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TIME AND DURATION OF THE SPAWNING
SEASON IN SOME MARINE TELEOSTS
IN RELATION TO THEIR DISTRIBUTION

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**Time and Duration of the Spawning Season
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AS part of a study of the biology of the common shore fishes *Blennius pholis* and *Centronotus gunnellus*, the times and durations of the breeding seasons were determined and the cycles of maturation and depletion of the gonads were followed throughout the year. It then appeared that the breeding cycles of the two species are very different. *B. pholis* breeds for about five months, in late spring and early summer. A nest of this species (a crevice, or space between stones, guarded by the male parent) was usually found to contain more than one batch of eggs. The stage of development varied between the different batches, showing that they had been deposited at different times. Gonad examination of monthly samples collected in the field showed that the ovaries did not become spent after early spawnings, and observations in aquaria confirmed that each individual spawns several times during the breeding season. *C. gunnellus*, however, breeds for only about two months, in late winter or early spring. In this species each egg mass consisted of eggs all at the same stage of development. The egg masses of this species are guarded mainly by the females, though both parents are found guarding them early in the spawning season. Guardian females were always found to be completely spent, and could not therefore have spawned again for a year. In this species it was clear that the entire annual egg-production of each female was being concentrated into a single spawning act.

To investigate whether the size distribution of oocytes, in maturing ovaries of the two species, would show corresponding peculiarities, ovaries of *C. gunnellus*, collected in November, and of *B. pholis* collected in March, were fixed in Bouin's fluid. After dehydration and clearing,

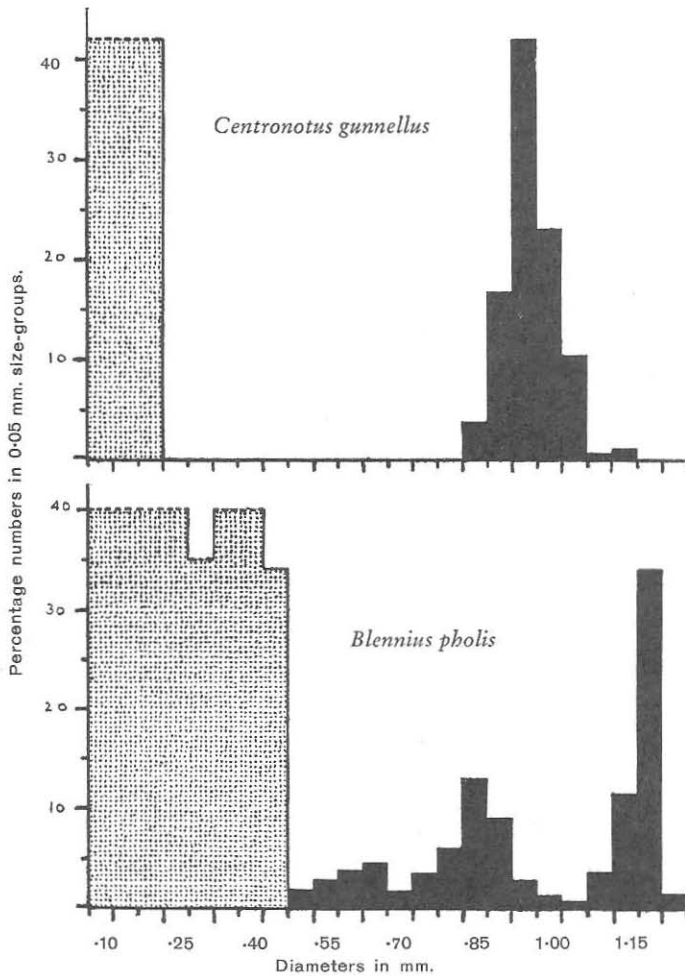


Figure 1. Size-distribution of maturing oocytes (black histograms) in ovaries of *Centronotus gunnellus* and *Blennius pholis*. The shaded areas indicate the sizes of small, apparently yolkless cells, which probably included follicle cells and oogonia. These were much more numerous than the oocytes, and they were therefore disregarded when calculating percentage size-distribution of the latter.

the ovaries were carefully opened in watch glasses and the oocytes removed and measured under a micrometer eye-piece. The percentages falling in each .05 mm. size-range are given in Figure 1. It is evident from the curves that in *C. gunnellus* there is a single stock of large oocytes which might all be spawned together. In *B. pholis*, on the other hand, the oocytes are of a wide range, evidently destined to be matured and shed periodically during the season.

Table 1.

Northern species (arctic-boreal)	Limits of Atlantic distribution	Known breeding range (European)
<i>Centrotonus gunnellus</i> (Gunnel)	Spitsbergen to English Channel. Greenland, Labrador to Woods Hole and Massachusetts (Sæmundsson, 1949; Duncker & Mohr, 1928; Breder, 1948).	Iceland (Sæmundsson, 1949); North Sea (Ehrenbaum, 1904); British coasts (Smith, 1887), and probably in English Channel.
<i>Clupea harengus</i> (Herring)	Spitsbergen to Bay of Biscay. Greenland to Cape Hatteras and rarely around New York (Sæmundsson, 1949; Hodgson, 1934; Breder, 1948).	Barents Sea (Rass, 1936); northern Norway (Hjort, 1914); Iceland to English Channel (Sæmundsson, 1949; Hodgson, 1934).
<i>Cottus scorpius</i> (Sea scorpion)	Spitsbergen to English Channel. Greenland and various North American coasts (Sæmundsson, 1949; Ehrenbaum, 1932).	Iceland (Sæmundsson, 1949); North Sea (Ehrenbaum, 1904); British coasts (Jenkins, 1936), and probably in English Channel.
<i>Gadus aeglefinus</i> (Haddock)	Spitsbergen to Bay of Biscay. Greenland to Cape Hatteras and New Jersey (Sæmundsson, 1949; Hjort, 1912; Breder, 1948).	Barents Sea (Rass, 1936); northern Norway (Raitt, 1936); Iceland to English Channel (Schmidt, 1909).
<i>Gadus callarius</i> (Cod)	Spitsbergen to Bay of Biscay. Greenland to Cape Hatteras and Virginia (Sæmundsson, 1949; Hjort, 1912; Breder, 1948).	Barents Sea (Rass, 1936); northern Norway (Hjort, 1914; Wiborg, 1948); Iceland to English Channel (Schmidt, 1909).
<i>Pleuronectes platessa</i> (Plaice)	Barents Sea and White Sea to Portugal and Morocco; also recorded from northern parts of Mediterranean (Sæmundsson, 1949; Hjort, 1912; Schnakenbeck, 1929).	Barent Sea (Rass, 1936; Milinski, 1938); Iceland (Sæmundsson, 1949); North Sea to English Channel (Wallace, 1909).

Similar differences in the size-distribution of oocytes from various species have been noticed earlier, by investigators studying the fecundity of fishes (Fulton, 1891; Mitchell, 1913). These workers found it difficult or impossible to determine the fecundity of some species, because of the almost continuous gradation in cell-size between the large oocytes and the smallest cells at the spawning season. The latter are presumably follicle cells, or destined to provide the oocytes of later years. This is the condition found in *B. pholis*. In *C. gunnellus*, on the other hand, the uniformly large maturing oocytes can easily be distinguished from the much smaller yolkless cells, which will mature in subsequent years. There is therefore no difficulty in determining the fecundity of this fish. Similar conditions have been found in other northern fishes, such as plaice (Simpson, 1951), haddock (Raitt, 1933), cod (Fulton, 1891), and herring (Farran, 1938; Hickling, 1940).

Table 1 (continued).

Southern species (Mediterranean-boreal)	Limits of Atlantic distribution	Known breeding range (European)
<i>Blennius pholis</i> (Shanny)	South-west Norway (Bergen) to Mediterranean (Duncker & Mohr, 1928; Ford, 1935; de Latil, 1954).	Non-migratory. As previous column.
<i>Clupea pilchardus</i> (Pilchard)	Southern Norwegian coasts to Mediterranean (Kyle & Ehrenbaum, 1927; D'Ancona, 1931).	North Sea (Furneston, 1939); English Channel (Corbin, 1951); Bay of Biscay to Mediterranean (Fage, 1920).
<i>Clupea sprattus</i> (Sprat)	South-west Norway (Trondheim) to Mediterranean (Kyle & Ehrenbaum, 1927; Robertson, 1938).	South-west Norwegian coast (Mulicki, 1947); North Sea, English Channel, Bay of Biscay and Mediterranean (Fage, 1920; D'Ancona, 1931).
<i>Gadus merlangus</i> (Whiting)	Iceland to Mediterranean (Sæmundsson, 1949; Hjort, 1912; D'Ancona, 1933).	South of Iceland, North Sea, and other British waters to Bay of Biscay (Schmidt, 1909).
<i>Merluccius merluccius</i> (Hake)	Iceland to Mediterranean (Sæmundsson, 1949; Hjort, 1912; D'Ancona, 1933).	North Sea and other British waters to Bay of Biscay (Schmidt, 1909); Mediterranean (D'Ancona, 1933).
<i>Scomber scombrus</i> (Mackerel)	Iceland to Mediterranean. Labrador to Cape Hatteras (Sæmundsson, 1949; le Gall, 1932; Breder, 1948).	Southern Norwegian coasts (Dannevig, 1947); Swedish coasts (Nilsson, 1914); British waters (Allen, 1897); North Sea to Mediterranean (Ehrenbaum, 1924).

A correlation between the size frequency distribution of oocytes and the duration of the spawning season was first pointed out by Hickling and RutenberG (1936). They showed that herring and haddock, which have short spawning seasons, have maturing oocytes all of approximately the same size, whereas pilchard and hake, which have long spawning seasons, have maturing oocytes of a wide range of sizes. These two conditions are also found in *C. gunnellus* and *B. pholis* respectively.

This difference between the breeding habits of *B. pholis* and *C. gunnellus* seemed at first to be rather surprising, for both species occupy a rather similar habitat (they may be found together under the same stone) and are fairly closely related systematically (both are placed in the Blenniiformes). The distribution of the two forms in other latitudes, however, is quite different. *B. pholis* is confined to the Atlantic coasts of Europe, from Bergen, in southern Norway (Duncker and Mohr, 1928; Ford, 1935), to the Mediterranean (de Latil, 1954). It therefore has its centre of distribution to the south of the British Isles. *C. gunnellus* on the other hand extends from Western Greenland, Iceland, and Norway to the English Channel (Sæmundsson, 1949). It is found on both sides of the Atlantic, like other arctic-boreal forms

from several phyla, and unlike mediterranean-boreal forms (Ekman, 1953). The lower sea temperature in the western Atlantic allows it to penetrate south as far as Massachusetts (Breder, 1948), but on the eastern side it has its centre of distribution to the north of the British Isles. It seemed probable that the differences observed between the breeding cycles of the two species were correlated with the fact that *B. pholis* is a southern form and *C. gunnellus* a northern form.

To test this hypothesis the breeding cycles of these species were compared with those of other marine teleosts of British waters, for which data are available (Tables 1 and 2). The species have been classified into northern and southern forms according to whether or not they have been recorded as breeding north of the arctic circle (Table 1). With the single exception of the plaice, the northern forms are found on both sides of the Atlantic. Of these forms the plaice appears to be the least adapted to cold conditions, for it alone extends to the Mediterranean, though it has not been found to breed there. Other migratory northern species, like herring, cod, and haddock, reach as far south as the Bay of Biscay in European waters, but *Centronotus gunnellus* and *Cottus scorpius* seem to reach their southern limits in the English Channel. The breeding range in all the northern forms seems to lie between the Arctic Ocean and the English Channel. Little is known about the breeding in extreme arctic regions, but it has been demonstrated in cod, by marking experiments, that mature individuals migrate during the breeding season, from polar regions to Iceland waters for spawning, and return to Greenland waters as spent (Hansen, Jensen, and Tåning, 1935).

The southern forms range mostly from the Mediterranean to the North Sea. Some of these species are also recorded from the south of Iceland and the Faroes during the summer, but they do not appear to breed in Icelandic waters, with the single exception of the whiting. The whiting seems to be less adapted to warm conditions than the others. The breeding range in most of these forms is from the Mediterranean to the northern parts of the North Sea, although the extreme northern limit of the breeding range varies in different species. The mackerel is found in American waters, as might be expected, since it is largely a fish of the open ocean. None of the other southern forms extends to the American side of the Atlantic.

Examination of Table 2 will show that all the southern species have breeding cycles similar to that of *B. pholis*, whilst all the northern species have cycles like that of *C. gunnellus*. The differences in breeding habits between the northern and southern groups may be summarized as follows:—

1. Southern forms spawn in late spring or summer, whereas northern forms spawn in late winter or early spring.
2. In southern forms the spawning seasons last for five or six months, but in northern forms they last only three or four months.
3. The maturing ovary of a southern species contains oocytes of a wide range of sizes, which are presumably destined to contribute to a

Table 2.

Fauna	Species	Size-range of oocytes in maturing ovary mm.	Time and duration of spawning in British waters											Area investigated	Authors	
			Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.			Nov.
Northern species (arctic-boreal)	<i>Centronotus gunnellus</i> (Gunnel)	0.84—1.10 (Present author)		+	+	+									Irish Sea	Present author
	<i>Clupea harengus</i> (Herring)	1.11—1.26 (Farran, 1938)		+	+	+									Southern North Sea	Hodgson, 1929
	<i>Cottus scorpius</i> (Sea scorpion)	1.20—1.27 (Fulton, 1891)		+	+	+	+								Irish Sea	Jenkins, 1936
	<i>Gadus aeglefinus</i> (Haddock)	1.20—1.39 (Fulton, 1891)			+	+	+	+							North Sea	Damas, 1909
	<i>Gadus callarias</i> (Cod)	1.20—1.40 (Fulton, 1891)				+	+	+							North Sea	Graham, 1924
	<i>Pleuronectes platessa</i> (Plaice)	0.90—1.00 (Fulton, 1891)		+	+	+	+								North Sea	Buchanan-Wollaston, 1914
Southern species (mediterranean-boreal)	<i>Blennius pholis</i> (Shanny)	0.05—1.22 (Present author)						+	+	+	+	+			Irish Sea	Present author
	<i>Clupea pilchardus</i> (Pilchard)	0.05—0.50 (Hickling & Rutenberg, 1936)						+	+	+	+	+	+	+	Cornish waters	Hickling, 1945
	<i>Clupea sprattus</i> (Sprat)	0.06—1.12 (Fulton, 1891)						+	+	+	+	+	+		North Sea	Ehrenbaum, 1909 Tesch, 1909
	<i>Gadus merlangus</i> (Whiting)	0.05—1.30 (Fulton, 1891)						+	+	+	+	+			Irish Sea	Bowers, 1954
	<i>Merluccius merluccius</i> (Hake)	0.05—0.50 (Hickling & Rutenberg, 1936)							+	+	+	+	+		South and west of Ireland	Hickling, 1930
	<i>Scomber scombrus</i> (Mackerel)	0.05—0.90 (Fulton, 1891)							+	+	+	+	+		Celtic Sea	Corbin, 1947

succession of spawnings. That of a northern species, on the other hand, contains oocytes which are all similar in size and which may therefore be spawned together. Evidence of spawning of individual fish more than once during a season has been obtained in several southern species, including the pilchard (Russell, 1930), the Californian sardine (Clark, 1934), the mackerel (Sette, 1943), the sprat (Heidrich, 1925), and *Blennius pholis* (present author).

Considering the adaptive significance of these differences between southern and northern forms, one thinks first of the well established fact that temperature is of great importance in controlling reproduction. This principle has been referred to by Thorson (1946) as Orton's rule, since it was first established by Orton (1920). Appellöf (1912) and others wrote of it earlier, but less precisely. Runnström (1927) dealt with it more recently. Amongst its corollaries is the rule that species which are nearer to the warmer limits of their range breed during the colder months of the year and, conversely, that species which are nearer to the colder limits of their range breed during the warmer months of the year. Such habits are of adaptive advantage, since the young are generally less tolerant of extreme conditions than are adults. Certainly newly hatched larvae of *C. gunnellus* are very sensitive to changes in temperature and soon die if the temperature rises above 12—13°C. Larvae of *B. pholis* can tolerate much higher temperatures. It may be presumed that northern fishes in British waters must breed very early in the year because their young larvae would be killed by the summer temperatures if they bred later.

There are several features of the breeding cycles of these fishes which are not fully explained by Orton's rule, however. We must still explain why the northern forms do not breed over a long period during the colder months of the year and why the southern forms do not go on breeding in autumn, when the water is at its warmest. We may consider why *C. gunnellus* in Iceland, as in British waters, breeds for only two or three months at the coldest time of the year (Samundsson, 1949). Turning to another group of animals, the barnacles, which resemble fishes in having a long embryonic stage in the development, followed by a planktotrophic larval stage, we again find several features of the breeding cycles which are not easily explained on the basis of Orton's rule alone. As in fishes, the southern barnacles, which breed in summer, produce a succession of spawnings over a long period of several months (Crisp, 1950; Crisp and Davies, 1955) whereas the northern forms, which breed in winter, spawn during a shorter period, each individual producing a single brood annually (Crisp, 1954). The common arctic-boreal shore barnacle, *Balanus balanoides*, which is at its southern limit in the English Channel, spawns in British waters during November (More, 1935), which is far from being the coldest season of the year. The embryonic development goes on within the mantle cavity of the parents until the spring, when the planktotrophic larvae are liberated. At higher latitudes the embryos are still retained throughout the coldest months, so that they are liberated in

the spring when conditions are favourable for feeding and growth of the larvae (Crisp, 1954).

This behaviour suggests a principle that may be generally applicable to the breeding cycles of marine animals which have planktotrophic larvae. The breeding cycles may be so regulated that the larvae hatch during the season which is most favourable for finding planktonic food, under the conditions that prevail over the greater part of their range. I should like to refer to this as Crisp's rule, since it was suggested to me by Dr. D. J. Crisp, who has deduced it from his work on the breeding of barnacles. We have here an explanation of why *C. gunnel-lus*, in Iceland, breeds so early in the year, and why breeding seasons are short in northern fishes. In higher latitudes organic production in the plankton is restricted to a short period during early summer, when it is intense (Steeemann Nielsen, 1935; Jespersen, 1940). The planktotrophic larval stage must occur during this period, so the fish must spawn much earlier, since at low temperatures spawning is separated from hatching by a fairly long phase of embryonic development. At the spawning season temperatures and food supply are at about their annual minimum, so presumably conditions of life, for the adult fish, are too poor to support the maturation of successive batches of eggs. Each fish therefore puts all its reserves into one batch. The eggs of northern fishes seem to be generally larger than those of southern forms, as in many invertebrates (Thorsen, 1950). Hence the hatching larvae are probably well supplied with yolk, which will maintain them for a time if they should have difficulty in finding food.

In middle latitudes plankton production goes on at moderate levels throughout the spring and summer. But northern forms, even in these warmer parts of their range, must continue to breed in winter or early spring to provide optimum conditions for their stenothermal young. Hence, even in these milder climates, their breeding cannot occur at a season when abundant food for the parents would favour a succession of broods.

In low latitudes plankton production is said to go on at a comparatively low level throughout the year. Optimum conditions must be affected by the weather and may therefore occur at almost any time. Southern species, by spawning at intervals, ensure that larvae are present in the plankton over a long period, ready to take advantage of optimum conditions whenever these occur. Conditions are favourable for the building up of reserves by the adult fish during the spawning season, so each female brings to maturation successive batches of eggs. In southern species, which guard the eggs during an incubation period, this duty is always performed by the males. Well known examples are *Blennius pholis*, *Blennius ocellaris* (Lebour, 1927), *Blennius gattorugine* (Brown, 1929; Wilson, 1949), *Blennius sphynx*, *Blennius montagui*, *Clinus argentatus* (Güitel, 1893), and *Gobius minutus* and other gobies (Jenkins, 1936). The females are therefore left free to take advantage of abundant food, and their successive batches of eggs may be added to the previously laid masses, as in *Blennius pholis*. In

northern forms which breed only once in the season, during winter, when conditions for the building up of reserves are not very favourable, it is immaterial which of the sexes guards the eggs. In such forms we find this duty taken up by females, as in the crested blenny (Schultz and DeLacy, 1932), or by males, as in *Cottus scorpius* (Ehrenbaum, 1904), or by both sexes, as in *Centronotus gunnellus* (Gudger, 1927).

In British waters, spawning of southern forms generally finishes before September (Table 2). The young therefore have a growth period of at least two or three months before the sea becomes really cold. In *B. pholis* the gonads recover remarkably quickly after spawning and remain large during the winter. This rapid recovery also occurs in hake (Hickling, 1930) and whiting (Bowers, 1954). It is probably a feature characteristic of southern forms living in boreal waters, which enables them to take advantage of the warmth and food still available to them in the autumn.

Crisp's rule (in conjunction with Orton's rule, for fish larvae are undoubtedly more stenothermal than adults) therefore provides a complete explanation for these differences between the breeding cycles of southern and northern fishes, in terms of adaptive advantage to the species. But the problems of which point in the cycle is linked to the cycle of the seasons, and of whether the link is to temperature, to length of day, or to some other factor, remain to be solved by future experiments.

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Summary.

The breeding cycles of marine teleosts in British waters are governed by the following general principles:—

1. Northern (arctic-boreal) forms breed during winter or early spring, and southern (mediterranean-boreal) forms during spring and summer.

2. The breeding of northern forms lasts for only three or four months, but that of southern forms lasts for five or six months.

3. In northern forms the maturing oocytes are all of similar size and the eggs are probably spawned in a single group. Southern forms have maturing oocytes of a wide range of sizes, destined to be matured and shed periodically.

It is suggested that the breeding cycles of all these forms are adapted to provide optimum conditions of food and temperature for the larvae. During the warm breeding seasons of southern forms, moreover, sufficient food is available for the adults to support the maturation of

successive batches of eggs. Northern forms, on the other hand, spawn at a season which is not very favourable for feeding, so the females put all their reserves into a single batch.

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