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Spawning of plaice *Pleuronectes platessa* L. around the Isle of Man, Irish Sea

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The locations and timing of plaice *Pleuronectes platessa* spawning around the Isle of Man were studied from distributions of recently spawned eggs recorded in plankton samples. The area of intense spawning activity south-east of the Isle of Man was found to be further north than indicated in the literature. A previously disregarded spawning ground off the west coast of the Isle of Man was identified in 1991, 1992 and 1993, although egg densities were lower than off the east coast. Production of stage I eggs on the west coast spawning site was estimated at approximately 2% of the total plaice egg production in the Irish Sea. This would be sufficient to supply the local nursery grounds on the west coast of the Isle of Man with plaice larvae. Plaice spawned between early February and early April off the west coast of the Isle of Man, with March as the main period of egg production. Plaice therefore spawn well before the spring plankton bloom in the Irish Sea.

Key words: plaice, *Pleuronectes platessa*, spawning, egg distribution

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Introduction

Brander and Dickson (1984) examined the low level of demersal fish production (including plaice *Pleuronectes platessa* L.) in the Irish Sea and attributed it to low recruitment and poor survival of the planktonic stages. The level of year-class strength of plaice in the North Sea appears to be set in the planktonic stages before settlement on nursery grounds (van der Veer, 1986). The number of individuals settling on the nursery ground is determined by the survival of the planktonic egg and larval stages and transport from the spawning ground to the nursery ground, but very little is known of these processes (van der Veer *et al.*, 1990). Predatory and feeding conditions are assumed to be the two major factors determining survival of these vulnerable life stages (Shelbourne, 1957; Harding *et al.*, 1978; Pommeranz, 1981; Hovenkamp, 1989, 1990). Brander and Dickson (1984) suggested that the timing of the plankton production cycle was responsible for poor survival of the planktonic stages in the Irish Sea, and that in order to understand the link between the planktonic production cycle and survival, the timing and locations of spawning should be investigated.

The spawning period of plaice in the Irish Sea is poorly documented compared to the profusion of studies in the North Sea (e.g. Simpson, 1959a; Harding *et al.*, 1978; Coombs *et al.*, 1990). Surveys in the Irish Sea have either not covered or not described the period of spawning (Simpson, 1959b; Colman, 1966; Harding and Talbot, 1973; Nichols *et al.*, 1993). Scott (e.g. 1913) and Bal (1941) published data on the duration of spawning in the Irish Sea, but the period of peak spawning was unclear because their investigations were not quantitative and development stages were not attributed to the eggs.

Transport to the nursery ground may also be important in determining year-class strength (Pihl, 1990). The population ecology of juvenile plaice on the Port Erin Bay nursery ground on the west coast of the Isle of Man, has received much attention (e.g. Riley and Corlett, 1966; Nash *et al.*, 1994), and yet the spawning ground from which the plaice derive is unknown (Colman, 1966). Simpson (1959b) showed that eggs are not transported far from the spawning grounds in the Irish Sea, and Harden Jones (1968) suggested settlement in nurseries close to the spawning grounds. Although Simpson (1959b) recorded low numbers of plaice eggs to

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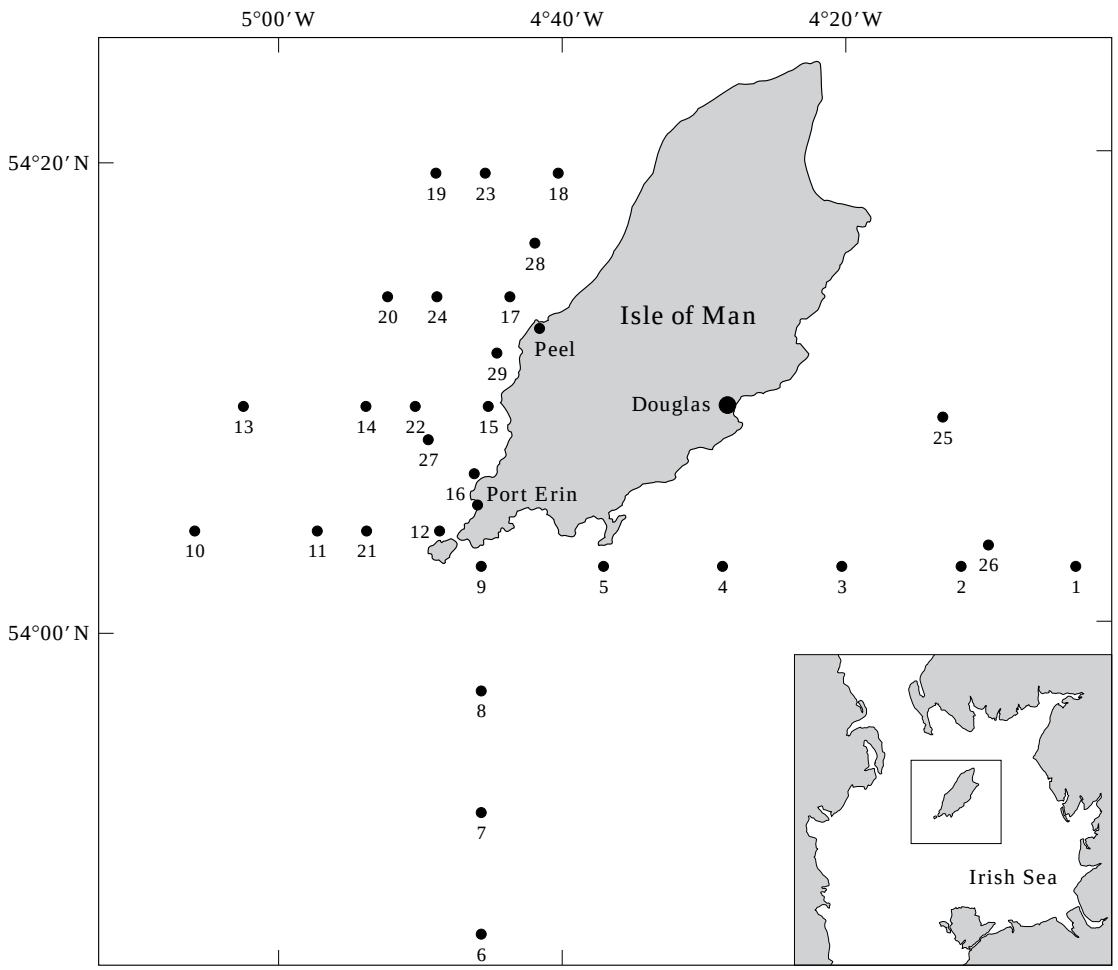

Figure 1. Positions of plankton sampling stations around the Isle of Man, in the Irish Sea (inset).

the west of the Isle of Man, Colman (1966) dismissed the possibility of a spawning ground local to Port Erin Bay and assumed that recruited larvae originated from one of the main spawning grounds. It is theoretically possible for Port Erin Bay plaice to originate from any of the main spawning grounds to the east of the Isle of Man (see Simpson, 1959b), based on development times and residual current speeds and directions (see Harvey, 1968; Norris, 1989).

The aims of the surveys of plaice egg distributions around the south and west of the Isle of Man described here were two-fold. First, to confirm the locations of plaice spawning around the south of the Isle of Man. Second, to define the period over which spawning occurred and the time of peak spawning on the west side of the Isle of Man. The hypothesis that sufficient eggs were produced on the west side of the Isle of Man to supply the local Manx nursery grounds was also examined.

Materials and methods

Sampling for plaice eggs was undertaken from RV "Cuma" in 1991 and RV "Roagan" in 1992 and 1993. In late February to early March 1991 a broad scale survey was undertaken to the east, west and south of the Isle of Man (Fig. 1; Stations 1–16). Between mid-January and mid-April 1992 four intensive surveys were made off the west coast of the Isle of Man (Stations 11–12, 14–24; Fig. 1), and two stations (25, 26) off the east coast were sampled in late March 1992. In 1993, seven surveys were made off the west coast between early February and early April (Stations 12, 15, 17, 18, 21–24, 28, 29) and a station (25) to the east of the Isle of Man was sampled twice in March. Two samples were typically taken at a station on each survey.

Plankton samples were taken with an un-encased Gulf III type high speed plankton sampler (Lockwood, 1974) fitted with a conical nose cone and 333 μm mesh. A

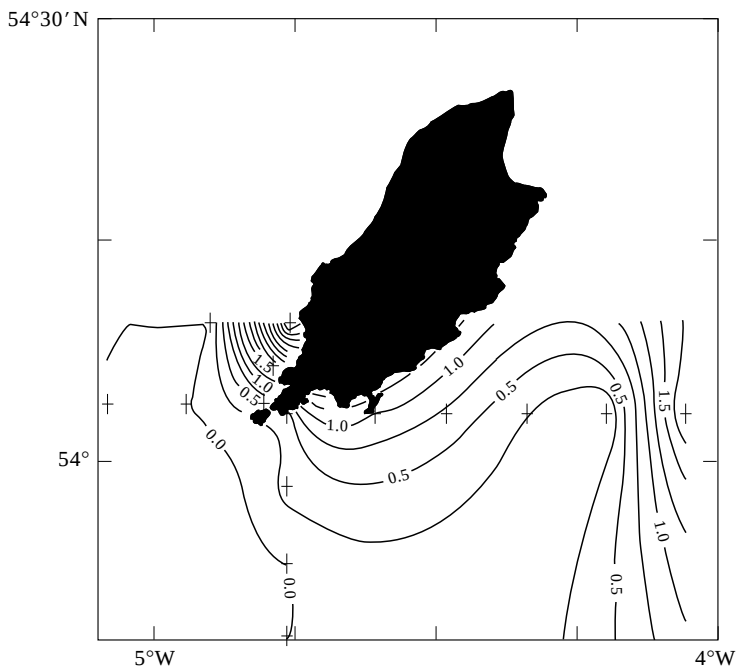

Figure 2. Contour plot of numbers of stage I plaice eggs m^{-2} sea surface recorded in 1991 survey (28 February to 7 March 1991) around the south of the Isle of Man. Sampling stations are indicated by +. Contour interval: 0.25 eggs m^{-2}.

General Oceanics flowmeter, mounted internally slightly off centre in the mouth of the conical nose cone, was used to estimate the volume of water filtered. The sampler was towed at 4–5 knots and deployed in a standard double oblique tow of 20 min duration, 10 min down and 10 min up. In 1992 and 1993, the depth of the sampler was monitored throughout the tow using a Furuno CN8 net sonde. In 1991, depth was estimated from the length of warp payed out, and a standard diver's depth gauge attached to the sampler recorded the actual maximum depth. The sampler was deployed to within approximately 2 m of the bottom. Surface water temperatures were recorded at sampling stations from a Furuno (model T2000) digital temperature sensor.

Upon recovery of the sampler, the net was gently hosed down with sea water, and the contents of the codend were preserved in 4% buffered formaldehyde in fresh water. Samples were sorted in the laboratory and plaice eggs were identified according to Russell (1976), and staged according to Apstein (1909) and Ryland *et al.* (1975). Contour plots of the number of stage I (A and B) plaice eggs m^{-2} were produced for each survey using SURFER™ (version 6, Golden Software). Kriging was used for the contouring.

Annual stage I egg production from the spawning ground to the west of the Isle of Man was estimated in 1992 and 1993 using the method described by Harding and Talbot (1973). The number of stage I eggs within the survey grid was estimated by integrating the area between density contours (see SURFER™). Daily egg production for each survey was estimated after correction for stage duration (Ryland *et al.*, 1975). Total egg production was estimated by both integrating the area under a quadratic equation fitted to the estimates of daily egg production over time, and integrating the area under the polygon joining the data points.

Results

The broad-scale survey (28 February to 7 March 1991) showed few stage I plaice eggs in the vicinity of the spawning ground described by Simpson (1959b) to the south-east of the Isle of Man when compared to the higher densities recorded off the west coast of the Isle of Man (Fig. 2). On 24 March 1992 there were significantly lower densities of stage I eggs (one-way ANOVA, $p<0.05$) at the centre of Simpson's (1959b) suggested spawning ground (0.81 m^{-2}; Station 26, Fig. 1) than at the centre of the egg distribution shown by Colman (1966), east of Douglas (9.7 m^{-2}; Station 25, Fig. 1). On 11 and 24 March 1993, higher densities of stage I eggs were recorded east of Douglas than on the west coast of the Isle of Man.

On the west coast of the Isle of Man there was a marked inshore–offshore gradient in the distribution of the stage I eggs (Figs 2–4), with eggs restricted to shallow inshore waters. In both 1992 and 1993, a distinct

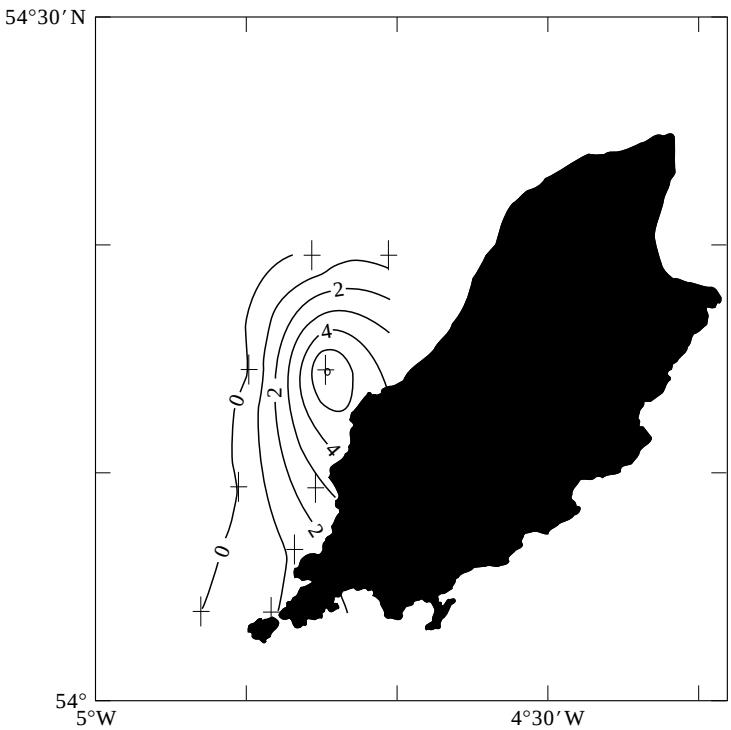

Figure 3. Contour plot of numbers of stage I plaice eggs m^{-2} sea surface recorded in third survey in 1992 (5 to 16 March 1992) around the south of the Isle of Man. Sampling stations are indicated by +. Contour interval: 1 egg m^{-2}.

centre of plaice egg distribution was typically recorded on the west side of the Isle of Man, in the vicinity of Peel (Figs 3 and 4).

In late February/early March 1991 the maximum development stage recorded on both the east and west coasts of the Isle of Man were stage III. Assuming a mean water temperature of 7°C this would suggest that spawning had started around 18 February. In 1992 stations on the west side of the Isle of Man were surveyed four times (13/14 January, 6/11 February, 5/16 March and 3/6 April). No plaice eggs were found in the survey in January. Low densities of stage I eggs were recorded in February and densities increased substantially by March (Fig. 3), and stage III eggs were also present. By the beginning of April there was a decrease in densities of stage I eggs, and up to stage V eggs were present. On the east side, off Douglas, on 24 March 1992 there were high densities of stage I eggs, and eggs up to stage V were found. This indicates that spawning on the east of the Isle of Man must have started by 6 March. However, by this sampling date (24 March) some eggs could have already hatched if spawned before the end of February.

In 1993, a series of seven surveys were undertaken on the west side of the Isle of Man between 9/10 February and 15 April (Fig. 4). Very few stage I eggs were found at the beginning of February. By early March substantial numbers of stage I eggs were recorded and up to stage IV eggs were also present. In late March there were still substantial numbers of stage I eggs, however, by mid-April there were very few in the area.

The numbers of stage I eggs within the survey area on the west coast of the Isle of Man were calculated for 1992 and 1993 (Fig. 5). In both cases the maximum abundance of stage I eggs occurred over the month of March with peak spawning occurring around the middle of March. The production of stage I eggs on the west side of the Isle of Man was estimated between 11.3 and 13.6×10^9 in 1992 and between 6.7 and 7.1×10^9 eggs in 1993.

Discussion

The distribution of stage I eggs reflects the location of spawning grounds. It appears that the plaice spawning ground to the south east of the Isle of Man is off Douglas (Station 25) as shown by Colman (1966), slightly further north than shown by Simpson (1959b) (Station 26) and indicated by Cole and Johnstone (1901). Although the centres of the spawning grounds are separated by only 5 nmi, there was a consistent difference. Few eggs were recorded at Simpson's spawning ground in late February 1991 and late March 1992,

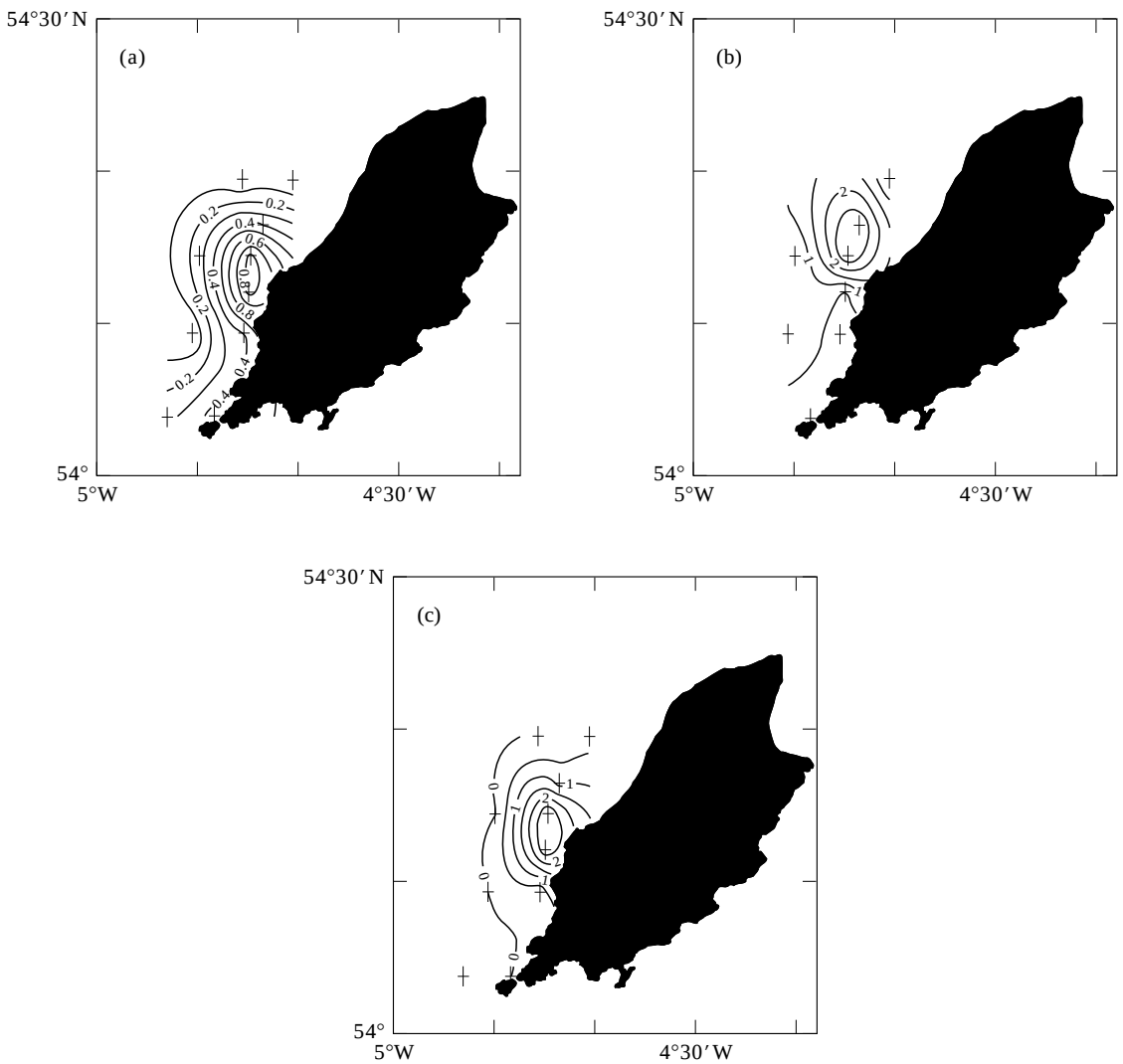

Figure 4. Contour plots of numbers of stage I plaice eggs m^{-2} sea surface recorded in 1993 surveys around the south of the Isle of Man. Sampling stations are indicated by +. (a) 22 to 23 February 1993, (b) 4 to 5 March 1993, (c) 31 March to 1 April 1993. Contour intervals: (a) 0.1, (b) 0.5, (c) 0.5 eggs m^{-2}.

whereas large numbers were recorded at Colman's location in late March 1992 and early and late March 1993. Nichols *et al.* (1993) also recorded high densities of plaice eggs off Douglas in early to mid-April, although their surveys did not extend further south than Douglas.

Recently spawned plaice eggs were recorded off the west coast of the Isle of Man in all surveys between February and April 1991–1993. Cole and Johnstone (1901) suggested that plaice spawn on the west side of the Isle of Man, and Scott (1913, 1915, 1919), Bal (1941) and Simpson (1959b) recorded plaice eggs in the area. There is, therefore, a well established spawning ground off the west coast of the Isle of Man. The significance to the Irish Sea plaice stock of the spawning ground on the west coast of the Isle of Man can be assessed by comparing production in this area (approximately 10×10^9 stage I eggs) with other estimates. Harding and Talbot (1973) estimated stage I egg production from the Great Orme spawning ground in 1965 at 2.75×10^{11}. The total production of stage I eggs from the Irish Sea plaice stock in 1993 was estimated at 4.76×10^{11} (see Table 1). The spawning ground on the west side of the Isle of Man therefore produces a small proportion (approximately 2%) of the total eggs spawned by the stock.

The stage I eggs were restricted to inshore waters off the west coast of the Isle of Man. Simpson (1959b) noted that plaice eggs are restricted to coastal or relatively shallow areas of the Irish Sea. The sharp depth gradient off the south and west coast of the Isle of Man into a

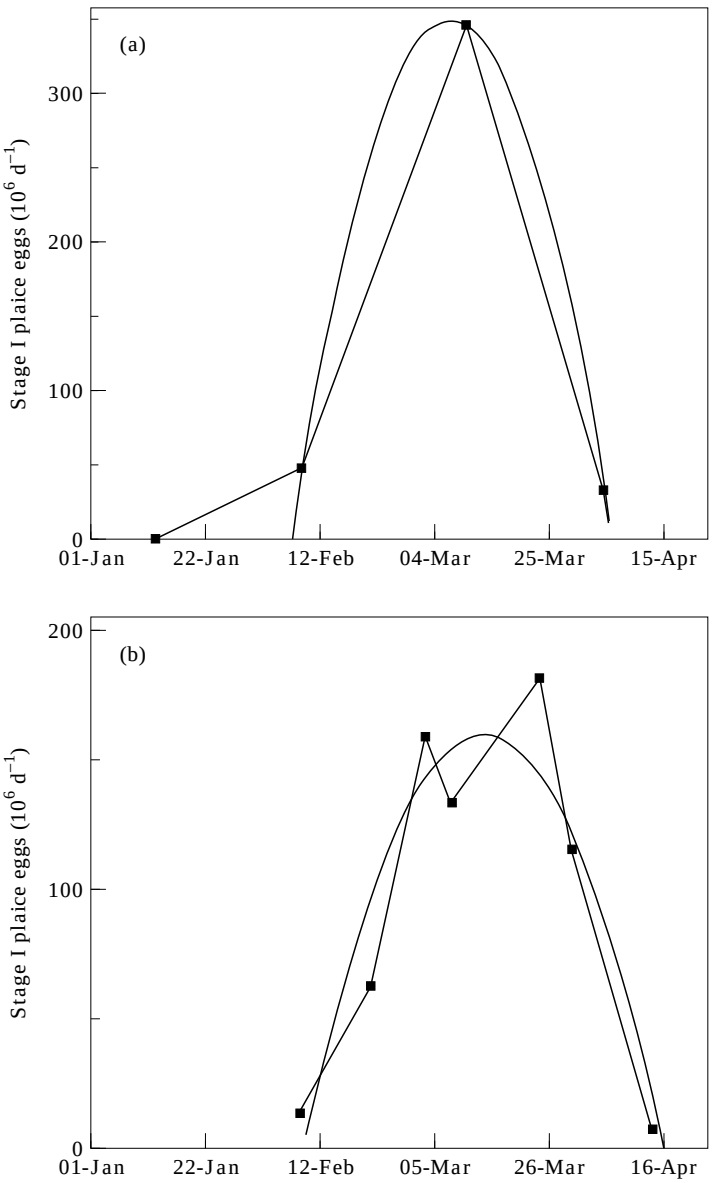

Figure 5. Production of stage I plaice eggs off the west coast of the Isle of Man with smoothed curve fitted by quadratic regression. (a) in 1992; (b) in 1993.

relatively deep trough (see Dickson *et al.*, 1988) could account for the limited distribution. In the North Sea, plaice spawn at depths <50 m (Harding *et al.*, 1978) and spawning in the Irish Sea is probably similarly restricted. The restricted distribution of eggs may have led to the potential for the spawning ground to supply Port Erin Bay being dismissed by Colman (1966). This was assessed by estimating the number of 0-group plaice that would be produced.

Total instantaneous mortality between stage I eggs and post-settlers has been estimated at 7.82 for North Sea plaice (Beverton and Iles, 1992). The estimated number of settling 0-group plaice which could be derived from the west coast of the Isle of Man spawning ground can therefore be estimated at between 2.7 and 5.5×10^6. Estimates of the population size of 0-group plaice in Port Erin Bay in mid-July, after completion of larval settlement, are in the order of 2×10^4 to 2×10^5 (Jones and Kain, 1964; Riley and Corlett, 1966; Ellis, 1994; Nash, unpubl. data). Theoretically, therefore, there would be sufficient production to supply the Port Erin Bay nursery ground and other local nurseries (e.g. Peel Bay) on the west coast of the Isle of Man.

Table 1. Production of stage I eggs from the Irish Sea plaice stock. Estimates of mean weight-at-age, numbers at age and maturity from Anon. (1993), assuming a sex ratio of 1:1. Fecundity estimated from relationship given by Bagenal (1960), atresia and fertilization rates taken from Horwood (1993) and Howell *et al.* (1991). Instantaneous mortality taken from Harding and Talbot (1973), with duration at 7°C estimated using Ryland *et al.* (1975).

Age	Mean weight (g)	Mean fecundity (10^3)	Number of females (10^3)	Maturity ogive	Number of mature females (10^3)	Total fecundity (10^9)
1	—	—	—	0.00	0	0
2	226	42	11 291	0.15	1694	71
3	270	54	5280	0.53	2798	150
4	321	68	2366	0.96	2271	156
5	378	86	517	1.00	517	46
6	440	107	533	1.00	533	57
7	508	131	366	1.00	366	48
8	582	158	170	1.00	170	27
9+	781	239	109	1.00	109	26
Total fecundity						5.79×10^{11}
Total number of eggs spawned (after atresia @ 2.7%)						5.63×10^{11}
Production of fertilized eggs (fertilization rate of 99.4%)						5.60×10^{11}
Production of stage I eggs (after mortality of 0.095 for 1.7 days)						4.76×10^{11}

Whether the eggs spawned off the west coast of the Isle of Man do supply the local nurseries with larvae will depend upon the local mortality rates and transport in the pelagic phase. Estimates of mortality of plaice eggs and larvae in the Irish Sea are restricted to one spawning ground in a single year (Harding and Talbot, 1973), but are within the range observed in the Southern Bight of the North Sea (Harding *et al.*, 1978). Although the time-averaged residual current in the Irish Sea is northward (Dickson *et al.*, 1988) and would carry the eggs and larvae away from the Isle of Man, the restricted coastal distribution of the eggs may reduce the impact of this flow.

The majority of eggs were produced in March, in agreement with the data of Simpson (1959b). This spawning period is also similar to that for the southern Celtic Sea (western approaches) where the majority of eggs are produced between early and late March (Horwood, 1993). In the Southern Bight of the North Sea peak spawning occurs between mid-January and mid-February (Harding *et al.*, 1978). Spawning in the Irish Sea is therefore later than in the Southern Bight, by some 4 to 6 weeks (Simpson, 1959b).

Cushing (1969) suggested that the time of spawning is linked to the timing of the spring plankton bloom, and Brander and Dickson (1984) found that the bloom occurs later in the Irish Sea than in the North Sea.

Cushing (1972, 1990) also suggested that larval survival is promoted by a close "match" in the times of the production cycles of larvae and their food. Plaice larvae are relatively large at hatching and feed primarily on zooplankton (Russell, 1976). Plaice larvae typically hatch after 3 to 5 weeks (Harding *et al.*, 1978). The phytoplankton bloom in the Irish Sea starts in March, and peaks later in the year (see Fig. 4 in Brander and Dickson, 1984). There is a time lag between the phytoplankton bloom and the zooplankton response (Savidge and Kain, 1990), so the zooplankton blooms between May and August (Herdman *et al.*, 1913; Colebrook, 1979; Scrope-Howe and Jones, 1985; Graziano, 1988). Plaice larvae therefore develop before the peak in food density in the Irish Sea. However, plaice also spawn well before the peak in the spring phytoplankton bloom in the Southern Bight of the North Sea (see Fig. 5 in Cushing, 1990). Plaice larval survival may, therefore, depend not only on the timing and intensity of the developing bloom, but also on the density of over-wintering zooplankton (see also Fortier *et al.*, 1995).

Despite the role of larval feeding conditions (Shelbourne, 1957; Hovenkamp, 1989), correlations between abundance indices in the North Sea suggest that plaice recruitment is determined before the larval stage, in the egg stages (Brander and Houghton, 1982; Zijlstra and Witte, 1985), and is therefore independent of larval feeding conditions. Predation is deemed to be the primary cause of mortality of plaice eggs (Harding *et al.*, 1978; Pommeranz, 1981; Rijnsdorp and Jaworski, 1990), and changes in the abundance, distribution and feeding activity of egg predators have been suggested to produce the positive correlation between temperature and mortality of plaice eggs (Bannister *et al.*, 1974; Zijlstra and Witte, 1985).

Plaice eggs will be preyed upon primarily by zooplanktivorous predators. Pepin (1987) showed theoretically that the density of alternative prey for planktivores has great potential for affecting the survival of planktonic stages of fish. As plaice eggs develop at a time of low zooplankton density, survival of eggs may be sensitive to the biomass of alternative prey for predators. It is therefore noteworthy that the over-wintering density of zooplankton is apparently lower in the Irish Sea than in the North Sea (Fig. 2 in Colebrook, 1979). Also, cold winters may advance the plankton bloom (Lockwood, 1990) and zooplankton density is negatively correlated with temperature (Colebrook, 1985). Mortality of plaice eggs may, therefore, be inversely related to the density of zooplankton prey for planktivores. However, there are problems with this hypothesis because temperature does not have an immediate effect on zooplankton density, but there is a time lag in the response of approximately nine months (Colebrook, 1985). Given the probable importance of the egg stage in the population dynamics of plaice, the factors affecting egg mortality are worthy of more intense study.

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