Vol. 30: 287–290, 1985 | MARINE ECOLOGY – PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published May 22

NOTE

Fate and possible effects of excessive sperm released during spawning

I. E. D. Dundas

Department of Microbiology and Plant Physiology, University of Bergen, Allegaten 70, N-5000 Bergen, Norway

ABSTRACT: A great number of marine animals rely on communal spawning for procreation. Male gonad material released during spawning represents a significant proportion of the total biomass of the population. Only insignificant proportions of this material are functional in fertilization, the remainder represents a nutritional input to phagotrophic and osmotrophic microbial food webs, allowing increased productivity at this level of the ecosystem. Degradation of male gonad material also results in increased nutrient availability for eventual phytoplankton productivity. The extent to which this might influence survival of fish larvae is discussed.

A great number of marine animals rely on sexual mechanisms involving external fertilization, spawning, for procreation. Spawning entails the release into the water of massive amounts of male gonad material, only a minimal fraction of which is directly involved in fertilization. Male gonads comprise from some 20 % (herring and mackerel) to about 10 % (codfish and haddock) of live spawn-ripe individual fish weight. Accordingly, material corresponding to some 5 % to 10 % of spawning fish biomass may be released into the water as sperm and sperm fluid during spawning. During spawning of herring under natural conditions the water may become visibly discolored, due to the massive release of sperm (Hourston & Rosenthal 1976).

Little work seems to have been done to investigate the fate of surplus sperm material. Microscope observations in our laboratory show that fresh cod sperm cells quickly lyse and release sperm head material on exposure to sea water. Less than 10 % of the sperm cells maintain structural integrity 10 min after exposure.

Diluting 1 ml of freshly stripped codfish milt into 1 l of sea water supports massive bacterial growth. Microscope observation shows that bacteria also rapidly colonize cellular debris remaining after sperm cell lysis (author's unpubl. results).

Influence of spawning location and timing on recruitment. Survival of cod larvae is dependent on food availability at a critical stage when the yolk sac just has been resorbed (Solberg & Tilseth 1984). Already in 1914 Hjort (1914) suggested that cod stock recruitment depended on the degree of temporal matching between peak spawning and peak production of adequate food for larvae. It has been shown that the minimum food requirement of cod larvae at the critical stage is higher than the average food availability in the environment (Solberg & Tilseth 1984). Vlymen (1977) suggested that larval survival is dependent on a spatial matching of larvae and patches of water with higher than average densities of larval prey. It has been proposed that recruitment is enhanced if fertilized eggs and emerging larvae of herring (Iles & Sinclair 1982) and haddock (Smith & Morse 1985) remain in a restricted water mass such as that represented by the rather stable gyre on Georges Bank off New England. This gyre has an extension of about 10,000 km^2 (Iles & Sinclair 1982) with a depth of some 40 m corresponding to a volume of 4×10^{11} m^3. The water in the gyre has a long volume replenishing time on the order of months (Hopkins & Garfield 1981). Iles & Sinclair (1982) also suggested that in general herring stock sizes are limited by the size of the larval retention areas available for the spawning populations. Serebryakov et al. (1984) argue that the magnitude of the spawning biomass is a major factor deciding recruitment efficiency of Arcto-Norwegian cod.

The 2 general views, that the retention of larvae in discrete water masses is important for recruitment, and that the size of spawning biomass is important for recruitment, may be reconciled if both mechanisms increase the probability of a temporal and spatial match between the fish larvae and their food in the critical survival period. Such would be the case if excess male gonad products released during spawning were partially instrumental in triggering microbial productivity and increasing the availability of ade-

0171-8630/86/0030/0287/$ 05.00

quate larval prey at the critical stage. Any mechanism increasing food availability at the critical stage, even if only marginally, may have significant effects on population recruitment.

Effect of excess spawning materials on microbial populations. The normal microbial food web in natural sea water includes bacterial populations with densities of 1×10^5 to 1×10^6 cells ml^{-1} utilizing both soluble and particulate material as nutrient, microbial populations of microflagellates with densities of about 1×10^3 cells ml^{-1} utilizing particulate material in the proper size range (including bacteria) as nutrient, and populations of larger phagotrophic microorganisms (Azam et al. 1983).

Fish sperm and sperm debris after lysis represent a nutritional input to phagotrophic microbial populations of flagellates and ciliates. Because cod sperm tend to lyse and disintegrate shortly after release, much of the soluble content of sperm, largely nucleic acid (DNA) and nucleohistones, represents a nutritional input to the normal bacterial flora in the water mass. The release of large amounts of 'excessive' male gonad products during spawning would accordingly increase productivity in microplankton food webs able to utilize and degrade the released particulate and soluble material.

It has been suggested that gonadal products may significantly increase secondary productivity when herring spawn in the Strait of Georgia (Hay & Fulton 1983). Nucleic acid and nucleohistones are so rich in organic nitrogen and phosphate that any organism utilizing such materials as nutrients must excrete large amounts of the ingested material as inorganic or organic nitrogen and phosphate. The degradation products from sperm material may later become available for primary productivity, possibly influencing timing, productivity and species composition of phytoplankton blooms. Such effects would depend on hydrologic conditions, transporting, dispersing and diluting sperm material and its degradation products.

Microbial degradation of excess male gonad material. Each year between the middle of March and the middle of April spawn-ripe codfish congregate off Lofoten islands in Norway. The size of the spawning population has been estimated to be 80 million individuals in 1982 (Nakken 1984), roughly corresponding to a biomass of some 320 million kg, assuming an average weight of 4 kg. Assuming a 50 % male population and a male gonad weight amounting to 10 % of body weight, rougly 16 million kg of male cod gonad material may be released during spawning. Cod male gonads have a dry matter content of about 16 % of wet weight (Boge & Braekkan 1974) while freshly stripped milt has a dry weight content as low as 8.1 % with a phosphorus content of 2.4 %, a nitrogen content of 12.8 % and a carbon content of 47 % (author's unpubl. results).

If 1.6 million kg dry weight male gonad material is released, 38 metric tons of phosphorus, 205 metric tons of nitrogen and 752 metric tons of carbon are made available as soluble and particulate organic material. This material would directly increase secondary productivity in the microbial food web while primary productivity would be enhanced only after degradation of the released material. The degraded material could increase phosphate concentration by some 0.1 $\mu g\text{-at } l^{-1}$ and the bound nitrogen concentration by more than 1.0 $\mu g\text{-at } l^{-1}$ in a water mass of 1.2×10^{13} l, corresponding to a water column 50 m deep with an extension of 240 km^2.

The above calculations refer only to the spawning biomass of codfish off Lofoten. In 1982 some 90 million individuals of Arcto-Norwegian codfish spawned at selected sites south and north of Lofoten (Nakken 1984). Simultaneous massive spawning by large populations of Norway pout in the same area also contributed to increased availabilty of nutrients for secondary and primary production.

Due to the permanence of the water mass on Georges Bank, all the various fish populations spawning on the bank will directly contribute in increasing nutrient concentrations in the water mass where their eggs will hatch and their larvae forage. In this case the same water mass functions as a spawning and as a nursery area. The more complex hydrological conditions off the Norwegian coast makes it difficult to infer to what extent excess sperm degradation products could affect conditions in the nursery areas. Relatively stable gyres do seem to occur also in this area (Sundby 1983), affecting the concentration patterns of fertilized eggs and larvae.

Table 1 lists some major actual and potential spawning populations of fish and gives the corresponding amounts of released male gonad material. The potential primary productivity calculated on the basis of released nitrogen is larger than the immediately available carbon from released sperm, reflecting the much higher N/C ratio of sperm material compared to phytoplankton biomass. Table 1 also attempts to compute the water masses in which the produced male gonad material could increase the concentration of phosphate and bound nitrogen by respectively 1 and 10 $\mu g\text{-at } l^{-1}$. While such concentrations only correspond to a doubling of the normal concentrations in deeper water, it must be reemphasized that even small effects, slightly enhancing the probability that larvae encounter a patch of suitable prey, may be significant for recruitment.

The time required for hatching of codfish eggs, some 2 to 3 wk, depending on the temperature (Solberg &

Table 1. Male gonad material released during spawning of some actual and potential fish stocks. SB: spawning biomass; GM: dry weight of spawned male gonad material; P: phosphorus in male gonad material; N: nitrogen in male gonad material; C: carbon in male gonad material; PP: potential primary productivity after complete mineralization; E: extension of a water column 50 m deep with a 10 µg-at l^{-1} increase in nitrogen due to release of milt

Species	Stock	SB ($\times 10^6$ kg)	GM ($\times 10^6$ kg)	P[h] ($\times 10^3$ kg)	N[h] ($\times 10^3$ kg)	C[h] ($\times 10^3$ kg)	PP[i] ($\times 10^3$ kg)	E (km^2)
Herring	Norwegian	10,000[a]	240 [d]	5,800	30,720	112,800	174,933	4,389
Herring	Nova Scotia	400[a]	9.6[d]	230	1,228	4,512	6,993	184
Herring	Icelandic	200[a]	4.8[d]	115	614	2,256	3,496	88
Herring	Georges Bank	1,000[a]	24 [d]	580	3,072	11,280	17,493	439
Codfish	Arcto-Norwegian (1982)	680[b]	3.4[e]	82	435	1,598	2,477	62
Codfish	Arcto-Norwegian (1946)	1,240[c]	6.2[e]	148	793	2,914	4,516	113
Codfish	Arcto-Norwegian		186 [f]	4,464	23,808	87,420	135,573	3,401
Codfish	Icelandic		22 [f]	528	2,816	10,340	6,035	402
Codfish	North Sea		1.7[g]	41	218	799	1,241	31
Haddock	North Sea		3.3[g]	79	422	1,550	2,403	60
Whiting	North Sea		5.7[g]	137	730	2,680	4,157	104

[a] From Iles & Sinclair (1982), assuming lightly harvested stocks
[b] From Nakken (1984), assuming an average individual weight of 4 kg
[c] From Serebryakov et al. (1984)
[d] Assuming 50% males, male gonads to be 20% of body weight with 24% dry weight (Boge & Braekkan 1974, Souci et al. 1962)
[e] Assuming 50% males, male gonads to be 10% of body weight and a gonad dry matter content of 10%
[f] From Garrod & Horwood (1984), assuming unharvested stock size, and dry weight of spawned male gonad material to be 50% of the dry weight of spawned eggs
[g] From Hislop (1984), assuming dry weight of spawned male gonad material to be 50% of dry weight of spawned eggs
[h] Assuming male gonad material to contain 2.4% P, 12.8% N and 47% C on a weight basis
[i] Carbon fixed by primary productivity, assuming complete mineralization of excess gonad material and a C/N ratio in phytoplankton of 41/7.2 on a weight basis

Tilseth 1984), allows ample time for extensive microbial degradation of excess sperm material. While increased productivity in heterotrophic food webs should be an immediate effect of sperm release, partial degradation products of sperm DNA, such as guanine and hypoxanthine, may also affect primary productivity (Antia et al. 1980) even before complete mineralization of excess sperm.

Acknowledgements. This work has been supported in part by the Norwegian Council for Fisheries Research, Grant No. I 101.07 The manuscript was written during a sabbatical leave at the Department of Microbiology, Oregon State University. I am grateful for help and advice from R. L. Smith and W. G. Pearcy on matters related to physical oceanography and fisheries biology and to R. Y. Morita for help, hospitality and lively discussions.

LITERATURE CITED

Antia, N. J., Berland, B. R., Bonin, D. J. (1980). Proposal for an abridged nitrogen turnover cycle in certain marine planktonic systems involving hypoxanthine-guanine excretion by ciliates and their reutilization by phytoplankton. Mar. Ecol. Prog. Ser. 2: 97–103

Azam, F., Fenchel, T., Field, J. G., Gray, J. S., Meyer-Reil, L. A., Thingstad, F. (1983). The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Ser. 10: 257–263

Boge, G., Braekkan, O. R. (1974). Inositol i norsk fisk og fiskeprodukter. Tidsskrift for Hermetikkindustri 60: 240–243

Garrod, D. J., Horwood, J. W. (1984). Reproduction strategies and the response to exploitation. In: Potts, G. W., Wootton, R. J. (ed.) Fish reproduction: strategies and tactics. Academic Press, New York, p. 367–384

Hay, D. E., Fulton, J. (1983). Potential secondary production from herring spawning in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 49: 109–113

Hislop, J. R., G. (1984). A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the North Sea. In: Potts, G. W., Wootton, R. W. (ed.) Fish reproduction: strategies and tactics. Academic Press, New York, p. 311–329

Hjort, H. (1914). Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 20: 1–228

Hopkins, T. S., Garfield, N., III. (1981). Physical origins of Georges Bank water. J. mar. Res. 39: 465–500

Hourston, A. S., Rosenthal, H. (1976). Sperm density during active spawning of Pacific herring *(Clupea harengus pallasi)*. J. Fish. Res. Bd Can. 33: 1788–1790

Iles, T D., Sinclair, M. (1982). Atlantic herring, stock discreteness and abundance. Science 215: 627–633

Nakken, O. (1984). Acoustic estimates of spawning cod in the Lofoten area in 1982 and 1983. In: Godo, O. R., Tilseth, S. (ed.) The proceedings of the Soviet-Norwegian symposium on reproduction and recruitment of Arctic cod. Institute of Marine Research, Bergen, Norway, p. 99–115

Serebryakov, V. P., Borisov, V. M., Aldonov, V K. (1984). Population fecundity and abundance of year-classes of the Arcto-Norwegian cod. In: Godo, O. R., Tilseth, S. (ed.) The Proceedings of the Soviet-Norwegian symposium on reproduction and recruitment of Arctic cod. Institute of Marine Research, Bergen, Norway, p. 139–156

Smith, W. G., Morse, W. W. (1985). Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. Mar. Ecol. Prog. Ser. 24: 1–13

Solberg, T., Tilseth, S. (1984). Growth, energy consumption and prey density requirements in first feeding larvae of cod (*Gadus morhuae* L.). Flodevigen rapportser 1: 145–166

Souci, S. W., Fachmann, W., Kraut, H. (1962). Die Zusammensetzung der Lebensmittel. Wissenschaftliche Verlagsgesellschaft, Stuttgart

Sundby, S. (1983). Influence of bottom tophography on the circulation at the continental shelf of northern Norway. Norwegian Fisheries Research Institute. Report No. FO 8308, p. 1–30 (Mimeo)

Vlymen, W. J., III. (1977). A mathematical model of the relationship between larval anchovy *(Engraulis mordax)* growth, prey microdistribution, and larval behaviour. Environ. Biol. Fish. 2: 211–233

Accepted for printing on January 14, 1986