J. Fish Biol. (1971) 3, 207–219

The interrelation of the size of fish eggs, the date of spawning and the production cycle

T. B. BAGENAL
Freshwater Biological Association, The Ferry House, Ambleside, Westmorland, England

(*Received 7 August 1970*)

The variability in size of pelagic and demersal marine and freshwater fish eggs is examined. The difference between the smallest and largest volumes, based on published figures for the diameters, is large in many species. In marine species with planktonic eggs, the median percentage difference is just over 100%, and this is similar in species with demersal eggs and in freshwater fish.

The available evidence suggests that geographical differences in egg size are small, but in marine fish there is a well-known seasonal decline in egg size. In herring it has previously been shown that egg size in different spawning groups can be correlated with the timing of the production cycle. A similar correlation can be seen in the seasonal shift in time and locality of spawning, and egg size, of the plaice. Sufficient data on seasonal freshwater fish egg variations are not available, but the time of spawning does appear to be linked with the availability of food for the larvae in both lake and stream species.

I. INTRODUCTION

Although some pelagic marine fish eggs have special markings or shape, most are identified by their size and pigment characters. Many newly fertilized eggs, however, are unpigmented and the diameter is the main distinguishing feature. For this reason the diameters of the commonest species are well documented (Ehrenbaum, 1905–09, 1911; Simpson, 1956; Hiemstra, 1962). The purpose of this paper is to examine the variability in egg size and compare that found in planktonic marine eggs with that of demersal marine and freshwater eggs. This variability will be considered in relation to its possible ecological significance, geographical variations, the fecundity of the female parent and the food supply of larvae.

II. THE VARIATION IN FISH EGG SIZE

1. MARINE PLANKTONIC EGGS

(a) *Total variation*

The ranges in diameter of planktonic eggs in the North Sea and adjacent areas (excluding the Baltic) are given by the International Council for the Exploration of the Sea (Ehrenbaum, 1911). The range is not ideal as a measure of variability since it increases with sample size, so the range in egg diameter is likely to be larger with the commoner species than with the rarer ones. However it is the only statistic available for most species and will be sufficient for our purposes here. From the diameters the volumes have been calculated for each species, and the difference between the smallest and the largest has been expressed as the percentage increase over the smaller volume. The results are given in Table I. The volumes have been used in the calculations since they reflect more closely than do the diameters the amount of yolk in the eggs. In herring *Clupea harengus* L. (Blaxter & Hempel, 1963) and trout *Salmo trutta* L., both of which lay demersal eggs, the egg size is related to the amount of yolk present. It has been shown by Holliday & Jones (1967) that the concentration of the yolk in plaice *Pleuronectes platessa* L. eggs can be regulated from the time of fertilization and in

TABLE I. The volume (mm^3) of large and small eggs and the difference expressed as a percentage of the smaller volume of 46 marine species of fish with planktonic eggs. Based on Ehrenbaum (1911)

Species	Smaller volume	Larger volume	% difference
Engraulis encrasicolus	0·18	0·90	403·8
Sardina pilchardus	1·77	3·05	72·8
Sprattus sprattus	0·29	0·97	237·5
Argentina silus	14·14	22·45	58·8
Argentina sphyraena	2·57	3·32	28·9
Merlangius merlangus	0·48	1·20	152·0
Trisopterus luscus	0·48	0·97	103·9
Trisopterus esmarkii	0·52	0·76	44·3
Trisopterus minutus	0·45	0·64	42·9
Pollachius pollachius	0·70	0·95	36·4
Pollachius virens	0·57	0·95	66·2
Gadus morhua	0·82	2·14	162·4
Melanogrammus aeglefinus	0·88	2·44	176·4
Brosme brosme	1·05	1·84	75·6
Physis blennoides	0·27	0·36	33·1
Merluccius merluccius	0·43	0·57	31·6
Molva molva	0·48	0·76	58·1
Raniceps raninus	0·22	0·39	78·6
Capros aper	0·38	0·54	41·3
Trachurus trachurus	0·28	0·59	111·7
Mullus surmuletus	0·28	0·39	41·8
Ctenolabrus rupestris	0·20	0·43	122·5
Trachinus vipera	0·5	1·1	101·2
Trachinus draco	0·43	0·72	64·7
Scomber scombrus	0·48	1·38	188·0
Callionymus lyra	0·17	0·43	152·8
Trigla spp.	0·70	2·14	207·7
Scophthalmus maximus	0·39	0·89	126·5
Scophthalmus rhombus	0·82	1·80	120·6
Zeugopterus punctatus	0·41	0·64	57·3
Phrynorhombus regius	0·38	0·51	33·1
Phrynorhombus norvegicus	0·20	0·49	152·2
Lepidorhombus whiffiagonis	0·64	0·95	48·2
Arnoglossus spp.	0·11	0·23	103·2
Limanda limanda	0·15	0·49	227·4
Platichthys flesus	0·29	0·76	161·7
Pleuronectes platessa	2·40	5·58	132·8
Microstomus kitt	0·76	1·60	111·3
Glyptocephalus cynoglossus	0·64	1·02	59·4
Hippoglossoides platessoides	1·38	22·45	1531·4
Hippoglossus hippoglossus	14·14	40·19	184·3
Pegusa lascaris	1·32	1·38	4·5
Solea solea	0·45	2·07	360·0
Buglossidium luteum	0·17	0·43	152·8
Microchirus variegatus	1·10	1·32	19·9
Lophius piscatorius	5·06	6·88	36·0

this way the buoyancy is maintained. The size of the eggs must therefore be related to the amount of yolk present even in these pelagic eggs. It has been shown by Gray (1928), Smith (1958), Blaxter & Hempel (1963) and Bagenal (1969) that the amount of yolk is of importance in larval growth and survival in trout and herring. It will be noticed in Table I that the variation in the egg volume of some species is very great.

(b) *Seasonal variation*

Planktonic eggs decrease in size as the spawning season progresses, and this is the basis of the correlation table proposed by Hiemstra (1962). Monthly mean egg size for some species are given in the International Council's key, and these are illustrated in Fig. 1.

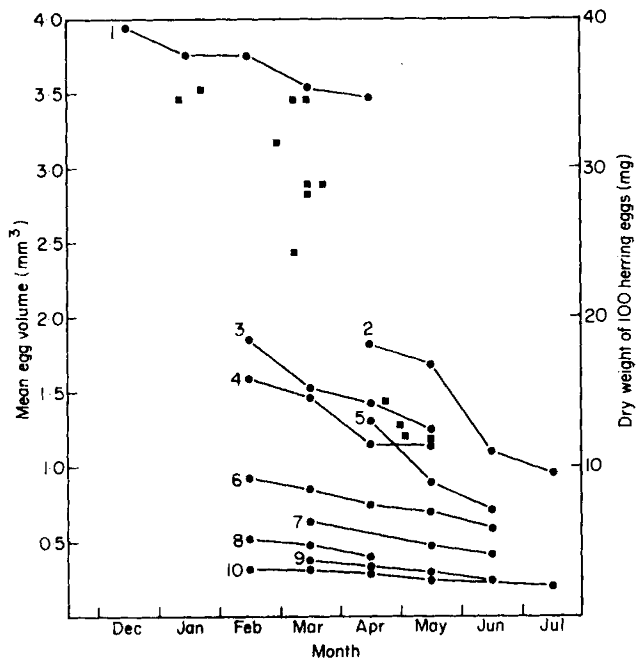

FIG. 1. The seasonal decrease in mean egg volume (mm³) of 1, *Pleuronectes platessa*; 2, *Trigla gurnardus;* 3, *Melanogrammus aeglefinus;* 4, *Gadus morhua;* 5, *Solea solea;* 6, *Merlangius merlangus;* 7, *Sprattus sprattus;* 8, *Platichthys flesus;* 9, *Rhinonemus cimbrius;* 10, *Limanda limanda* (data from Ehrenbaum, 1911).

■, The mean dry weight (mg) of 100 herring eggs derived from different spawning groups (data from Hempel & Blaxter, 1967).

The seasonal decrease in volume cannot be correlated with either sea temperature or salinity. The range of salinity in the North Sea is from about 34 to 35‰, so the volume difference of an egg moved between these extremes would only be in the order of 3%. The temperature tends to reach a minimum in March and then rise steadily. If the size changes were adjusting to temperature induced density changes, the eggs would decrease in volume to March and then increase in size. Fish egg volumes follow a different pattern and fall continuously from January to August. In any case, a temperature change *per se* will not affect the density (Sundnes *et al.*, 1964). It appears therefore that the seasonal change in egg size is a biological rather than a physical phenomenon. Simpson (1959*a*) states that there is a progressive change in the age composition of the spawning female plaice *Pleuronectes platessa* L. in the southern North Sea. The older fish spawn first and the mean age is progressively reduced until catches made over the spawning grounds towards the end of the season are dominated by younger fish. Therefore it seems that in this species the older fish produce the larger eggs, and this is probably true of other species.

Cushing (1967) has shown that the variation in egg size between different spawning groups of herring *Clupea harengus* L. can be correlated with the different timing of the onset of the production cycle as measured by the phytoplankton colour, given and defined by Colebrook & Robinson (1965). The species with planktonic eggs listed in Table I, probably, like the herring, eat little adult plankton when they first feed but mainly eat nauplii and young copepodite stages of copepods and the appendicularians *Oikopleura* and *Fritillaria* (Shelbourne, 1953). Nevertheless as an index of these smaller organisms we can follow Cushing and rely on the abundance of phytoplankton on which they feed rather than rely on the larger stages into which they grow and whose production cycle was lumped by Colebrook & Robinson as "copepods". Cushing gives the form of the production cycle for smaller areas than published by Colebrook & Robinson, and the reproduction of North Sea plaice can be associated with production in these areas.

Some plaice spawn in the Straits of Dover in late December, but the bulk of the Southern Bight stock spawn in late January and the larvae drift northeasterly towards the Dutch coast (Simpson, 1959*a*) through areas labelled Ow in Cushings' fig. 2 reproduced as Fig. 2 in this paper. In this area the production cycle starts in mid-

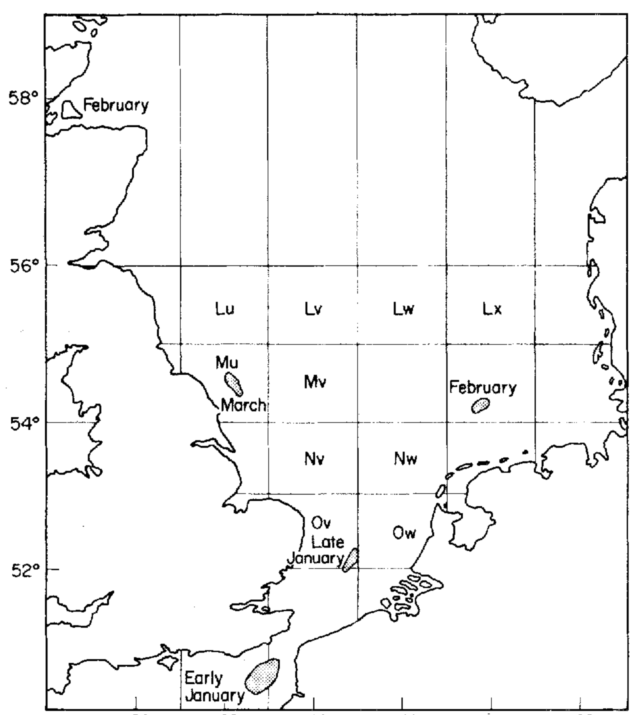

FIG. 2. The stippled areas indicate the centres of spawning activity of plaice *Pleuronectes platessa* and the dates of peak spawning (from Simpson 1959*a*). The sizes of the stippled areas do not indicate the relative importance of the different spawning grounds. The areas whose primary production is mentioned in the text are also indicated (from Cushing, 1967).

February and remains high into July. As the spawning season progresses the areas of peak spawning shift northeasterly across Ow to Nw where the onset of the production cycle is about 1 month later. Using Simpson's figures of 60 days pelagic life at 6·5° C and 144 miles drift, we can see that the earliest spawned plaice in the Straits of Dover would become demersal in Ow, while the bulk of the Southern Bight plaice, spawning further north-east, later, and developing more slowly in water of falling temperature would have drifted to about 54° N and 5° E and so have passed their planktonic feeding life in area Nw where the production cycle commences a month later. This suggests an association between spawning place and time with water temperature and the production cycle.

This association is also illustrated to some extent by the other plaice spawning areas in the North Sea. The peak spawning of Borkum plaice is in mid-February, but unfortunately no production data are available for the area of larval drift in the German Bight and to the Dutch coast, though the nearest area Lx has its peak production in mid March. The peak spawning at the Flamborough Off ground is in March and the eggs and larvae drift in a north westerly direction (Simpson, 1959*a*) over the area Lu where the production rises through April to a peak in May. Turning next to the sizes of these eggs, it has been shown with other species, trout and herring that fry from larger eggs survive longer without food, and it has been shown by Riley (1966) that even slight food scarcity affects plaice larval survival under hatchery conditions. Riley's observations confirm the conclusions reached by Shelbourne (1957) concerning the dependence of the condition of larval Southern Bight North Sea plaice larvae in nature on adequate planktonic food. It is, therefore, reasonable to consider if the egg size variations in plaice and other fish can be linked with the production cycle in a similar way as was suggested by Cushing for herring. The earlier spawned larger eggs hatch to give larvae with larger yolk sacs which are able to survive longer and make more attempts to find food. This search for food has been described by Riley (1966) as follows: "Plaice larvae attempting to feed for the first time took several seconds to adopt the S-flexing of the tail which always precedes the feeding snap; if a larva failed to take a nauplius at the first attempt it would snap three or four times at about 5-sec intervals, but if it failed each time the snapping action was not repeated for some time, often over half an hour, by which time, at least at feeding levels F and E, the food density would already have been appreciably grazed down by those fish which had already established feeding". (Feeding levels F and E were 0·25 and 0·125 of the control level.) Bearing in mind that it has been established with herring and trout that larvae from larger eggs survive longer without food than those from small eggs, it is reasonable to suggest that plaice larvae from large eggs would survive longer searching for food. Those from smaller eggs would require to have hatched nearer the peak of the production cycle, and it seems that the smaller, later spawned eggs hatch to give larvae which are in fact seeking food when the cycle is more advanced, though in some areas, such as Eastern Dogger and Eastern Buchan, the primary production may return to a minimum again by June and July. However the mid-summer decrease does not appear to lead to a reduction in the groups lumped as "copepods" by Colebrook & Robinson.

(c) *Geographical variation*

Egg size data for some species have been published for the Irish Sea (Bal, 1943) and Faxa Bay, Iceland (Einarsson & Williams, 1968) and these have been compared with the North Sea data. The results are given in Table II.

TABLE II. The range in volumes (mm³) of fish eggs from the North Sea, Irish Sea and Faxa Bay, Iceland

Species	North Sea	Irish Sea	Faxa Bay
Sprattus sprattus	0·29–0·97	0·28–0·95	
Argentina sphyraena	2·57–3·32	2·57–3·26	
Merlangius merlangus	0·48–1·20	0·46–1·23	1·07–1·15
Trisopterus esmarkii	0·52–0·76		0·52–0·61
Trisopterus minutus	0·45–0·64	0·38–0·64	
Gadus morhua	0·82–2·14	0·80–2·14	0·80–1·88
Melanogrammus aeglefinus	0·88–2·44		1·05–1·84
Molva molva	0·48–0·76	0·46–0·70	0·61–0·90
Ctenolabrus rupestris	0·20–0·43	0·39–0·62	
Callionymus lyra	0·17–0·43	0·20–0·42	
Trigla spp.	0·70–2·14	0·84–2·19	
Scophthalmus maximus	0·39–0·89	0·43–0·68	
Zeugopterus punctatus	0·41–0·64	0·38–0·66	
Limanda limanda	0·15–0·49	0·20–0·51	0·11–0·52
Pleuronectes platessa	2·40–5·58	2·19–4·45	0·82–4·19
Microstomus kitt	0·76–1·60	0·78–1·70	0·90–1·29
Glyptocephalus cynoglossus	0·64–1·02	0·64–1·00	0·97–1·38
Solea solea	0·45–2·07	0·97–1·56	
Buglossidium luteum	0·17–0·43	0·18–0·24	
Microchirus variagatus	1·10–1·32	1·10–1·50	

The production cycle off southern Iceland is of the "deep water Atlantic" type (Colebrook & Robinson, 1965) and starts about one month later than in the North Sea or "coastal Atlantic" areas. In the North Sea plaice eggs were surveyed by Simpson (1959*a*) from about mid-December to late April. The data given by Einarsson & Williams suggest that plaice eggs could be caught from March to early June. Data for other species are given in Table III, from which it appears that the time of spawning of many Icelandic fish is related to the later start of the production cycle in April.

Production in the Irish Sea itself is not given by Colebrook & Robinson, but if we assume that it is of the "coastal Atlantic" type, we could expect it to increase through February and reach a peak in May, when in the North Sea it is already declining. The Irish Sea plaice have been shown to spawn from late January to the end of March (Simpson 1959*b*) which is later than in the Southern Bight of the North Sea.

It has been shown by Bagenal (1966) that the Irish Sea plaice of 37 cm would be expected to contain about 141 thousand eggs compared with 84 thousand for a comparable fish from the North Sea, which is an increase of about 68 %. Table II indicates that this difference cannot be correlated with egg size. Neither the salinity (33·8 to 34·2‰ Irish Sea; 34 to 35‰ North Sea), nor temperature (4·5 to 7·0° Irish Sea; 4·5 to 6·0° C North Sea) differences can have any significant effect on egg size differences between the two areas.

2. MARINE DEMERSAL EGGS

The size of herring eggs has been studied from numerous points of view, and large differences have been found between spawning groups. Some data taken from

TABLE III. Dates when eggs of various species were collected in Faxa Bay, Iceland in 1948–57 and reported on by Einarsson & Williams (1968)

Brosme brosme	4 June
Molva molva	28 May to 3 June
Trisopterus esmarkii	20 April to 7 June
Merlangius merlangus	20 May to 7 June
Gadus morhua	11 April to 7 June
Melanogrammus aeglefinus	16 April to 7 June
Hippoglossoides platessoides	9 April to 4 June
Pleuronectes platessa	8 April to 4 June
Limanda limanda	11 April to 7 June
Microstomus kitt	30 April to 7 June
Glyptocephalus cynoglossus	4 June

Blaxter & Hempel (1963) are given in Table IV. The data have been treated in a similar way to those of other fish in this paper, but refer to weight and not volume. The significance of the differences in relation to the production cycle has been discussed by Cushing (1967) and need not be considered further here.

TABLE IV. Mean and range of eggs weights of six stocks of North Atlantic herring (from Blaxter & Hempel (1963) table 11)

Group	Spawning time	Mean	Smallest Largest	Range as % of smallest
Norway (old fish)	Early March	34·5	25–44	76·00
(recruits)	Late March	28·9	18–44	144·44
Clyde	Late Feb.–early March	30·0	19–47	147·37
Buchan	Aug.–early Sept.	15·9	12–20	66·67
Dogger	October	26·7	17–42	147·06
Downs	Nov.–Dec.	36·6	27–47	74·07
Kiel	April–May	12·6	9–20	122·22

The range is expressed as a percentage of the smaller weight.

If the mean egg size is considered in relation to the time of spawning, there is a decrease from mid February to May that is greater than the egg size decrease found in planktonic eggs. From June to December mean egg size increases; species with planktonic eggs do not spawn at this time.

The amount of size variation found in the eggs of a few other species which lay marine demersal eggs is given in Table V.

3. FRESHWATER EGGS

Although several freshwater fishes from a number of families lay planktonic eggs, in most the eggs are demersal.

Very few data are available on the geographical and seasonal variations in freshwater egg size. The total variation is given in Table VI, based on data from a variety of sources.

TABLE V. Variation in egg volume of marine fish with demersal eggs (other than herring) from various sources

Species	Smaller volume	Larger volume	Range as a % of smaller volume
Agonus cataphractus	2·57	3·59	39·6
Myxocephalus scorpius	1·77	4·19	137·0
Ammodytes sp.	0·18	0·27	49·3
Taurulus bubalis	2·57	3·59	39·6
Blennius ocellaris	0·74	0·90	23·0

TABLE VI. The volume (mm^3) of large and small eggs and the difference expressed as a percentage of the smaller volume of 27 species of freshwater fish

Species	Smaller volume	Larger volume	% difference	Authority
Esox lucius	8·18	14·14	72·80	Bracken
Cyprinus carpio	1·05	2·62	149·96	&
Abramis brama	2·03	4·19	106·72	Kennedy (1967)
Tinca tinca	0·52	1·44	174·40	
Gobio gobio	1·15	2·35	104·47	
Rutilus rutilus	3·59	5·13	42·88	
Scardinius erythrophthalmus	1·32	2·81	113·06	
Phoxinus phoxinus	1·77	3·05	72·80	
Leuciscus leuciscus	4·19	8·18	95·31	
Noemacheilus barbatulus	0·52	0·90	72·80	
Pungitius pungitius	1·77	2·57	45·57	
Gasterosteus aculeatus	1·77	2·57	45·57	
Salmo salar	65·45	190·59	191·20	Nikolskii (1963)
Oncorhynchus gorbuscha	47·71	143·79	201·37	
Cyprinus carpio	0·38	0·90	137·04	
Perca fluvialitis	4·19	8·18	95·31	
Salmo salar (Norway)	77·95	179·59	130·39	Rounsefell (1957)
(U.S.A.)	82·45	164·64	99·69	
Salmo trutta	54·36	113·10	108·05	
Salmo clarki	41·63	69·46	66·84	
Oncorhynchus tshawyscha	130·92	258·16	97·18	
Cristivomer namaycush	61·60	82·45	33·84	
Salvelinus fontinalis	33·51	44·60	33·10	
Oncorhynchus nerka	77·51	150·53	94·21	Foerster (1968)
Phoxinus phoxinus	1·77	3·05	72·70	Frost (1943)
Salmo salar	65·45	179·59	174·40	Schindler (1953)
Salmo trutta	33·51	87·11	159·96	
Salvelinus alpinus	33·51	47·71	42·38	
Thymallus thymallus	17·16	33·51	95·31	
Coregonus albula	3·05	6·37	108·62	
Esox lucius	8·18	14·14	72·80	
Cyprinus carpio	1·77	4·19	137·04	
Lota lota	0·27	1·77	559·18	
Stizostedion lucioperca	0·52	1·77	237·50	
Perca fluvialitis	4·19	8·18	95·31	
Cottus gobio	4·19	8·18	95·31	

The limited data given in Table VII show geographical variations. Carp egg sizes given by Bracken & Kennedy (1967) for Ireland are considerably larger than those quoted by Nikolskii (1963), and larger than the range for Europe given by Schindler (1953). The differences for pike, minnow, perch and salmon from widely scattered

TABLE VII. The range in egg volumes of 6 freshwater fish species from different localities

	Russia	Germany	Windermere	Ireland	Norway	U.S.A.
Salmo salar	65·45–190·59	65·45–179·59	—	—	77·95–179·59	—
Salmo trutta	—	33·51–87·11	—	—	—	54·36–113·10
Esox lucius	—	8·18–14·14	9·20–12·77	8·18–14·14	—	—
Cyprinus carpio	0·38–0·90	1·77–4·19	—	1·05–2·62	—	—
Phoxinus phoxinus	—	—	1·77–3·05	1·77–3·05	—	—
Perca fluviatilis	4·19–8·18	4·19–8·18	—	—	—	—

Russian data from Nikolskii (1963), German from Schindler (1953), Irish from Bracken & Kennedy (1967), Norway and U.S.A. from Rounsefell (1957), Windermere from Frost (1943) and Frost & Kipling (1967).

localities are either non-existent or negligible. The sizes of some salmonid eggs can vary significantly from one lake or river to another, and some data illustrating this are given in Table VIII.

TABLE VIII. The diameter (mm) of sockeye salmon eggs from 3 localities from 1914 to 1920

	Morris Creek	Harrison Rapids	Cutlus Lake
1914	6·02	6·58	5·49
1915	6·14	6·67	5·46
1916	6·10	6·53	5·52
1917	6·00	6·68	5·40
1918	6·13	6·51	5·39
1919	6·15	6·67	5·43
1920	6·05	6·60	5·48
Average	6·09	6·61	5·46

The figures, adapted from Robertson (1922), are based on the number of eggs filling a trough 1 m long.

The timing of spawning of freshwater fish cannot be as closely linked with primary production curves owing to less dependence of zooplankton in freshwater than in the sea on the primary production. The primary production cycle in Windermere (Talling, personal communication) usually starts to rise in mid-March and reaches a peak in mid-May. The variation in the timing of the spring increase of freshwater planktonic

Crustacea is so great between species that each has to be considered separately (Smyly, personal communication). In most years *Cyclops leukarti* and *C. strenuus* start to increase in numbers around 7 to 14 March and often reach a high level in mid-April which may be continued until July or August. *Bosmina*, which is also an important food of small perch and pike in Windermere, starts to increase later, in early May, and becomes very plentiful in late June and through July. *Daphnia* is plentiful throughout the year apart from December to mid-April.

The spawning and development times of six species that spawn in Windermere are given in Table IX. The autumn spawning char probably find food scarce when they are ready for first feeding in the second half of March, but it is clear that the other species start to feed at a time when the secondary production has already increased considerably. The early diet of perch for example is largely *Bosmina* and the food in the stomachs of fry shows a good correlation with what is in the water (Smyly, 1952). Very small pike eat *Bosmina* and *Chydorus* (Frost, 1954) both of which have increased by mid-May when pike start to feed. The first food of pike is entirely entomostraca until the fish reach about 17·5 mm when aquatic larval insects are also taken. When pike reach about 35 mm they begin to feed on fish (Frost, 1954) and this size is reached in early June, four to seven days after the peak hatching of perch which is their main prey (Table IX). It appears that the spawning season of pike in Windermere is as closely associated with the hatching of perch as with the production cycle of entomostraca which is the first food.

The link between primary production and secondary production in streams is probably even more tenuous than in lakes, owing to the greater importance of detritus and other material of terrestrial origin in the food of invertebrates. The food of brown trout fry in streams when, at about 2·5 cm in length, they first begin to feed, is to a large extent (>50%) dependent on drifting chironomid larvae (McCormack, 1962). In Dartmoor streams in southern England the trout fry of 2·5 cm emerge from the gravel in March and April (Elliott, 1966, 1967) at which time there is a marked increase in the chironomid larvae in the benthos and drift (Elliott, 1967). Although the size variation in trout eggs is well known, how this is associated with the size of the parent or the time of spawning has not been adequately investigated.

III. DISCUSSION

The median percentage difference in egg volume given in Table I for marine species with planktonic eggs is just over 100% and the range is 4·5 to 403% (excluding *Hippoglossoides platessoides* (Fabricius) which has a very large and variable perivitelline space). This variation in egg size is very similar to that found in herring (whose percentage differences in weight range from 66·7 to 147%. Median 122%) and other marine species with demersal eggs (Range 23 to 137%. Median 40%). Furthermore the variation in egg size of marine species is of the same order as is found in freshwater fish (Range 33 to 559%. Median 95%). It is not true to suggest (Simpson, 1951) that planktonic marine fish eggs are less variable in size than those from fresh water.

The data on geographical size variations are meagre but suggest that there are not any very great differences even over quite large distances, except with the anadromous sockeye salmon *Oncorhynchus nerka* which shows consistent differences in egg size between nearby rivers.

TABLE IX. Approximate dates of spawning hatching and first feeding of Windermere fish

Species	Spawning Range	Spawning Approx peak	Incubation days	Peak hatching	Yolk sac absorbed after about	First feeding	Authority
Esox lucius	14 April–7 May	21 April	14–21	*c.* 7 May	9–10 days	*c.* 15 May	Frost & Kipling (1967)
Perca fluviatilis	7 May–7 June	20 May	8 days	28 May	4 days	1 June	Personal observation
Cottus gobio	31 March–15 May	20 April	4 weeks	18 May	4 weeks	15 June	Smyly (1957)
Noemacheilus barbatulus		*c.* 14 May	14–16	*c.* 29 May	6 days	4 June	Smyly (1955)
Salvelinus alpinus		8 Nov.	60–80	1 March		*c.* 20 March	Frost (1965)
		22 Feb	70–80	Late April		*c.* 21 May	Frost (1965)
Phoxinus phoxinus	May–July	June	4–5	Mid June	13–14 days	Late June	Frost (1943)

The seasonal decrease in egg size is characteristic of planktonic and demersal marine eggs but the data are not available for freshwater species. The seasonal decrease in egg size, and the associated with spawning time which in herring (Cushing, 1967), plaice, trout and other freshwater fish, appear to be linked with the availability of food. In the case of marine species this is indicated by the spring increase in the production cycle. In the case of Windermere pike the timing of spawning is such that plankton is available at the time of first feeding and newly hatched perch fry are available when the young pike change to a piscivorous diet.

References

Bagenal, T. B. (1966). The ecological and geographical aspects of the fecundity of the plaice. *J. mar. biol. Ass. U.K.* **46,** 161–186.

Bagenal, T. B. (1969). Relationship between egg size and fry survival in brown trout *Salmo trutta* L. *J. Fish Biol.* **1,** 349–353.

Bal, D. V. (1943). A study of fish eggs and larvae from Manx waters. *J. Univ. Bombay* **11B,** 54–90.

Blaxter, J. H. S. & Hempel, G. (1963). The influence of egg size on herring larvae (*Clupea harengus* L.). *J. Cons. perm. int. Explor. Mer* **28,** 211–240.

Bracken, J. J. & Kennedy, M. P. (1967). A key to the identification of the eggs and young stages of coarse fish in Irish waters. *Scient. Proc. R. Dubl. Soc.*, Ser. B **2,** 99–108.

Colebrook, J. M. & Robinson, G. A. (1965). Continuous plankton records: seasonal cycles of phytoplankton and copepods in the north-eastern Atlantic and the North Sea. *Bull. mar. Ecol.* **6,** 123–139.

Cushing, D. H. (1967). The grouping of herring populations. *J. mar. biol. Ass. U.K.* **47,** 193–208.

Ehrenbaum, E. (1905–09). *Eier und Larven von Fischen des Nordischen Planktons.* Kiel und Leipzig, 1905–09.

Ehrenbaum, E. (1911). Tables for the determination of the plankton eggs of fishes occurring in the North Sea and the neighbouring waters (excluding the Baltic). Copenhagen 1911. *Rapp. Cons. Explor. Mer* **13.** Appendix to reports 1 & 3.

Einarsson, H. & Williams, G. C. (1968). Planktonic fish eggs of Faxafloi, southwest Iceland, 1948–1957. *Rit Fiskideild.* **4,** 1–15.

Elliott, J. M. (1966). Downstream movements of trout fry (*Salmo trutta*) in a Dartmoor stream. *J. Fish. Res. Bd Can.* **23,** 157–159.

Elliott, J. M. (1967). The food of trout (*Salmo trutta*) in a Dartmoor stream. *J. appl. Ecol.* **4,** 59–71.

Foerster, R. E. (1968). The sockeye salmon *Oncorhynchus nerka*. *Bull. Fish Res. Bd Can.* **162,** 1–422.

Frost, W. E. (1943). The natural history of the minnow (*Phoxinus phoxinus*). *J. Anim. Ecol.* **12,** 139–162.

Frost, W. E. (1954). The food of pike *Esox lucius* L. in Windermere. *J. Anim. Ecol.* **23,** 339–360.

Frost, W. E. (1965). Breeding habits of Windermere charr, *Salvelinus willughbii* (Günther), and their bearing on speciation of these fish. *Proc. R. Soc.* B. **163,** 232–284.

Frost, W. E. & Kipling, C. (1967). A study of reproduction, early life, weight-length relationship and growth of pike *Esox lucius* L. in Windermere. *J. Anim. Ecol.* **36,** 651–693.

Gray, J. (1928). The growth of fish II. The growth rate of the embryo of *Salmo fario*. *Br. J. exp. Biol.* **6,** 110–121.

Hempel, G. & Blaxter, J. H. S. (1967). Egg weight in Atlantic herring (*Clupea harengus* L.). *J. Cons. perm. int. Explor. Mer* **31,** 170–195.

Hiemstra, W. H. (1962). A correlation table as an aid for identifying pelagic fish eggs in plankton samples. *J. Cons. perm. int. Explor. Mer* **27,** 100–108.

Holliday, F. G. T. & Jones, M. P. (1967). Some effects of salinity on the developing eggs and larvae of the plaice (*Pleuronectes platessa*). *J. mar. biol. Ass. U.K.* **47,** 39–48.

McCormack, Jean C. (1962). The food of young trout (*Salmo trutta*) in two different becks. *J. Anim. Ecol.* **31,** 305–316.

Nikolskii, G. V. (1963). *The Ecology of Fishes.* London & New York: Academic Press.

Riley, J. D. (1966). Marine fish culture in Britain VII. Plaice (*Pleuronectes platessa* L.) post-larval feeding on *Artemia salina* L. nauplii and the effects of varying feeding levels. *J. Cons. perm. int. Explor. Mer* **30,** 204–221.

Robertson, A. (1922). Further proof of the parent stream theory. *Trans. Am. Fish. Soc.* **51,** 87–90.

Rounsefell, G. A. (1957). Fecundity of the North American Salmonidae. *Fish. Bull. Fish Wildl. Serv. U.S.* **57,** 451–468.

Schindler, O. (1953). *Unsere susswasserfische.* Stuttgart. (Translated by Orkin, P. A. 1957. *Freshwater Fishes.* London & New York: Thames & Hudson).

Shelbourne, J. E. (1953). The feeding habits of plaice post-larvae in the Southern Bight. *J. mar. biol. Ass. U.K.* **32,** 149–159.

Shelbourne, J. E. (1957). The feeding and condition of plaice larvae in good and bad plankton patches. *J. mar. biol. Ass. U.K.* **36,** 539–552.

Simpson, A. C. (1951). Book review. *J. Cons. perm. int. Explor. Mer* **17,** 198–199.

Simpson, A. C. (1956). *The Pelagic Phase* In *Sea Fisheries: Their Investigation in the United Kingdom* (Ed. M. Graham). London: Arnold.

Simpson, A. C. (1959*a*). The spawning of plaice in the North Sea. *Fish. Invest.*, Ser. 2 **22,** 1–111.

Simpson, A. C. (1959*b*). The spawning of plaice (*Pleuronectes platessa*) in the Irish Sea. *Fish. Invest.*, Ser. 2 **22,** 1–30.

Smith, S. (1958). Yolk utilization in fishes. In *Embryonic Nutrition* (Ed. D. Rudnick). Chicago: University of Chicago Press.

Smyly, W. J. P. (1952). Observations on the food of the fry of perch (*Perca fluviatilis* L.) in Windermere. *Proc. Zool. Soc. Lond.* **122,** 407–416.

Smyly, W. J. P. (1955). On the biology of the stone-loach *Nemacheilus barbatula* (L.). *J. Anim. Ecol.* **24,** 167–186.

Smyly, W. J. P. (1957). The life history of the bullhead or miller's thumb (*Cottus gobio* L.). *Proc. zool. Soc. Lond.* **128,** 431–453.

Sundnes, G., Leivestad, H. & Iversen, O. (1964). Buoyancy determination of eggs from the cod (*Gadus morhua* L.). *J. Cons. perm. int. Explor. Mer* **29,** 249–252.