg / m^3.

Fine-scale environmental fluctuations in relation to spawning

Male spawning began early on 17 June at 0500 h (Fig. 2). At that time, only a few isolated males released their gametes in the water. Seven hours later, the proportion of spawning individuals had increased to attain 5 per cent of the 300 observations made. However, the male spawning only became generalised in the entire population around 1400 h, when more than 65 per cent of males were spawning. The highest number of spawning individuals was recorded at 1500 h, comprising 83 per cent of males.

Female spawning began at 1400 h, with numerous isolated individuals starting to release oocytes. When the first isolated female spawnings were recorded, they always occurred in proximity to a spawning male (less than 5 m). Following a drop in the male spawnings to less than 32 per cent of males (at 1700 h), maximum female spawning (87 per cent of the population) was observed. Around 1800 h, less than 12 per cent of females were still releasing gametes (Fig. 2). A small proportion of male and female individuals continued to spawn until 0700 h the next morning (18 June). No spawning individual was observed in the following 10 h of diving at the study site.

The data on tidal oscillation at the study site (Fig. 2) indicated that the first isolated spawnings of male and female individuals occurred during the lower slack tide. Spawning was initiated in both sexes when the current was minimum (0.5 to 1.5 cm / s). At that time, the underwater visibility was maximum, attaining around 4.7 m, associated with a net decrease in the concentration of chlorophyll a (Fig. 2).

The male spawning began at sunrise (0500 h), as the water temperature increased rapidly, passing from 3° to 7°C in less than 2 h. Female spawning also occurred as the visibility increased rapidly to attain 3.6 m, and the temperature increased rapidly, passing from 3° to 6°C in 2.5 h. The chlorophyll a was at its minimum (around 2.5 mg / m^3).

The maximum number of male individuals spawning (7 h after the first isolated one) occurred at the next slack tide, when again the concentration of chlorophyll a was minimum. However, the time of greatest abundance of female individuals spawning coincided with the beginning of the flood

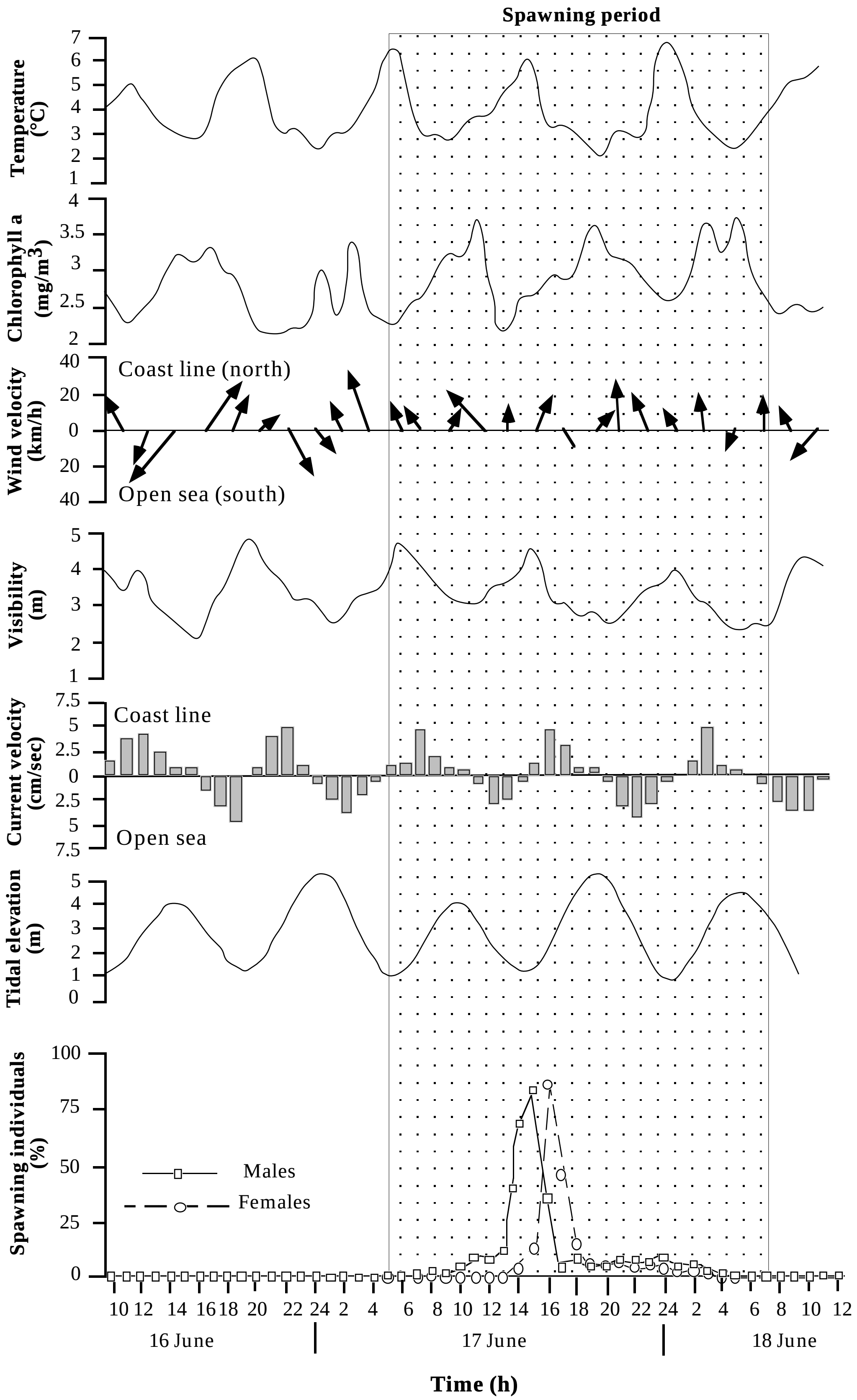


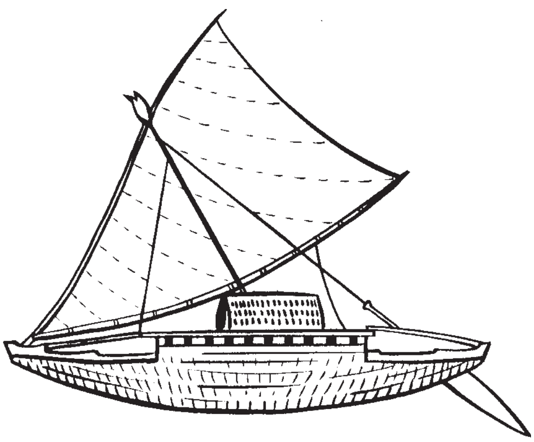
Figure 2. *Cucumaria frondosa*. Evolution of water temperature, chlorophyll a concentration, wind velocity, underwater visibility, direction and velocity of the current and tide level recorded every hour at Les Escoumins

The proportion of spawning males and females based on 300 observations every hour is also indicated. All measurements were recorded between 16 and 18 June 1992.

tide, when the current increased (passing from 0.5 to >4 cm/s) and both underwater visibility and water temperature decreased rapidly. During the spawning event of both sexes the wind blew relatively constantly, mainly in the north-north-west direction towards the coast at 5 – 35 km/h (Fig. 2).

Proportion of individuals implicated in spawning events

In summer 1991, 1992 and 1993 the proportions of males and females ready to spawn and those implicated in spawning were roughly the same. A maximum of 85 per cent of males and 84 per cent of females collected were ready to spawn a few days before the spawning event. A few days after the spawning event, our data indicated that the vast majority of individuals had spawned, since less than 14 per cent (considering males and females together) still possessed gonadal tubules at maturity.



Discussion

For many species of echinoderms, spawning events extend over a long period, but the reproductive season may be shortened when the environmental conditions are only favourable for a short time (Giese & Kanatani, 1987; Chia & Walker, 1991; Pearse & Cameron, 1991).

We observed in the St Lawrence Estuary that more than 80 per cent of the individuals ready to spawn had done so just after the massive spawning event recorded in the field (within a one-week period), suggesting that the conditions for an extended breeding season were not found in the St Lawrence Estuary. In contrast, Jordan (1972) and Coady (1973) indicated that the breeding season of *Cucumaria frondosa* was spread over a month in Newfoundland and along the coast of Maine.

The short duration of the phytoplanktonic bloom and the restrained warm season may in part explain the difference from these other locations where *C. frondosa* was studied. Varying lengths of spawning periods in relation to latitudes are very common among marine invertebrates and have been observed in other echinoderms (Giese & Kanatani, 1987).

The spawning periods reported for the numerous locations where *Cucumaria frondosa* was studied also showed a great variability. Occurring in July in the highest latitudes, spawning was noted in March and April in more southern locations. In the St Lawrence Estuary, the spawning of *C. frondosa* occurred in mid-June, when the stratification of the water column was well established, with a defined warmer surface layer.

Those conditions appeared as the fresh-water run-off dropped drastically. At that time, the primary production also increased, as the day-length progressively reached about 15 h/day. Highly variable at that time of the year, the temperature fluctuated over more than 7°C every day and does not seem to be the factor that stimulated *C. frondosa* to spawn (Fig. 2). The fact that days had gradually been growing longer well before the spawning, and continued to do so, minimises the likehood of a relationship between daylength and spawning event.

However, the male and female spawnings in 1992 and 1993 coincided with a drastic increase in primary production, as demonstrated by the significant increase of chlorophyll a. Simultaneously, individuals were found to have a higher content of phytoplanktonic cells in the digestive tract (unpublished data), strongly suggesting that the phytoplankton initiated spawning in *Cucumaria frondosa*. Starr et al. (1990, 1992, 1993) also demonstrated this with the sea urchin *Strongylocentrotus droebachiensis* and Hamel et al. (1993) suggested it for the sea cucumber *Psolus fabricii* at the same study site. For *C. frondosa*, Jordan (1972) and Coady (1973), also suggested that phytoplankton may induce spawning.

Moreover, the distinctive breeding seasons found in July for the Arctic (Runnstrôm & Runnstrôm, 1919); in mid-June for our research; in May–June for Newfoundland (Coady, 1973) and in April–May along the coast of New England (Jordan, 1972) again suggest that the primary production plays an important role in the initiation of spawning. The phytoplanktonic bloom occurs sooner in lower latitudes than in higher ones such as the Arctic waters.

Nonetheless, a closer look at the fine-scale spawning of *Cucumaria frondosa* informed us that the spawning correlation with environmental conditions was not as simple as suggested by the previous data (Fig. 2). In fact, male C. *frondosa* spawned first, a piece of information that was not revealed by the large-scale correlations. This phenomenon was also observed in other sea cucumbers by McEuen (1988).

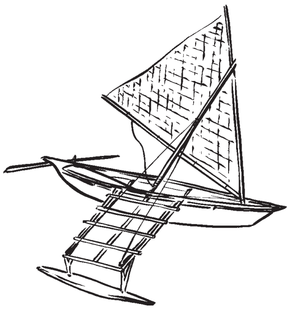
The female spawning began much later in *C. frondosa* (Fig. 2). More precisely, the male spawning initiated at first in a few isolated individuals coincided with low tide, minimum current, a drop in chlorophyll a concentration and a drastic increase in temperature as the sun rose (Fig. 2).

After those isolated individuals, spawning became epidemic, spreading away from the first individuals to spawn. This suggests that the environmental cue perceived by the males was not similarly effective for all members of the population. It strongly suggests that the spawning became epidemic in males following the direct effect of the sperm or pheromones issued from spawning individuals, as previously proposed by Pearse et al. (1991).

The female spawning also began with a few isolated females. Moreover the delay between male and female spawnings suggests that the female spawnings were stimulated by the sperm and not directly by the environmental factors.

Epidemic spawning, in which individuals take their cues from others, may play a role in the synchronicity of the phenomenon in entire populations. Sperm has been experimentally demonstrated to stimulate spawning in a few species, such as the green sea urchin *Strongylocentrotus droebachiensis* (Starr et al., 1992), the sea star *Leptasterias polaris* (Hamel & Mercier, 1995) and was also suggested by Young et al. (1992) for the bathyal sea urchin *Stylocidaris lineata*.

However, what is the cue for the spawning of the first few isolated individuals? Despite the apparent correlation with phytoplankton demonstrated in the large-scale correlative experiment, laboratory experiments with ripe female and male *C. frondosa* (Hamel & Mercier, unpublished data) demonstrated that no spawning success was obtained by stimulation of the phytoplankton species found at the study site during the spawning period.



The spawnings seem to be triggered by a progressive increment of the temperature and a drastic change of the light intensity. These conditions closely resemble those found at sunrise, when *C. frondosa* began to spawn in the field. A closer look at the fine-scale fluctuations of the environmental factors showed that, if the spawning cue came from phytoplankton in many species, in *C. frondosa* the correlation was not very convincing or was more complex than suggested by the large-scale experiment (Fig. 2). It seems to demonstrate the synergetic effect of numerous factors, such as tidal height, inter-individual communication (via sperm or pheromone), current, temperature, time of the day and phytoplanktonic biomass.

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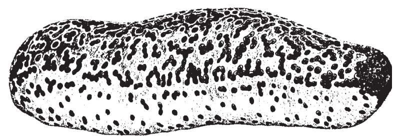

Japanese sea cucumber *Cucumaria japonica* in the far eastern seas of Russia

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Most commercially harvestable species of sea cucumbers belong to the order Aspidochirotida and are basically distributed in the tropics.

The only two representatives of the order Dendrochirotida occur far to the north. One of them is the Japanese cucumaria, *Cucumaria japonica,* which is distributed in the far eastern seas of Russia.

The Japanese cucumaria (called 'kinko' in Japanese) is a fairly large sea cucumber (Fig. 1). Its body length is up to 20 cm, the live weight is up to 1.5 kg (average 0.5 kg), and the weight of the body wall is 20 per cent of the total weight. The body is roundish, smooth, with 5 rows of tube feet. Its colour is grayish purple, but in some regions pure white specimens can be found.