Reprinted from

Réimpression du

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Occurrence of the toxic phytoflagellate *Prymnesium parvum* and associated fish mortality in a Norwegian fjord system

S. Kaartvedt, T. M. Johnsen, D. L. Aksnes, U. Lie, and H. Svendsen

Volume 48 • Number 12 • 1991

Pages 2316–2323

Canada

Fisheries and Oceans / Pêches et Océans

Printed in Canada by The Runge Press Limited
Imprimé au Canada par The Runge Press Limited

Occurrence of the Toxic Phytoflagellate *Prymnesium parvum* and Associated Fish Mortality in a Norwegian Fjord System

S. Kaartvedt,[1] T. M. Johnsen,[2] D. L. Aksnes, and U. Lie

Department of Fisheries and Marine Biology, University of Bergen, Bergen High Technology Center, N-5020 Bergen, Norway

and H. Svendsen

Geophysical Institute, University of Bergen, Allégt. 70, N-5007 Bergen, Norway

Kaartvedt, S., T. M. Johnsen, D. L. Aksnes, U. Lie, and H. Svendsen. 1991. Occurrence of the toxic phytoflagellate *Prymnesium parvum* and associated fish mortality in a Norwegian fjord system. Can. J. Fish. Aquat. Sci. 48: 2316–2323.

At the end of July 1989, toxin-producing *Prymnesium parvum* was spread through a fjord system in the surge of freshwater released from a hydroelectric power plant. In total, 750 tonnes of Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) died in fish farms. *Prymnesium parvum* germinated in the brackish surface layer of a fjord branch which, during July, was characterized by longer residence time, higher temperatures, and lower nitrogen and silicate concentrations than the rest of the fjord system. Nutrient loading (especially phosphate) from fish farms may, however, have stimulated local growth of the alga. At the time of the first observed fish mortality, the salinity was 5‰ and the temperature 18°C. Pelagic concentrations of *P. parvum* were generally low, with a maximum of 2.2×10^6 cells·L^{-1} found close to a fish farm. Denser concentrations of *P. parvum* were, however, found in association with benthic substrates. Phosphorus limitation was probably important for the production of toxin by *P. parvum*.

À la fin du mois de juillet 1989, *Prymnesium parvum*, algue productrice de toxine, s'est répandue dans un système de fjords à partir de rejets d'eau douce provenant d'une centrale hydroélectrique. Au total, 750 tonnes de saumons de l'Atlantique (*Salmo salar*) et de truites arc-en-ciel (*Oncorhynchus mykiss*) ont péri dans des exploitations piscicoles. *Prymnesium parvum* s'est multiplié dans la couche d'eau saumâtre d'une branche d'un fjord qui, en juillet, se caractérise par un temps de séjour plus long, des températures plus chaudes et des concentrations d'azote et de silicate plus faibles que dans les autres fjords du système. Toutefois, les éléments nutritifs (en particulier, le phosphate) provenant des exploitations piscicoles peuvent avoir stimulé la croissance locale de l'algue. Lorsque les premiers poissons morts ont été observés, la salinité de l'eau était de 5 ‰ et sa température de 18°C. Les concentrations pélagiques de *P. parvum* ont été généralement faibles, la valeur la plus élevée ($2,2 \times 10^6$ cellules·L^{-1}) ayant été observée à proximité d'une exploitation piscicole. Par contre, les concentrations de *P. parvum* ont été plus élevées dans les substrats benthiques. La limitation de phosphore a probablement joué un rôle important dans la production de toxine par *P. parvum*.

Received June 14, 1990
Accepted June 12, 1991
(JA611)

Reçu le 14 juin 1990
Accepté le 12 juin 1991

In July–August 1989, 750 tonnes of Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) died in aquaculture enclosures in a fjord system of southwestern Norway. The total economic cost was 35 million Norwegian kr ($5 million (U.S.)). Some mortalities were also reported among free-living fish, but these apparently were not affected as severely (Johnsen et al. 1989; Johannessen 1989).

Mortality of salmon was initially observed in the inner part of the fjord branch Hylsfjorden and thereafter spread outwards through the fjord system (Fig. 1). The fish deaths coincided with the appearance of the prymnesiophycean *Prymnesium parvum*, an oval flagellate about 10 μm long with two flagella and characterized by a short and stiff haptonema. This alga has previously caused fish deaths in brackish fish ponds and other brackish environments in Europe and Asia (Otterstrøm and Steemann Nielsen 1939; Reich and Aschner 1947; Valkanov 1964; Krasnoshchek and Abramovich 1971; Hickel 1976; Comin and Ferrer 1978; Holdway et al. 1978), but to our knowledge, this is the first incident in a large marine (estuarine) system.

At the time of the first observed fish death, the Research Vessel *Håkon Mosby*, with a team of scientists from the University of Bergen, was operating in the fjords to study the effect of onset of freshwater discharge from Hylen hydroelectric power plant, which had been closed during July. Discharge from the power plant, situated at the head of Hylsfjorden (Fig. 1), was initiated the day after the first observed fish mortality in inner Hylsfjorden. Therefore, we were incidentally at the right spot with appropriate equipment. In the present paper, we describe the distribution of *P. parvum* in the fjord system during July–August 1989 and evaluate factors influencing its growth, toxicity, and dispersal in an attempt to identify conditions which led to the event.

[1]Present address: Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.

[2]Present address: Norwegian Institute for Water Research, Breiviken 5, N-5035 Sandviken-Bergen, Norway.

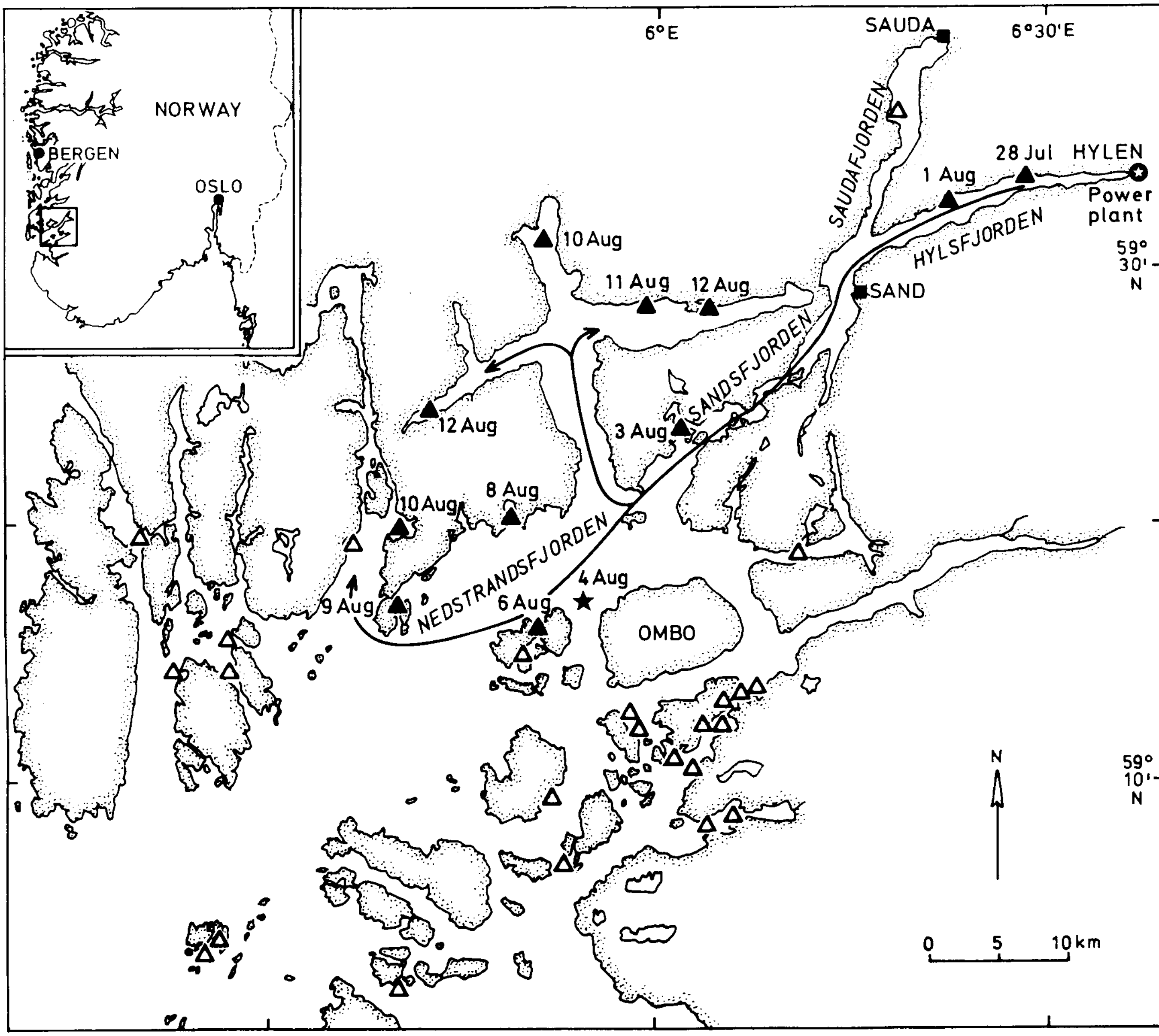

FIG. 1. Time of first observed fish mortality with path of outflowing toxic water indicated. Triangles represent fish farms; star represents well boat. Open triangles show nonaffected fish farms.

Study Area and Methods

The investigation was carried out during 25 July to 6 August 1989, mainly in Hylsfjorden, Saudafjorden, and Sandsfjorden, all of which share a common narrow connection to the outer fjord waters (Fig. 1). Due to high freshwater input and restricted exchange potential, this fjord system is characterized by a marked brackish surface layer (Svendsen 1981; Kaartvedt and Svendsen 1990a). Tidal amplitudes are weak along the southwestern coast of Norway. Amplitude at the mouth of Sandsfjorden is approximately 0.5 m, and tidal current velocities are negligible compared with wind- and freshwater-driven currents (Svendsen 1981; Kaartvedt and Svendsen 1990b).

Currents were measured in Hylsfjorden (Stns. 51, 53, and 55), Saudafjorden (Stn. 58C), and Sandsfjorden (Stns. 64 and 68) by moored Aanderaa and Gytre current metres (Fig. 2). Effects of tides were removed by using a 25-h moving average filter of hourly values.

Transverse recordings of surface (1 m) salinity and temperature were obtained with a Meerestechnik CTD attached to a float which was towed from shore to shore throughout the fjord system. Another Meerestechnik CTD with an oxygen sensor was attached to the hose of a pump during plankton sampling.

Nutrients and phytoplankton samples were obtained with Niskin bottles and a plankton pump. Subsamples (30 mL) for nutrient analysis were preserved with chloroform and refrigerated for later analysis. Weekly sampling of nutrients in the main freshwater sources (Suldalslågen and Hylen power plant) had been undertaken since March 1989. Both live (after *P. parvum* was first identified on 2 August) and Lugol-fixed phytoplankton were examined in samples drawn from the Niskin bottles. Water samples for Chl *a* analysis were taken with the plankton pump. Subsamples (100 mL) were filtered through

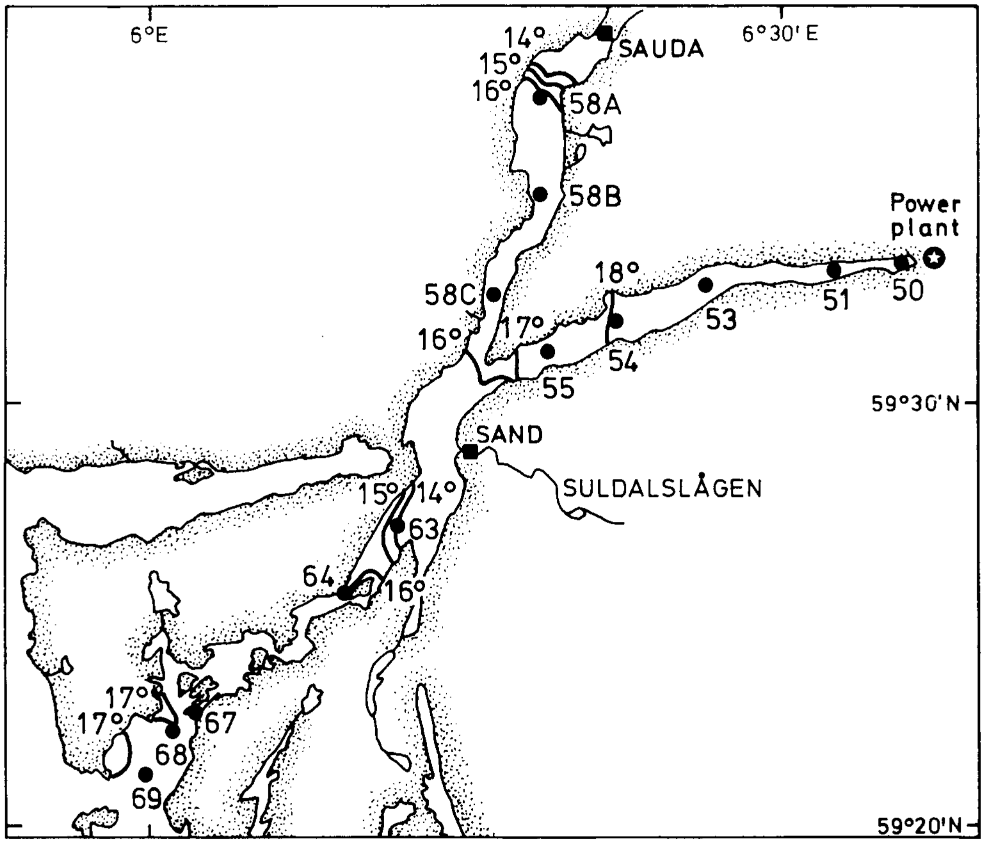

FIG. 2. Sampling stations referred to in the text, and surface temperatures (1 m), 27–28 July 1989.

0.45-μm Sartorius membrane filters. The filters were frozen and later analyzed following the method of Holm-Hansen et al. (1965).

Prymnesium parvum was first observed in a sample from fouling on a fish net, which appeared as a monoculture of the alga. We therefore searched for *P. parvum* on benthic substrates along the shores of the fjord. Benthic sampling was concentrated on macroalgae. The cell numbers obtained from this sampling were not quantitative and could only be used as an indication of high benthic concentrations of the species. On a later cruise (15 August), benthic abundance of *P. parvum* was estimated. Macroalgae covering an area of about 1 m^2 were removed from the substrate and the algae were shaken in a known volume of water to detach affiliated cells of *P. parvum* prior to subsampling for analysis.

Freshwater data (cubic metres per second) were provided for the main freshwater sources by the Norwegian State Power Board.

Results and Discussion

Dispersal of Fish Kills

The first fish mortality was recorded in inner Hylsfjorden on 28 July (Fig. 1). Following the start of discharge from the Hylen power plant on 29 July, mortality spread out through the fjord system. The first pulse of outgoing water was apparently more lethal, but did not affect the adjacent Saudafjorden (Fig. 1). Rain and snowmelt in the mountainous watersheds gave marked increase in runoff at Sauda coincidentally to start of the power plant (Fig. 3). Resulting outward flow of brackish water from

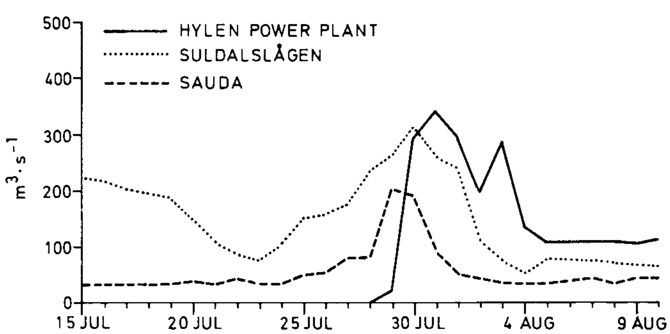

FIG. 3. Freshwater discharge in July–August (daily means) from Suldalslågen, Hylen power plant, and Sauda.

this fjord branch, which on 30 July at least spanned the upper 5 m (not shown), probably reduced intrusion of water from Hylsfjorden into Saudafjorden at that time. Fish died with successively later deaths with increasing distance from Hylsfjorden. While all fish farms located north of the outlet of Sandsfjorden were affected, no mortalities occurred in the large number of fish farms located south of the island of Ombo (Fig. 1). Outflowing water was probably deflected northward by Coriolis force and by the northward heading Norwegian Coastal Current.

Cause of Fish Kills

Prymnesium parvum, which is known as a nuisance alga from other brackish environments, was the most probable agent causing fish mortality and the dispersal of mortality followed

TABLE 1. Numbers of *P. parvum* ($10^6 \cdot L^{-1}$).

Station	Depth (m)	Live samples Aug. 3	Aug. 5	Aug. 8	Fixed samples July 27	July 29	July 30	Aug. 3	Aug. 4	Aug. 5
Hylsfjorden										
51	0					0.08				
	4					0.23				
53	0		0.50	1.10						
	4		0.00	0.00						
Fish farm	0					1.61				
	1					2.26				
	2					1.68				
	4					1.57				
	6					0.03				
54	1	0.60								
	4	0.06								
	8	0.00								
	12	0.00								
55	0			0.80		0.05	0.55		1.61	
	4					0.05	0.53		0.51	
	6								0.95	
Saudafjorden										
58A	0			0.65						
	4			0.04						
58B	0		0.60		0.00					0.25
	4		0.00							0.14
Sandsfjorden										
63	0			0.50	0.01			0.15		
	4			0.04	0.00			1.55		
64	1	0.70	0.80	0.60						
	4	0.00	0.08	0.00						
	8	0.00		0.00						
	12	0.00		0.00						
69	0		0.08							
	1	0.00								
	4		0.00							
	12	0.00								

the outflowing brackish water containing *P. parvum*. Our results rule out oxygen deficiency as a cause. In Hylsfjorden, 150% saturation was measured just beneath the brackish layer, and the lowest oxygen content observed at the time of first fish mortality was 110% saturation inside net cages in Hylsfjorden. Nitrogen supersaturation or other characteristics of the water from the power plant can also be ruled out, since fish in inner Hylsfjorden started to die prior to the freshwater discharge. No disease was observed in the fish by veterinarians.

Pelagic Distribution of *P. parvum*

In accordance with the chronology of fish kills, the *Prymnesium* distribution data imply that the alga was first established in Hylsfjorden (Table 1). Prior to discharge from the power plant, *P. parvum* was almost exclusively found in this fjord branch, where it was confined to the brackish surface layer. On 29 July, 1 d after the first observed fish mortality, concentrations were 10–40 times higher in the immediate vicinity of the affected fish farm (maximum concentration of 2.2×10^6 cells$\cdot L^{-1}$) than midfjord concentrations in Hylsfjorden (Stns. 51 and 55). The following day, after start of the power plant, concentrations at the outlet of Hylsfjorden (Stn. 55) had increased 10-fold (Table 1), and fish mortality was thereafter observed in the outer part of the fjord branch (Fig. 1). In the beginning of August, *P. parvum* was also present in Sandsfjorden (Stn. 63) and Saudafjorden (Stns. 58A and 58B) (Table 1).

We found low concentrations of *P. parvum* outside Sandsfjorden. Eighteen samples on 4–5 August (mainly from Nedstrandsfjorden; Fig. 1) gave 0 to 0.2×10^6 cells$\cdot L^{-1}$. Later, during the main fish kills outside Sandsfjorden, outflowing brackish water generally contained *P. parvum* in pelagic concentrations of 0.5 to 1.5×10^6 cells$\cdot L^{-1}$ (J. Aure, Institute of Marine Research, Bergen, pers. comm.).

Algal Transport as Revealed from Chl *a* and Water Movements

Strong mixing between cold freshwater and fjord water took place near the power plant outlet in inner Hylsfjorden (Stn. 50)

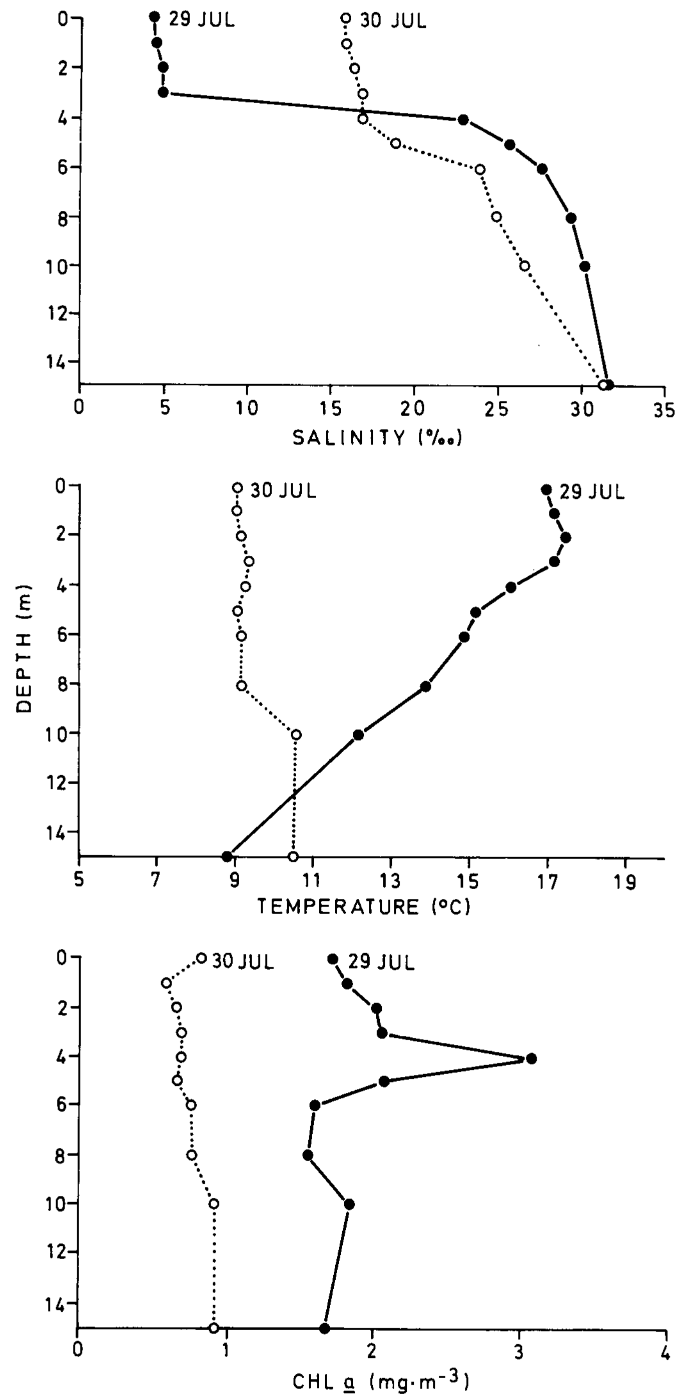

FIG. 4. Salinity, temperature, and Chl *a* at the head of Hylsfjorden (Stn. 50) prior to and after the start of the power plant.

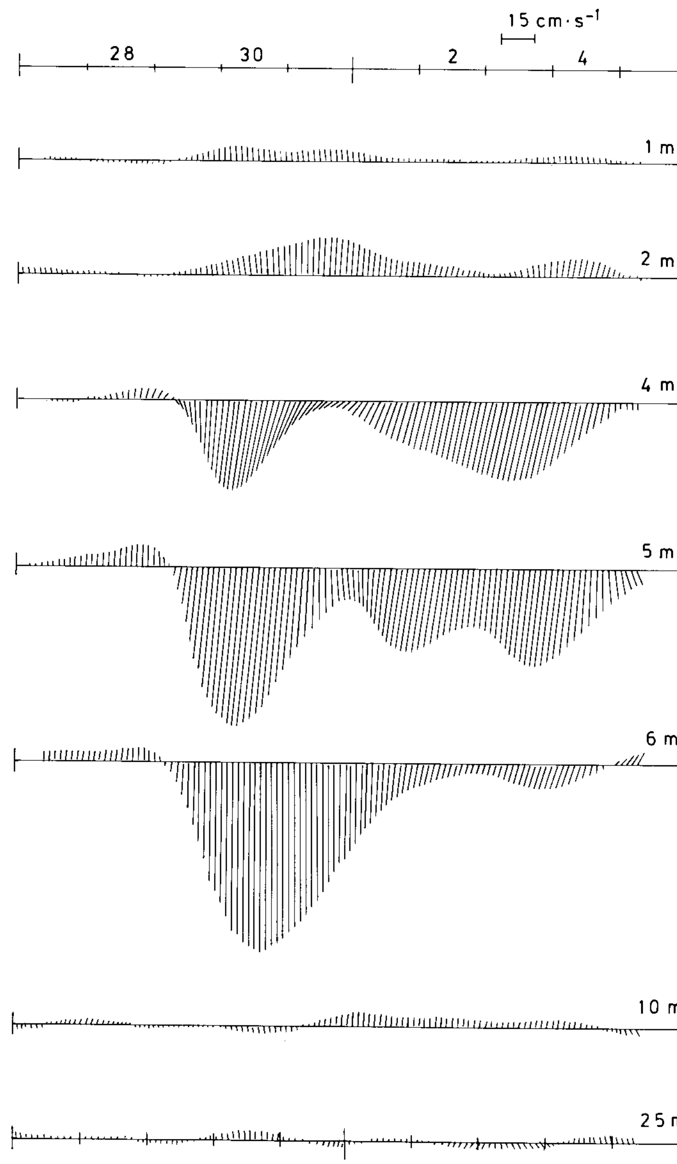

FIG. 5. Current velocities in the inner part of Hylsfjorden (Stn. 51) showing low velocities prior to the start of the power plant and an outwardly directed current beneath the surface layer in response to freshwater discharge from the power plant. The horizontal axis represents dates in July–August 1989. Downward lines represent outgoing currents and upward lines represent ingoing currents.

at the onset of the discharge from the Hylen power plant (Fig. 4). Temperature decreased by 8°C and salinity increased by 12‰ in the upper layer of the mixing zone. This new water mass (henceforth denoted discharge water mass; DWM) consequently had higher density than the surface water elsewhere in the fjord system, and a normal estuarine circulation was not generated. Instead, the DWM submerged beneath the existing surface water in a clearly separate frontal zone in inner Hylsfjorden (located between Stns. 50 and 51) and proceeded as an outwardly directed current at between 3 and 8 m (Fig. 5 and 6).

Algae were transported outwards with the freshwater-driven currents, and Chl *a* decreased considerably at the head of the fjord (Stn. 50) from 29 to 30 July (Fig. 4). Further out in Hylsfjorden, the DWM appeared as a cold core with reduced Chl *a* values (Fig. 6). This cold-water core was observed throughout Hylsfjorden, but on 30 July there were no recognizable effects further out in the fjord system.

Observations on 2 August demonstrated that relatively low-salinity water flowed out of the fjord. At the outlet of Sandsfjorden, the salinity was 17‰ towards the northern shore, i.e. 10‰ lower than 5 d earlier (see later). Current meters at the outlet of Sandsfjorden revealed outgoing currents in the upper 10 m.

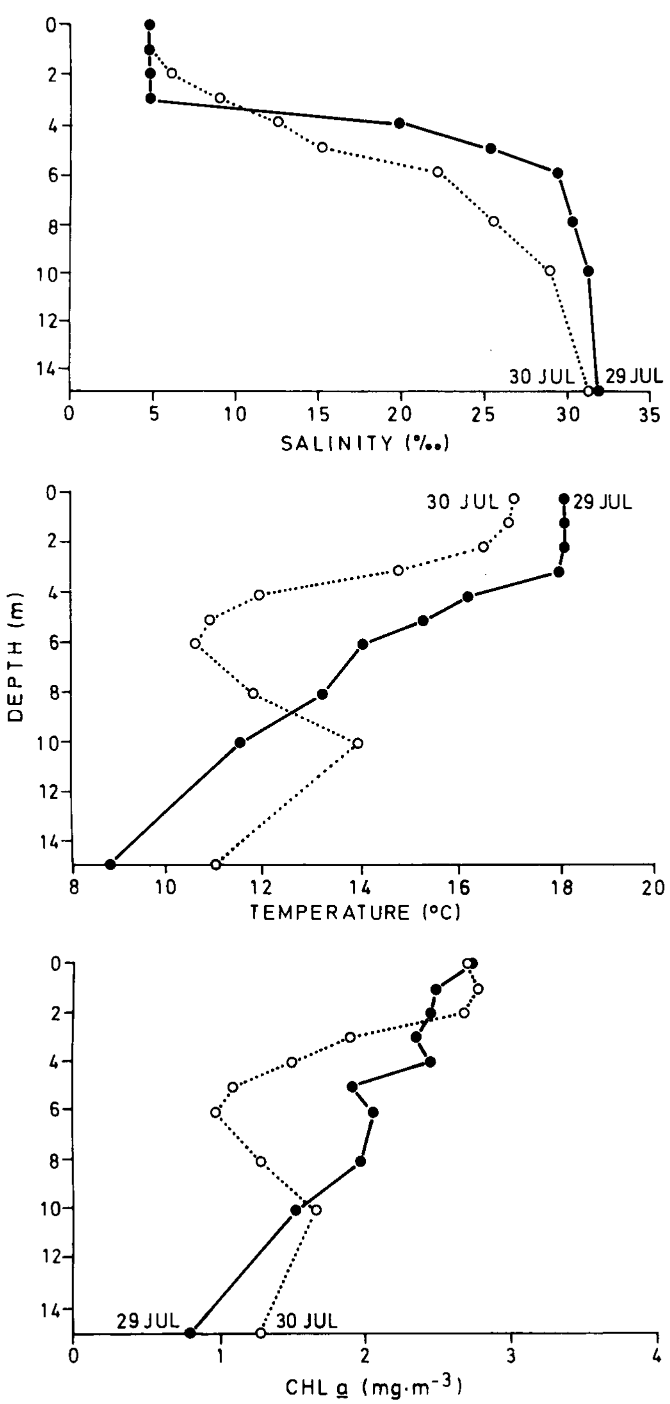

FIG. 6. Salinity, temperature, and Chl *a* near the location of first fish mortality (St. 53) prior to and after the start of the power plant. The discharge water mass (DWM) is recognized as a cold core with reduced Chl *a* content.

Algal Concentrations and Fish Kills

Pelagic algal concentrations were an order of magnitude lower than generally found in association with fish kills, and Holdway et al. (1978) stated that 10^7–10^8 cells·L^{-1} is necessary to provoke mortality. However, we repeatedly observed high concentrations of *P. parvum* from benthic samples, a previously unreported association (Johnsen and Lein 1989). *Prymnesium parvum* seemed to be specifically associated with the green macroalgae *Cladophora* spp. By shaking *Cladophora* in water, concentrations up to 400 × 10^6 cells·L^{-1} were obtained. Estimates based on a sample taken from 1 m^2 of shoreline (15 August) densely covered with *Cladophora* gave an abundance of 10^{10} cells·m^{-2}.

Toxic pockets of water, without high concentrations of cells, may have developed nearshore or at other benthic accumulations of *P. parvum*, since *P. parvum* excretes its toxins into the surrounding water (Otterstrøm and Steemann Nielsen 1939; Shilo and Aschner 1953). It is likely that accumulation of *P. parvum* took place on nets of fish cages, which may have caused toxic waters in the vicinity of large concentrations of fish. *Prymnesium parvum* had a high affinity for attachment to benthic substrate, and repeated fouling of fish nets (*P. parvum*) was observed even when these had been in the water for only a few hours. Accumulations on fish cages cannot, however, explain all incidences of mortality in the fjord system, as salmon also occasionally died in boats used to monitor the distribution of poisonous water (Institute of Marine Research, Bergen).

Phosphorus-limited growth was probably essential for the poisonous effect of *P. parvum*. With phosphorus limitation, toxicity increases with a factor of 10–20 (Shilo 1967), and without phosphorus limitation, the species may be found in large concentrations without affecting fish (Holdway et al. 1978; Shilo 1981). The freshwater supplying the brackish fjord water with nutrients had relatively high concentrations of silicate and nitrate, but low concentrations of phosphate (Table 2). The N:P values in the surface layer of the fjord system accordingly were much higher than the Redfield ratio of 16 (Table 3). Phosphorus limitation in the brackish layer was also indicated by high phosphatase activity in August 1989 (T. F. Thingstad, Department of Microbiology and Plant Physiology, University of Bergen, pers. comm.).

TABLE 2. Concentrations (μM) of silicate (S), nitrate (N), and inorganic phosphate (P) in the main freshwater sources during spring and summer 1989. Phosphate values were below the detection level of 0.05. Number of samples is given by *n*.

	n	S	N	P
Suldalslågen, March–July	17	15.0	12.6	<0.05
Hylen power plant, March–June	12	13.8	10.3	<0.05

TABLE 3. Average ratios between nitrate and inorganic phosphate (N:P) with 95% confidence intervals showing values much higher than the Redfield ratio in freshwater and in surface waters inside the fjord system. When phosphate was below the detection level, the value was set at 0.05 μM. Results from previous investigations are given, where data from all stations and times of the year are combined. Number of samples is given by *n*.

	n	N:P
Surface water		
Inside Sandsfjorden, 1987–89	102	47 ± 6
Inside Sandsfjorden, July–August 1989	18	64 ± 10
Outside Sandsfjorden, 1987–89	50	12 ± 3
Freshwater		
Suldalslågen, 1988–89	18	173 ± 42
Hylen power plant, 1988–89	16	143 ± 28
Other sources, 1988–89	10	165 ± 134

Conditions for Growth of *P. parvum*

In determining favorable conditions for *P. parvum* to multiply, it is essential to identify ecological characteristics which distinguished Hylsfjorden (where *P. parvum* apparently was first established) from the rest of the fjord system. These include the residence time, temperature, and nutrient dynamics of the brackish water. Human impacts on the environment comprise aquaculture, which expanded markedly in the 1980s, and the establishment of the Hylen power plant which started operating in 1980.

Salinity

All fjord branches were characterized by a conspicuous brackish surface layer. During the end of July (27–28), surface salinities were 4–5‰ through most of the fjord system. In outer regions (outside Stn. 64), surface salinity increased seaward and was 27‰ at the outlet of Sandsfjorden (Stn. 69). The low salinity of the brackish layer probably was important for the occurrence of *P. parvum*. The salinity of the brackish layer in July–August 1989 was similar to that found in many other systems where *P. parvum* has caused fish mortalities (Otterstrøm and Steemann Nielsen 1939; Krasnoshchek et al. 1972; Hickel 1976; Comin and Ferrer 1978; Holdway et al. 1978), and laboratory experiments with *P. parvum* from the fjord system showed that growth was inhibited in salinities exceeding 20‰ (Kaartvedt et al. 1990). The salinity alone, however, can neither explain why the event was initiated in Hylsfjorden nor why *P. parvum* appeared in 1989. There were no differences in salinity between the fjord branches, and results from baseline studies prior to the hydroelectric development show nearly identical surface salinities (Svendsen 1981; Kaartvedt et al. 1990).

Temperature

The highest temperature (18.5°C) was recorded in Hylsfjorden (Fig. 2), where the surface water represents a backwater when the power plant is shut down. *Prymnesium parvum* thrives in "a mild climate" (Collins 1978), and the high temperatures in Hylsfjorden in July 1989 may have favored the alga in this fjord branch compared with the colder water in other parts of the fjord system. However, while *P. parvum* flourishes in warmwater fish ponds in Israel (e.g. Shilo 1971), blooms with associated fish deaths have also been reported in waters with temperatures down to 5°C (Otterstrøm and Steemann Nielsen 1939; Krasnoshchek and Abramovich 1971).

Nutrients

Nutrient concentrations in the "old" brackish layer of Hylsfjorden were much lower than in Sandsfjorden (Fig. 7) and Saudafjorden, which received large amounts of nitrate and silicate from river runoff. Phosphate levels of the brackish water were, on the other hand, low throughout the fjord system (0.05–0.1 μM). The two fish farms in Hylsfjorden do, however, represent major nutrient sources. Fertilization associated with fish farming seems to create favorable conditions for *P. parvum* (Collins 1978; Holdway et al. 1978), and *P. parvum* has repeatedly been found in association with fish farming in brackish water (Reich and Aschner 1947; Shilo 1967, 1971; Krasnoshchek and Abramovich 1971; Krasnoshchek et al. 1972; Hickel 1976). Estimated phosphorus loading from the two fish farms in Hylsfjorden is about 10 kg water-soluble phosphate$\cdot d^{-1}$ (Kaartvedt et al. 1990). This amount of phosphate could theoretically lead to a daily increase of 10^{16} *P. parvum* cells, given the same phosphorus cell content as in *Chrysochromulina polylepis* (Dahl et al. 1990). Averaged over the entire Hylsfjorden,

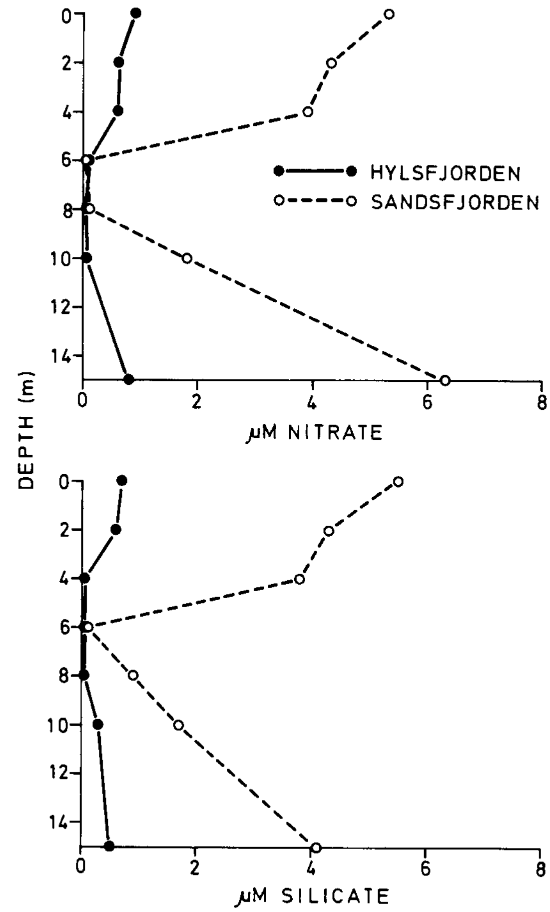

FIG. 7. Nitrate and silicate levels in Hylsfjorden (Stn. 51; 29 July) and Sandsfjorden (Stn. 63; 27 July) prior to initiation of freshwater discharge from the Hylen power plant. Biological consumption had nearly depleted the nutrient reservoir in the "old" Hylsfjord water.

this corresponds to a daily new production of 10^{9}–10^{10} cells$\cdot m^{-2}$, and an accumulated effect involving recycling of nutrients may be expected in the backwaters of this fjord branch. While only a portion of the phosphorus loading will provide growth of *P. parvum*, it is also unrealistic to average the nutrient supply over the entire fjord branch. Currents in Hylsfjorden were weak in July prior to the start of the power plant (e.g. Fig. 5), which enables local establishment of the alga without substantial advective loss and facilitates local utilization of nutrient sources. The results from 29 July, when 10–40 times higher concentrations of *P. parvum* were found close to the fish farm than at midfjord stations (Table 1), substantiate this argument. Benthic settlement of *P. parvum* may also have facilitated increased efficiency in utilization of nutrient release from the fish farms.

Also, discharge from the power plant increases the nutrient input to Hylsfjorden. The power plant is usually not operated in June–July, but in June 1989, extra silicate and nitrate were supplied due to ancillary operation of the plant. The freshwater discharge, however, makes the nutrient regime of this fjord branch more similar to the rest of the fjord system. Actually, the low silicate level which develops in Hylsfjorden when the power plant is shut down should favor flagellates over diatoms in this part of the fjord system (Officer and Ryther 1980).

Conclusion

Prymnesium parvum germinated in the low-salinity water of a fjord branch characterized by long residence time of the brackish water. This led to relatively high temperatures, depletion in nitrogen and silicate derived from the freshwater, and low advective loss of algae. Low exchange rates and benthic association may also have facilitated an accumulated effect of continuous nutrient supply from fish farms. *Prymnesium parvum* was advected outwards in currents generated by controlled freshwater discharge from a hydroelectric power plant, which was initiated at the time of the first observed fish mortality. Coincident large runoff from other sources contributed to far-reaching dispersal of the alga out of the fjord system. Phosphorus-limited growth probably was important for the toxicity of the alga.

The present case represents the first report of fish kill by *P. parvum* in a large marine (estuarine) ecosystem and the first example of extensive growth of this phytoflagellate in association with benthic substrate. This extension in type of environment and of growth mode suggests that the alga may become a threat to an expanding marine aquaculture industry, as it has proved to be in inland brackish fish ponds. Our results give a clue to one type of environment which may favor outbreaks. However, the peculiar set of ecological conditions of the microenvironment in which the core population of *P. parvum* developed was in many respects rather similar to previous described locations and atypic to most marine aquaculture sites. In this particular fjord system, the development of future incidents possibly can be manipulated by human control of the freshwater discharge.

Acknowledgements

Berit R. Heimdal and Neil Swanberg gave valuable suggestions for improvements of the manuscript. We thank A. Aadnesen for technical assistance. Figures were drawn by B. Biskopshavn and E. Holm. We thank the captain and crew of RV *Håkon Mosby* for their cooperation and assistance. The investigation was funded by Konsesjonsavgiftsfondet (Norwegian Water Resources and Energy Administration) and Statkraft (Norwegian State Power Board).

References

COLLINS, M. 1978. Algal toxins. Microbiol. Rev. 42: 725–746.

COMIN, F. A., AND X. FERRER. 1978. Desarollo masivo del fitoflagelado *Prymnesium parvum* Carter (Haptophyceae) en une laguna costera del delta del Ebro. Oecol. Aquat. 3: 207–210.

DAHL, E., O. LINDAHL, E. PAASCHE, AND J. TRONDSEN. 1990. The *Chrysochromulina polylepis* bloom in Scandinavian waters during spring 1988, p. 383–405. *In* E. M. Cosper, K. M. Bricelj, and E. J. Carpenter [ed.] Novel phytoplankton blooms. Causes and impacts of recurrent brown tides and other unusual blooms. Springer-Verlag, New York, NY.

HICKEL, B. 1976. Fishsterben in einem Karpfenteich bei einer Massenentwicklung des toxischen Phytoflagellaten *Prymnesium parvum* Carter (Haptophyceae). Arch. Fishereiwiss. 27: 143–148.

HOLDWAY, P. A., R. A. WATSON, AND B. MOSS. 1978. Aspects of the ecology of *Prymnesium parvum* (Haptophyta) and water chemistry in the Norfolk Broads, England. Freshwater Biol. 8: 295–311.

HOLM-HANSEN, O., C. J. LORENZEN, R. W. HOLMES, AND J. D. H. STRICKLAND. 1965. Fluorometric determination of chlorophyll. J. Cons. int. Explor. Mer 30: 3–15.

JOHANNESSEN, T. 1989. Undersøkelser ved algeoppblomstringen i Ryfylkefjordene august 1989, og gjennomgang av lignende oppblomstringer andre steder. Flødevigen Meldinger 8: 29 p. (Available from Institute of Marine Research Flødevigen, N-4817 His, Norway.)

JOHNSEN, T. M., S. KAARTVEDT, AND D. L. AKSNES. 1989. Identifikasjon og tidlige observasjoner av *Prymnesium parvum* blomstringen i Ryflykefjordene, juli–august 1989. IMB Rapp. 15, 1989: 19 p. (Available from Department of Fisheries and Marine Biology, University of Bergen, Norway.)

JOHNSEN, T. M., AND T. E. LEIN. 1989. *Prymnesium parvum* Carter (Premnesiophyceae) in association with macroalgae in Ryfylke, southwestern Norway. Sarsia 74: 277–281.

KAARTVEDT, S., AND H. SVENDSEN. 1990a. Advection of euphausiids in a Norwegian fjord system subject to altered freshwater input by hydro-electric power production. J. Plankton Res. 12: 1263–1277.

1990b. Impact of freshwater runoff on physical oceanography and plankton distribution in a western Norwegian fjord: an experiment with a controlled discharge from a hydroelectric power plant. Estuarine Coastal Shelf Sci. 31: 381–395.

KAARTVEDT, S., T. M. JOHNSEN, D. L. AKSNES, U. LIE, AND H. SVENDSEN. 1990. Giftalgen *Prymnesium parvum* i Ryfylkefjordene, juli–august 1989. IMB Rapp. 2, 1990: 68 p. (Available from Department of Fisheries and Marine Biology, University of Bergen, Norway.)

KRASNOSHCHEK, G. P., AND L. S. ABRAMOVICH. 1971. Mass development of *Prymnesium parvum* Cart. in fish-breeding ponds. Hydrobiol. J. 7(3): 54–55.

KRASNOSHCHEK, G. P., L. S. ABRAMOVICH, AND V. R. SHEMCHUK. 1972. A new case of massive development of *Prymnesium parvum* (Cart.). Hydrobiol. J. 8(5): 80.

OFFICER, C. B., AND J. H. RYTHER. 1980. The possible importance of silicon in marine eutrophication. Mar. Ecol. Prog. Ser. 3: 83–91.

OTTERSTRØM, C. V., AND E. STEEMANN NIELSEN. 1939. Two cases of extensive mortality in fishes caused by the flagellate *Prymnesium parvum* Carter. Rep. Danish Biol. Stn. 44: 5–24.

REICH, K., AND M. ASCHNER. 1947. Mass development and control of the phytoflagellate *Prymnesium parvum* in fishponds in Palestine. Palest. J. Bot. Ser. 4: 14–23.

SHILO, M. 1967. Formation and mode of action of algal toxins. Bacteriol. Rev. 31: 180–193.

1971. Toxins of crysophyceae, p. 67–103. *In* S. Kadis, A. Ciegler, and S. J. Ajl [ed.] Microbial toxins 7. Algal and fungal toxins. Academic Press, London.

1981. The toxic principle of *Prymnesium parvum*, p. 37–47. *In* W. W. Carmichael [ed.] The water environment. Plenum Press, New York, NY.

SHILO, M., AND M. ASCHNER. 1953. Factors governing the toxicity of cultures containing the phytoflagellate *Prymnesium parvum* Carter. J. Gen. Microbiol. 8: 333–343.

SVENDSEN, H. 1981. A study of circulation and exchange processes in the Ryfylkefjords. Doctoral thesis, University of Bergen, Norway.

VALKANOV, A. 1964. Untersuchungen über *Prymnesium parvum* Carter und seine toxische Einwirkung auf die Wasserorganismen. Kiel. Meeresforsch. 20: 65–81.