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**A LITERATURE REVIEW OF STUDIES ON
FISH EGG MORTALITY: IMPLICATIONS FOR THE
ESTIMATION OF SPAWNING STOCK BIOMASS BY THE
ANNUAL EGG PRODUCTION METHOD**

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1. INTRODUCTION

In 1995 a series of egg production surveys were conducted in the Irish Sea. Using the annual egg production method, the aim was to provide fisheries independent estimates of the spawning biomass of cod, plaice and sole for comparison with results derived from virtual population analysis (VPA). Egg production estimates of spawning biomass were much higher than VPA estimates, by a factor of 2.75 for cod, 4.75 for plaice and 2.99 for sole (Anon., 1998(a)). A study of Bristol Channel sole in 1990 yielded similar results; spawning biomass of this stock was calculated to be 2.2 times greater using the egg production method (Horwood, 1992). In either case, a satisfactory explanation for the observed discrepancy was not found. By contrast, values obtained for the spawning biomass of the Western mackerel stock (North East Atlantic) using the two methods were comparable (Anon., 1996). These calculations differ to the other studies because they use mortality estimates generated from the abundance of stage Ia eggs, instead of extrapolation back to time zero, i.e. the time of spawning. Nonetheless, the variation between models has caused concern about the accuracy of both types of assessment and hence the adequacy of scientific advice based upon them. In order to provide some measure of validation and to allow reliable comparisons, inconsistencies need to be identified. For the egg production method these may include inadequate coverage of spawning areas (both temporally and spatially), incomplete estimates of fecundity, or mis-identification of early stage eggs (Heessen and Rijnsdorp, 1989). VPA-type assessments may be biased by false reporting of landings, by the assumption that only one stock contributes to egg production in any particular area, and by other errors in the basic catch and catch per unit effort data (Horwood,

1992). In addition, they may be assessing only part of the stock in comparison to egg based methods.

Total egg production in many surveys is estimated by fitting a mortality function to the data for each egg stage, extrapolating back to the number of eggs at the time of spawning, then calculating the area under the curve. In general, an exponential decay model is the standard used. However, patterns in the residuals obtained from fitting such a function to the 1995 egg production data indicated that mortality might be lower during the early stages of egg development compared with later stages. This could suggest that a sigmoidal mortality curve might be fitted (Figure 1). The number of eggs spawned would then be predicted to be closer to the abundance of stage Ia eggs. The exponential model predicts a larger number of eggs spawned compared to the abundance of stage Ia eggs. The consequences of this for the estimates of the spawning biomass are significant; overall abundance would be 50% lower for cod and sole, and 40% lower for plaice (Anon., 1998(a)). As noted above, the Irish Sea calculations used mortality estimates extrapolated to time zero, whereas the N.E. Atlantic calculations did not. VPA estimates from the latter surveys were tuned to the egg production data because no commercial effort data is available for these stocks. Such factors may suggest why spawning biomass estimates using the two methods were so similar. However, even without the tuning, egg production and VPA estimates of biomass differed by only 6% (pers. comm., C. Darby, CEFAS, Lowestoft).

This review aims to discover whether there is any evidence in the literature to support the hypothesis that mortality rates during early egg development are initially low. The probable causes of fish egg mortality are also considered in an attempt to identify plausible mechanisms for such a pattern.

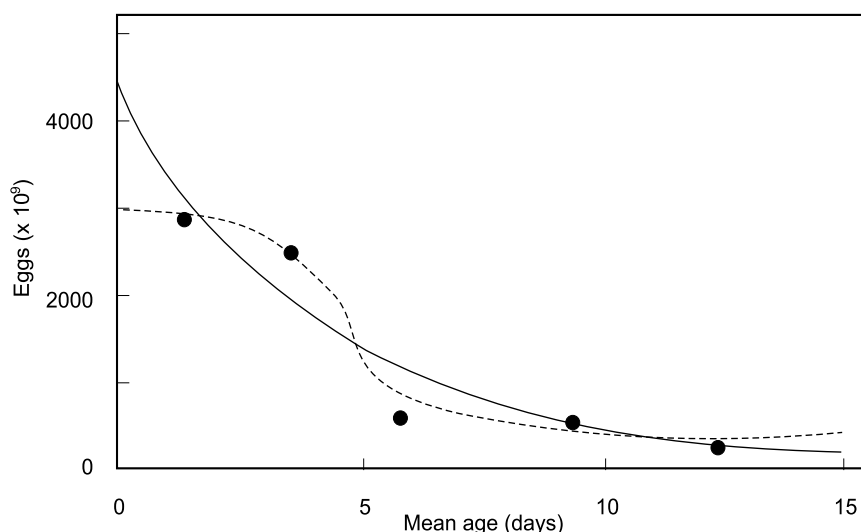


Figure 1. Impact of fitting a sigmoidal mortality function (dashed line) compared with an exponential function (solid line) to total number of cod eggs produced in the Irish Sea in 1995

2. PATTERN OF DEVELOPMENT IN TELEOST EGGS

The eggs and planktonic stages of British marine fish have been described by Russell (1976), the ichthyoplankton of the western North Atlantic by Fahay (1983) and the morphological characteristics of pelagic fish eggs by Ahlstrom and Moser (1980). Blaxter (1988) detailed the pattern of development in embryos and larvae, from which the following summary is adapted.

Pelagic marine eggs are typically single, positively buoyant, and range from 0.6 to 4.0 mm in diameter. During the final stages of ovarian maturation, eggs of fish such as cod, whiting, haddock and plaice, undergo a large influx of water. Water content may reach as high as 92% of the egg weight and because the fluid is hypotonic, the egg becomes buoyant. After fertilisation the perivitelline space is formed and the chorion hardens (Figure 2). The width of the perivitelline space varies between species. The embryo develops initially as a blastodisc, the periphery of which grows over the yolk in a process known as epiboly. Eventually the yolk is enclosed to form a gastrula, but leaving an opening called the blastopore (Figure 3). As the embryo continues to develop, the head and eye cups become identifiable and the trunk lengthens and separates from the yolk. The heart begins to beat well before hatching and in some demersal eggs a vitelline circulation can be seen within the yolk sac. The length of incubation differs between species and is determined by external factors such as temperature (Pepin, 1991), and salinity (Alderdice and Forrester, 1971). Before hatching the embryo becomes active and the chorion softens as a result of enzymes secreted by hatching glands. The degree of development of the larvae at hatching also depends on the species.

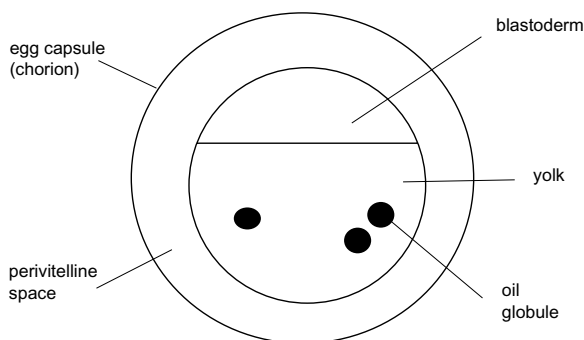


Figure 2. Structure of an early stage fish egg

2.1 Spawning environment

Marine teleost eggs are spawned at a range of depths, and the pattern of vertical distribution is highly variable between species (Coombs and Pipe, 1979; Solemdal and

Sundby, 1981). Sundby (1996) divided early stage fish eggs into three groups determined by buoyancy characteristics. Firstly, pelagic eggs, e.g. mackerel, plaice and cod, have a specific gravity which makes them positively buoyant in the upper mixed layer of the water column. Their neutral buoyancy, measured as salinity, is lower than the salinity of the upper layer and so they rise towards the surface after release. In controlled experiments, fertilised plaice eggs from the North Sea have been estimated to ascend vertically at a mean rate of 5.2 m h^{-1} (Coombs *et al.*, 1981(a)). The next group of eggs, termed bathypelagic, are heavier than the upper layer, but lighter than the density of the deep layer. Bathypelagic distributions are less common than those of pelagic eggs and are usually confined to deeper water species, or to fish found at depth during spawning, such as halibut, blue whiting (Coombs *et al.*, 1981(b)), and hake (Bailey and Yen, 1983). Lastly, benthic eggs are heavier than the density of the bottom layer, and are found attached to rock or other bottom substrate and in beach sediments. Herring and capelin spawn demersal eggs.

As development proceeds, changes in density of pelagic and bathypelagic eggs alter their position in the water column, i.e. the eggs become slightly heavier, so later stages tend to be found deeper in the water. The pattern of vertical distribution is also affected by temperature (Kendall *et al.*, 1994) and salinity conditions, and by mixing within the water column caused by turbulence (Sundby, 1996). In stratified waters, the presence of a thermocline or halocline effectively creates a barrier preventing the movement of eggs across it and restricting them to the upper mixed layer (Coombs and Pipe, 1979). In calm weather at sea, many eggs may be present at the surface.

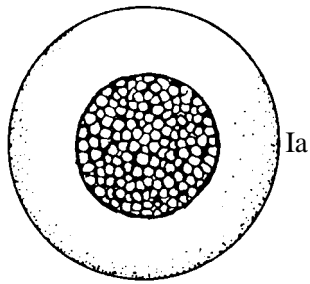
3. EGG PRODUCTION STUDIES

Assessment of the spawning biomass of marine fishes based on ichthyoplankton data generally follow one of three approaches. The first, the annual egg production method was described by Saville (1964) and is based on a series of surveys that cover the whole of the spawning season and area of a particular stock. The basic model, as given by Lo (1985), is

$$P_0 = B_\alpha R (E/W) \quad [1]$$

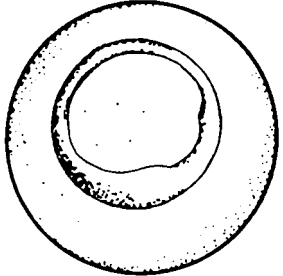
where P_0 = egg production at time zero,
 B_α = spawning biomass,
 R = proportion of biomass being female,
 E = average annual fecundity,
 W = average mature female weight

Estimates of daily production are obtained by calculating the total number of staged eggs produced over the total surface area sampled, and dividing by the mean stage duration derived from laboratory experiments, e.g. Thompson and Riley (1981) for cod



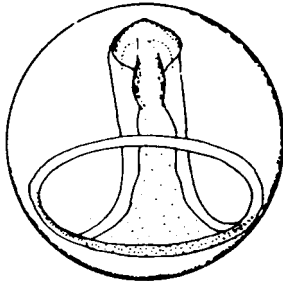
Ia

From fertilization until cleavage produces a cell bundle in which the individual cells are not visible.



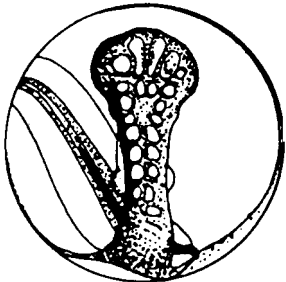
Ib

Formation of the blastodisc, visible as a 'signet ring', and subsequent thickening at one pole.



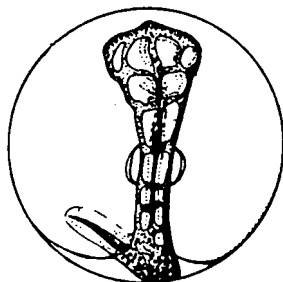
II

From the first sign of the primitive streak until closure of the blastopore. By the end of this stage the embryo is half-way round the circumference of the egg.



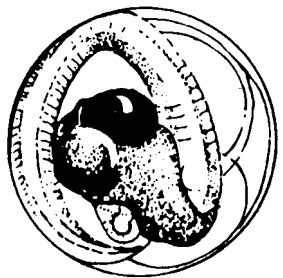
III

Growth of the embryo from half-way to three-quarters of the way round the circumference of the egg. There is development of the eye, and pigment spots develop on the embryo (and in some species, on the yolk and/or oil globule).



IV

Growth of the embryo until it spreads round the full circumference of the egg.



V

Growth of the embryo until the tail is past the head. (Not all species progress to this stage: some hatch at the end of stage IV.)

Figure 3. Development stages of teleost eggs (after Thompson and Riley, 1981)

and Ryland and Nichols (1975) for plaice. Total seasonal production of the population is then calculated by integrating the estimates of daily egg production in each survey over the time interval between the midpoints of the surveys (Figure 4). At the same time, adult fish are sampled to estimate the number of eggs produced per fish weight (E/W), and sex ratio (R). This method is adequate for species that spawn only once during a season, such as cod and plaice, and assumes fecundity is determinate, i.e. fixed before the onset of spawning (Hunter *et al.*, 1992). Potential annual fecundity is estimated from the number of vitellogenic oocytes in the ovaries of females collected immediately prior to spawning. However, a proportion of these can be resorbed before ovulation in a process known as atresia (Greer Walker *et al.*, 1994). The rate of atresia is estimated histologically at successive stages during the spawning season and is then used to estimate the realised specific fecundity. Annual egg production models have been applied to sole from the Bristol Channel (Horwood and Greer Walker, 1990), plaice and cod in the North Sea (Land *et al.*, 1990), and stocks of Western mackerel (Anon., 1998(b)).

In multiple spawners (e.g. anchovy and sardine), annual fecundity cannot be determined from counts of vitellogenic oocytes in the ovaries of females, since these are continued to be produced after the onset of spawning. In such instances, integrated annual egg

production is replaced by an estimate of the daily egg production for a particular survey. This model requires estimates of the spawning frequency to be made as demonstrated by Parker (1980). If the proportion of mature spawning females (F) is incorporated into equation [1], it becomes

$$P_0 = B_\alpha R \cdot F(E/W) \quad [2]$$

To obtain the spawning biomass, daily egg production is divided by an estimate of the daily fecundity of the spawning population. Daily fecundity is the product of spawning frequency and the number of eggs released per spawning. One advantage of the daily egg production method, also known as the 'batch-fecundity' method, is that sampling can be completed within a matter of days rather than months. In addition, no assumption about the shape of the seasonal egg production curve is required. This method has been used to estimate spawning biomass of pelagic stocks such as anchovy (Stauffer and Picquelle, 1981; Picquelle and Hewitt, 1984; Lasker, 1985), and sardine (Wolf and Smith, 1986).

Lastly, a relatively new approach to the estimation of spawning biomass has been developed called the daily fecundity reduction method. This method is based on the daily decline in reproductive potential of a population and the numbers of planktonic eggs during part of the spawning season. Reproductive potential is defined as

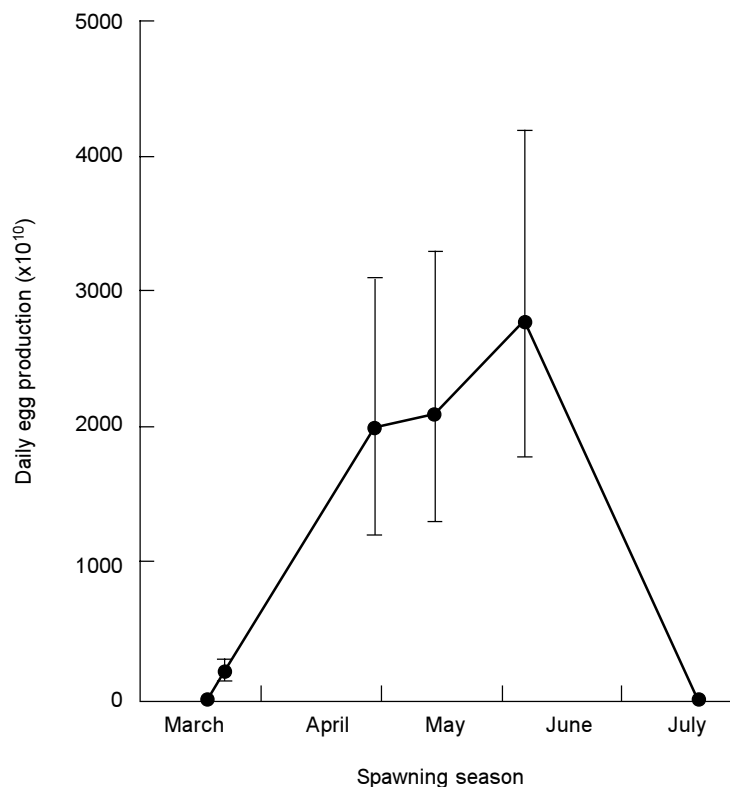


Figure 4. The total Western mackerel production curve (1977). The points on the line represent the sum of egg production in each of the rectangles in the survey grid. Total egg production for the spawning season is estimated by the area under the line joining the point estimates (Lockwood, 1988)

the daily reduction in the number of mature oocytes identified in the parent ovary, and the numbers of females with active ovaries. Like the annual egg production model, the method is restricted to fish species with determinate annual fecundity. However, unlike the annual egg production method it can be carried out after the time of peak spawning. Another advantage of the procedure is that estimates of spawning frequency are not required. The daily fecundity reduction method has been illustrated for Dover sole on the west coast of North America (Lo *et al.*, 1992).

Egg production studies often incorporate estimates of the rate of natural egg into their models. This is designed to account for the mortality suffered during the period between the release of eggs into the water and the time at which they are sampled. Instantaneous daily egg mortality (Z) is normally expressed by

$$N_t/N_0 = \exp[-Zt] \quad [3]$$

where N_0 is the initial number of eggs, N_t the number of eggs remaining at time $t > 0$, and Z the instantaneous mortality coefficient. The equation can be re-arranged to give

$$N_t = N_0 e^{-Zt} \quad [4]$$

An exponential decline implies that mortality occurs at a constant rate, i.e. that in any given time period a fixed proportion of the eggs at the start of that period will die. This model has been used by numerous workers to estimate the instantaneous egg mortality for a range of stocks and species. These include sole in the River Blackwater (Riley, 1974), bay anchovy in Chesapeake Bay (Purcell *et al.*, 1994), and Biscayne Bay (Leake and Houde, 1987), North Sea sole (Land, 1991) and plaice (Heessen and Rijnsdorp, 1989; Land, 1991), black drum (Cowan *et al.*, 1992) and Nova Scotian cod and haddock (Campana *et al.*, 1989). Usually, Z is estimated by plotting the log-transformed numbers of eggs at each developmental stage against the average age of the egg stage. The y-intercept of the linear regression of this plot represents the number of fertilised eggs at age 0, and the slope of the regression gives an estimate of the instantaneous rate of mortality (Heessen and Rijnsdorp, 1989; Land, 1991).

Many of the studies that have used the exponential decay model have reported problems in the fitting of this equation to their data. For instance, Riley (1974) observed from his regression that the production estimates for stage Ib sole eggs appeared too low and those for stage II eggs too high. As a result, egg mortality in the early and later stages appeared reduced compared to the mid-stages. A similar effect was noted by Land (1991) with egg production estimates of sole and plaice in the North Sea. In both studies, the apparent decrease in mortality during the early stages was

associated with problems in the staging of eggs in preserved material, leading to an overestimation of the number of stage II eggs and a corresponding underestimate of eggs at stage I. Thompson (1989) used a version of the exponential decay model to fit mortality curves to mackerel egg counts. However, the data showed a tendency, particularly at higher temperatures, for the daily production of stage IV eggs to exceed that of stages II and III. Again, erroneous stage identification was suggested as a possible cause, but it was also noted that incorrect calculation of the stage durations used may have affected the results.

Another problem workers face is that often the data is not comprehensive enough to justify fitting an alternative function. For example, Campana *et al.* (1989) found that because the eggs of cod and haddock in Nova Scotia could only be distinguished from each other at stage IV, a constant rate of mortality had to be assumed when estimating numbers of stage I eggs for each species. In species with rapid egg development such as bay anchovy (*Anchoa mitchilli*), a similar difficulty arises. In Biscayne Bay, anchovy have been shown to hatch after a period of between 18 to 25 hours at temperatures above 20°C (Leake and Houde, 1987; Purcell *et al.*, 1994). Egg mortality has been estimated from the difference in \log_e abundances of mid-term embryos and 1-day old larvae, meaning that only a constant value of Z could be fitted to the data (Leake and Houde, 1987).

Because of problems with both the sampling and statistical analysis, instantaneous mortality rates of fish eggs and larvae are not easily estimated (Ware, 1975). The above studies suggest that a constant model may not always be appropriate. However, in order to determine whether a genuine biological basis to the observed patterns of mortality exists, and hence whether a departure from the exponential model could be justified, it is necessary to examine egg mortality studies for supporting evidence.

4. ESTIMATES OF EGG MORTALITY

Table 1 summarises some of the estimates of egg mortality given in the literature for a variety of marine teleosts. Daily egg mortality rates can reach as high as 3.64 d⁻¹, but are more commonly below 1.0 d⁻¹. Mortality during the egg stage accounts for a significant proportion of the lifetime mortality of *Anchoa mitchilli* (Leake and Houde, 1987), and in species such as plaice, egg mortality may largely determine year-class strength in recruited populations (Coombs *et al.*, 1990; van der Veer *et al.*, 1990; Hovenkamp, 1992; Ellis and Nash, 1997). However, despite the importance of mortality during the egg phase to studies of recruitment and egg production, very little is known about the processes which may influence it.

Table 1. Egg mortality rates of marine teleosts

Species	Area	Year	Daily egg mortality (Z)	Reference
<i>Anchoa mitchilli</i>	Biscayne Bay, Florida	1979-1980	1.94	Purcell <i>et al.</i> , 1994
	Chesapeake Bay	1977-1981	0.69	Houde, 1987*
<i>Clupea harengus</i>	Atlantic		0.05	Houde, 1987*
<i>Chrysophrys auratus</i>	Hauraki Gulf, New Zealand	1980	0.3-1.01	McGurk, 1986*
<i>Engraulis anchoita</i>	SW Atlantic	1969	0.6	Ciechomski & Capezzani, 1973
<i>Engraulis capensis</i>	S. African coast	1984-86	0.24	Armstrong <i>et al.</i> , 1988
<i>Engraulis japonica</i>	Japan	1966	0.33	Pepin, 1991*
<i>Engraulis mordax</i>	Peruvian coast	1989	0.23	Smith <i>et al.</i> , 1989
	California	1980-1981	0.13-0.39	Lo, 1986
	California	1983	0.18	Picquelle & Hewitt, 1984
<i>Engraulis ringens</i>	Peruvian coast	1988-89	1.12	Smith <i>et al.</i> , 1989
	Peruvian coast	1983	0.91	Pepin, 1991*
<i>Etremeus teres</i>	Gulf of Mexico	1977	1.09	Pepin, 1991*
<i>Gadus morhua</i>	Southern Bight	1970-74	0.03-0.4	Daan, 1981
	Southern North Sea	1987-88	0.14-0.22	Heesen & Rijnsdorp, 1989
	Southern North Sea	1989	0.205	Land <i>et al.</i> , 1990
	Atlantic		0.05	Houde, 1987*
	Lofoten	1983-84	0.1	Fossum, 1988
<i>Harengula jaguana</i>	Gulf of Mexico	1977	3.64	Pepin, 1991*
<i>Melanogrammus aeglefinus</i>	Browns Bank	1983	0.21-0.54	Koslow <i>et al.</i> , 1985
<i>Pleuronectes platessa</i>	German Bight	1947-1971	0.02-0.14	Harding <i>et al.</i> , 1978
	North Sea	1987-88	0.07-0.17	Heesen & Rijnsdorp, 1989
	Southeastern North Sea	1989	0.096	Land <i>et al.</i> , 1990
	Southeastern North Sea	1981-82	0.11-0.2	Coombs <i>et al.</i> , 1990
<i>Sardinops caerulea</i>	Pacific coast	1951-59	-0.31	Smith, 1973
<i>Sardinops melanostica</i>	Japanese coast	1962	0.5	Tanaka, 1974*
<i>Sardinops sagax</i>	Peruvian coast	1988-89	2.12	Smith <i>et al.</i> , 1989
<i>Scomber scombrus</i>	Biscay & Western Approaches	1977-1986	0.05-0.16	Thompson, 1989
	Gulf of St. Lawrence	1985	0.44	Ware & Lambert, 1985
<i>Solea solea</i>	River Blackwater	1969-70	0.6-1.0	Riley, 1974
	North Sea	1988	0.46	Beek, 1989
	Southeastern North Sea	1984-1990	0.4-0.61	Land, 1991
	Irish Sea	1990	0.2	Horwood, 1992
<i>Sprattus sprattus</i>	German Bight	1986	0.04	Alheit <i>et al.</i> , 1987
<i>Theragra chalcogramma</i>	Shelikof Strait, Gulf of Alaska	1981	0.1-0.4	Kim & Gunderson, 1989
<i>Trachurus symmetricus</i>	S. California coast	1951-54	1.64	Pepin, 1991*

* see author for original citation

5. FACTORS CONTROLLING SURVIVAL

The survival of fishes during early life history stages has long been recognised as a probable source of variability in recruitment to adult stocks (Hjort, 1914). Fish egg and larval mortality rates are high (up to 67% d⁻¹, Fossum, 1988) and changeable between years and populations. The mortality rate of North Sea cod eggs is estimated at 22% d⁻¹, which results in only 2% of the eggs spawned surviving to produce larvae (Daan, 1981). Houde (1989) argued that subtle variability in mortality rates will have a more profound effect on survival to recruitment than critical factors such as aberrant drift, failed egg production or acute toxic events. Such incidents are episodic, and considered a threat to recruitment only if a large fraction of the fecundity of a population is lost. On the other hand, less catastrophic events such as pollution, or environmental stressors that moderately increase mortality rates or lower growth rates, could have a large impact. To illustrate this, the author predicted that an increase of just 3% in the daily instantaneous mortality rate of eggs from a theoretical population could result in a ten-fold reduction in recruitment. However, a comparable reduction would only be seen if more than 80% of the egg production was lost as the result of an episodic event. In reality this would mean that although 60% of striped bass eggs spawned in the Potomac River, Chesapeake Bay, were lost because of low temperatures in 1987, the remaining 40%, spawned later in the season, could still produce an average number of recruits.

Factors that have been proposed to alter fish egg mortality rates can be broadly divided into two categories; 'exogenous' and 'endogenous' (Heath, 1992). Exogenous causes include predation, and abiotic (or environmental) effects from changes in temperature and salinity, oxygen concentration, wave action, UV radiation and pollutants. Endogenous sources of mortality stem from inherited genetic abnormalities, or from a decline in egg quality arising from poor parental condition prior to spawning.

5.1 Environmental

5.1.1 Temperature

Based upon extensive laboratory studies (see review by Rombough, 1996), the upper and lower lethal limits of temperature marine fish embryos can withstand differs between species (Table 2). However, the absolute temperature change that most eggs can tolerate is roughly the same, i.e. plus or minus about 6°C. In the open seas and oceans, direct lethality caused by rapid changes in water temperature is rarely expected to be a source of high fish egg mortality (Thompson and Riley, 1981). Under natural conditions, marine fish appear to spawn within a few degrees of the temperature determined to produce the maximum number of total or

viable larvae. Eggs that develop beyond the upper limit of their optimum range may still be fertile but tend to develop abnormally (Ciechomski, 1967(a); Kraak and Pankhurst, 1996), because of damage to critical enzymes (Laurence and Rogers, 1976). The range of temperatures that marine teleost eggs can tolerate is often restricted by other environmental variables such as salinity and oxygen concentration. These influences are discussed in Sections 5.1.2 to 5.1.4.

Apart from the observed direct effect on egg mortality rates caused by extremes of temperature, the survival of incubating fish eggs may be influenced by temperature in other ways. Dannevig (1895) was the first to show experimentally that egg development times were significantly shortened with increases in temperature. Length of egg incubation varies between species at the same temperature and is related to egg size; larger embryos developing at a slower rate than eggs of smaller diameter. Pepin (1991) described the statistical relationship between temperature and time of development for 124 species using previously published values (Figure 5(a)). Residuals from his equation showed a highly significant positive correlation with egg size (Figure 5(b)). The effect of varying incubation period with temperature on the rate of fish egg mortality in the field is not easily estimated. Thompson (1989) anticipated that if temperature acts principally on time of development, then mortality over the egg stage should be less at higher temperatures; low temperatures prolong the period of egg incubation, and hence the time in which fish remain in this highly vulnerable phase. However, some studies have inferred that daily instantaneous mortality rates of pelagic fish eggs increase in relation to a rise in environmental temperature. For example, in laboratory experiments to determine the temperature tolerance of early developmental stages of sole, Irvin (1974) described a clear time/temperature relationship for mortality during incubation. The time to 50% mortality of the sole eggs decreased significantly as incubation temperature increased. Field observations of North Sea sole by Land (1991) appear to confirm that egg mortality increases with increasing sea water temperature at the time of spawning. Pepin (1991) also noted that daily mortality rates of eggs increased with increasing environmental temperature, based on information collated from a number of field reports (Figure 6). In both cases, values of egg mortality used were estimates of the total mortality and not just that attributed to temperature. Despite this, temperature and daily mortality rates appeared to be highly correlated.

The temperature-mortality relationship is not always as straightforward. Land (1991) discovered that when water temperatures were comparatively high in the period before spawning had begun, mortality rates were reduced. This discrepancy was reasoned by the author to have occurred because spawning was induced earlier than usual by temperatures that, although above average, were still lower than later in the year when spawning

Table 2. Temperature tolerance of fish embryos and yolk-sac larvae (from Rombough, 1996)

Family	Species	Stage	Age	Salinity (ppt)	Test duration (d)	Tolerance limits (°C)				Reference
						Lower	Upper	Range	Centre	
Atherinidae	<i>Atherinops affinis</i> (topsmelt)	embryo	f-h	34	20-50	<12.8	26.8	>14.0	19.8	Hubbs, 1965
	<i>Leuresthes tenuis</i> (grunion)	embryo	f-h	34	20-50	14.8	26.8	12.0	20.8	Hubbs, 1965
		embryo	f-h			15.0	28.5	13.5	21.75	Ehrlich & Farris, 1971
Cyprinodontidae	<i>Fundulus parvipinnis</i> (California killifish)	embryo	f-h	34	20-50	16.6	28.5	11.9	22.55	Hubbs, 1965
	<i>Cyprinodon macularius</i> (desert pupfish)	embryo	f-h	35	4.6-53	16.0	33.0	17.0	24.5	Kinne & Kinne, 1962
Blennidae	<i>Hypsoblennius</i> sp. (blenny)	embryo	f-h	34	20-50	<12.0	26.8	>14.8	19.4	Hubbs, 1965
Clupeidae	<i>Sardinops caerulea</i> (Pacific sardine)	embryo	f-h	34		14.0	21.0	7.0	17.5	Lasker, 1962
	<i>Clupea harengus</i> (Atlantic herring)	embryo	f-h	34	7.9-40	2.0	16.0	14.0	9.0	Blaxter, 1956
		larva	yolksac	34	1	-1.8	22-23.5	25.3	10.9	Blaxter, 1960
	<i>Clupea pallasii</i> (Pacific herring)	embryo	f-h	17	9-34.7	1.6	15.2	13.6	8.4	Alderdice & Velsen, 1971
Scaridae	<i>Calotomus japonicus</i>	embryo	f-h	34	0.5-2.4	20.5	28.6	8.1	24.6	Seno <i>et al.</i> , 1926
Scombridae	<i>Scomber scombrus</i> (Atlantic mackerel)	embryo	f-h	34	2-8.6	11.0	21.0	10.0	16.0	Worley, 1933
Gadidae	<i>Gadus macrocephalus</i> (Pacific cod)	embryo	f-h	26.5	7-20	2.0	8.0	6.0	5.0	Forrester, 1964
	<i>Gadus morhua</i> (Atlantic cod)	embryo	f-h	23-27		-1.0	12.0	13.0	6.5	Johansen & Krogh, 1914
		embryo				<-1.8				Valerio <i>et al.</i> , 1992
Pleuronectidae	<i>Parophrys vetulus</i> (English sole)	embryo	f-h	25.9	3.5-11.8	4.5	12.5	8.0	8.5	Alderdice & Forrester, 1968
	<i>Pleuronectes platessa</i> (plaice)	embryo	f-h	23-27		0	14.0	14.0	7.0	Johansen & Krogh, 1914
	<i>Pseudopleuronectes americanus</i> (winter flounder)	embryo	f-h			-1.8	15.0	16.8	6.6	Williams, 1975
		embryo	f-h			3.0	14.0	12.0	8.5	Rogers, 1976
	<i>Eopsetta jordani</i> (petrale sole)	embryo	f-h	28	6.6-13.5	5.3	8.2	2.9	6.8	Alderdice & Forrester, 1971
	<i>Hippoglossoides elassodon</i> (flathead sole)	embryo	f-h	29.5	7.2-16.8	3.8	13.0	9.2	8.4	Alderdice & Forrester, 1974
		embryo	f-h	34	4	7.0	17.0	10.0	12.0	Irvin, 1974
	<i>Solea solea</i> (Dover sole)	larva	yolksac	34	4		23.0			
		embryo	f-h	35	1.4-3.1	10.4	22.3	12.0	16.4	Gadomski & Caddell, 1991
Sparidae	<i>Sparus aurata</i> (guilthead seabream)	embryo	f-h	33	1-3.7	14.2	24.2	10.0	19.2	Polo <i>et al.</i> , 1991
		embryo	f-h	31	3.3-6.7	9.7	16.8	7.1	13.3	Jennings & Pawson, 1991
Sciaenidae	<i>Bairdiella icistia</i> (bairdiella)	embryo	f-h	15-40	0.7-1.3	20.0	30.0	10.0	25.0	May, 1975(a)
		larva		25-35	1		29-31			May, 1975(b)
Mullidae	<i>Mugil cephalus</i> (striped mullet)	embryo	f-h	36.5	1.1-2.9	19.8	31.5	11.7	25.7	Walsh <i>et al.</i> , 1991
Carangidae	<i>Caranx mate</i>	embryo	f-h	34	0.4-1.5	20.2	33.0	12.8	26.6	Santerre, 1976
Polynemidae	<i>Polydactylus sexfilis</i> (moi)	embryo	f-h	34	0.5-1.0	19.0	29.0	10.0	24.0	Santerre & May, 1977
Synentognathidae	<i>Belone belone</i> (garfish)	embryo	f-h	10-45	10-45	12.0	24.0	12.0	18.0	Fonds <i>et al.</i> , 1974

f-h; period between fertilisation and hatching

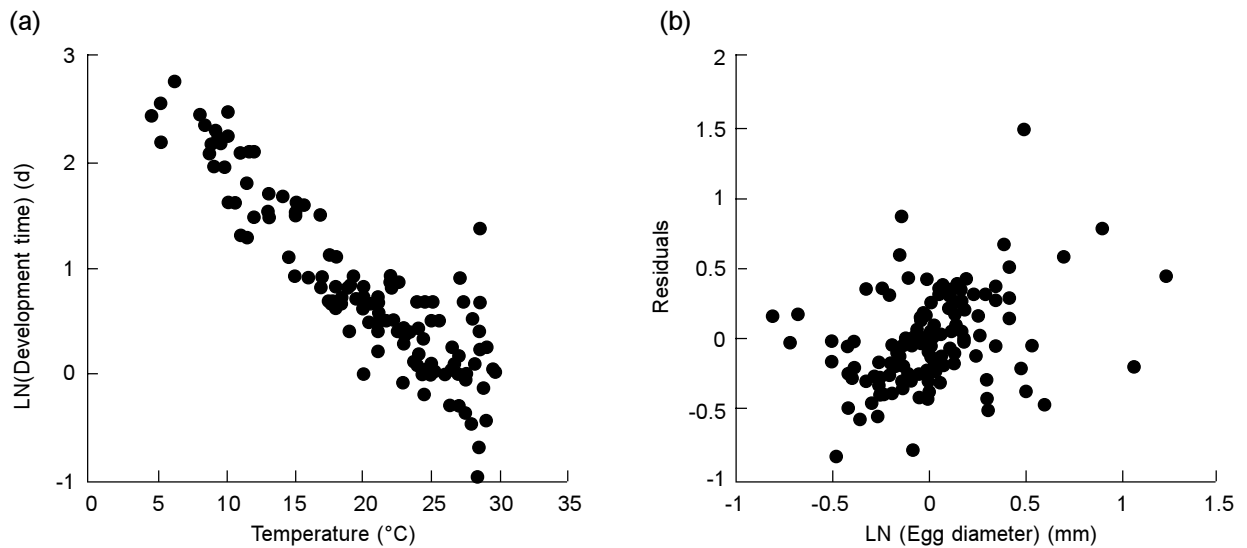


Figure 5. (a) Incubation time plotted in relation to temperature. (b) Residuals from temperature-dependent relationship of incubation times plotted in relation to the diameter of the egg

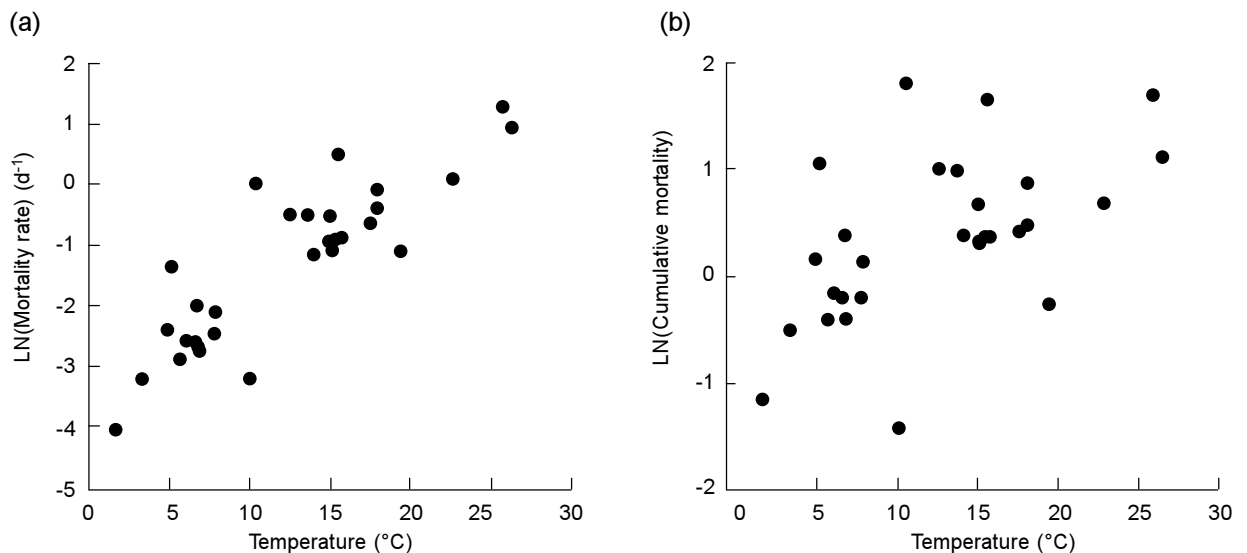


Figure 6. (a) Daily instantaneous mortality rates of pelagic fish eggs estimated from field surveys, in relation to environmental temperature. (b) Cumulative stage-specific egg mortality rates plotted in relation to environmental temperature (from Pepin, 1991)

normally takes place. In addition, Laurence and Rogers (1976) found that despite the shortening of incubation time, egg mortality was independent of temperature for cod, while haddock appeared to have lower mortalities at intermediate temperatures. There is also some evidence that varying water temperatures pre-dispose developing fish embryos to the impact of pollutants. Westernhagen and Dethlefsen (1996) found that the prevalence of malformed embryos of dab and other species in the North Sea was significantly higher at low surface water temperatures. At the same time, a significant correlation existed between water temperature and environmental pollutants.

Embryos of fish are generally considered to be most sensitive to temperature change early in development, particularly during cleavage (Thompson and Riley, 1981) and gastrulation (Rombough, 1996). Mortality rates at higher temperatures are reduced when eggs are exposed at later stages of development (Iversen and Danielssen, 1984). Bonnet (1939) concluded that mortality of Atlantic cod eggs was noticeably reduced during closure of the blastopore (stage II) over the range of temperatures examined. The author also identified a sharp increase in mortality as hatching approached. A similar period of high susceptibility appears to exist in eggs of the Pacific cod (Forrester, 1964).

Temperature affects the rate of development of pelagic fish eggs and the instantaneous and overall mortality suffered. However, sea temperatures change relatively slowly in the open ocean due to the thermal capacity of water. Changes in temperature will influence egg mortality when considered between years or across the length of the spawning season. But, given the time taken for a batch of eggs to develop through to hatching, water temperature is unlikely to change rapidly enough to influence the rates of stage-dependent mortality.

5.1.2 Salinity

In general, an inverse relationship exists between salinity and mortality in pelagic fish eggs (Holliday and Jones, 1967; Laurence and Rogers, 1976). The ability of early life stages to survive different salinities depends on the functioning of internal fluids in a range of conditions. The exact mechanisms controlling osmotic and ionic regulation in teleost eggs are described in detail by Alderdice (1988). In extremes of salinity, malformation of the embryo occurs (Figure 7). Development is aborted and the egg capsule swells in size by up to 20% (Rogers, 1976). Mortality occurs when the embryo is unable to restore levels of osmotic pressure to normal because of an unfavourable ionic gradient. Holliday and Jones (1967) reported that marine fish eggs do regulate their osmotic contents in response to small changes in salinity. The stage of egg development at which regulative capacity is acquired varies between species and is suggested to depend upon life history traits. For example, the pelagic embryos of plaice are able to osmoregulate from the time of fertilisation. If no such mechanism to control seawater uptake existed at this stage the eggs would sink and subsequently die. On the other hand, demersal eggs such as herring are unable to osmoregulate until after gastrulation is complete. At spawning, the eggs become isosmotic with the external medium. The resulting negative buoyancy ensures that they quickly sink and are able adhere to suitable substrate (Wood, 1981).

The effect of salinity on developmental stage appears to vary. In plaice eggs, Holliday and Jones (1967) found that in general resistance to fluctuations in salinity was lowest during the blastula and early gastrula stages. At low salinities (i.e. less than about 15 ‰), authors have reported that many embryos died just prior to hatching or when partly emerged (Rogers, 1976). Holliday (1969) suggested that the low specific gravity of lower salinities makes it difficult for emerging larvae to free themselves from the egg capsule. In addition, he proposed that, compared to higher salinities, the chorion may not rupture as easily. In the demersal eggs of Pacific herring, egg mortality increased at higher salinity levels. Susceptibility was greatest before closure of the blastopore and just prior to hatching (Taylor, 1971).

As with temperature, salinity might influence egg mortality indirectly via its effect on rates of development. For instance, low salinities have been

shown to prolong incubation periods in winter flounder (Rogers, 1976) and Pacific cod (Forrester and Alderdice, 1966). However, the effect of this on stage-specific egg mortality under natural conditions is likely to be negligible. Marine teleost eggs are expected to be spawned in salinities within their tolerated range. Fluctuations in salinity might produce variations in the overall, or between-year rates of egg mortality. But, the survival of teleost eggs over a broad range of salinities in rearing experiments indicates that in most waters, salinity will not be a limiting factor to successful incubation. Even in populations that migrate to brackish water to spawn, the eggs can survive in a constantly varying salinity environment due to their euryhaline properties (e.g. winter flounder, Rogers, 1976).

5.1.3 Temperature and salinity

Temperature effects on fish eggs are modified by salinity, and for this reason the two factors are normally studied in combination. Numerous laboratory rearing experiments have determined the optimal temperature and salinity ranges for the incubation of eggs of several marine teleosts (Table 3). Optimum conditions vary between species. In comparative experiments, the embryos of cod tolerated a wider range of temperatures and salinities than those of haddock (Laurence and Rogers, 1976). In addition, total mortality over all identical combinations was higher for haddock than cod.

In general, the effect of temperature on the embryos of fish is greater than that of salinity (Alderdice and Forrester, 1968; Fonds *et al.*, 1974), particularly on the length of incubation. Often though, there is a low-low/high-high interaction between the two variables, i.e. maximum viability during development is maintained at higher salinities only by a corresponding increase in temperature, and vice-versa. This phenomenon has been reported in a number of studies; (Holliday, 1965; Alderdice and Forrester, 1968; Alderdice and Velsen, 1971; Fonds *et al.*, 1974). Shifts away from the optimum salinity are concluded to reduce the range of temperatures tolerated (Rombough, 1996).

In temperature-salinity experiments, Laurence and Rogers (1976) reported that stage IV was statistically the most significant period of mortality for cod eggs. In contrast, embryo mortality of haddock was greatest at stage II over all combinations, with no apparent relationships. The authors suggested that this indicated a general susceptibility of haddock embryos in the gastrula stage, independent of the two physical factors tested. To conclude, with respect to natural mortality in the sea, it is unlikely that changes in both temperature and salinity would significantly alter the proportions of egg mortality between stages. Instead, over the geographic range of a species, temperature-salinity conditions, particularly temperature, are inferred to limit the abundance of eggs at its boundaries (Alderdice and Forrester, 1968; Alderdice and Forrester, 1971).

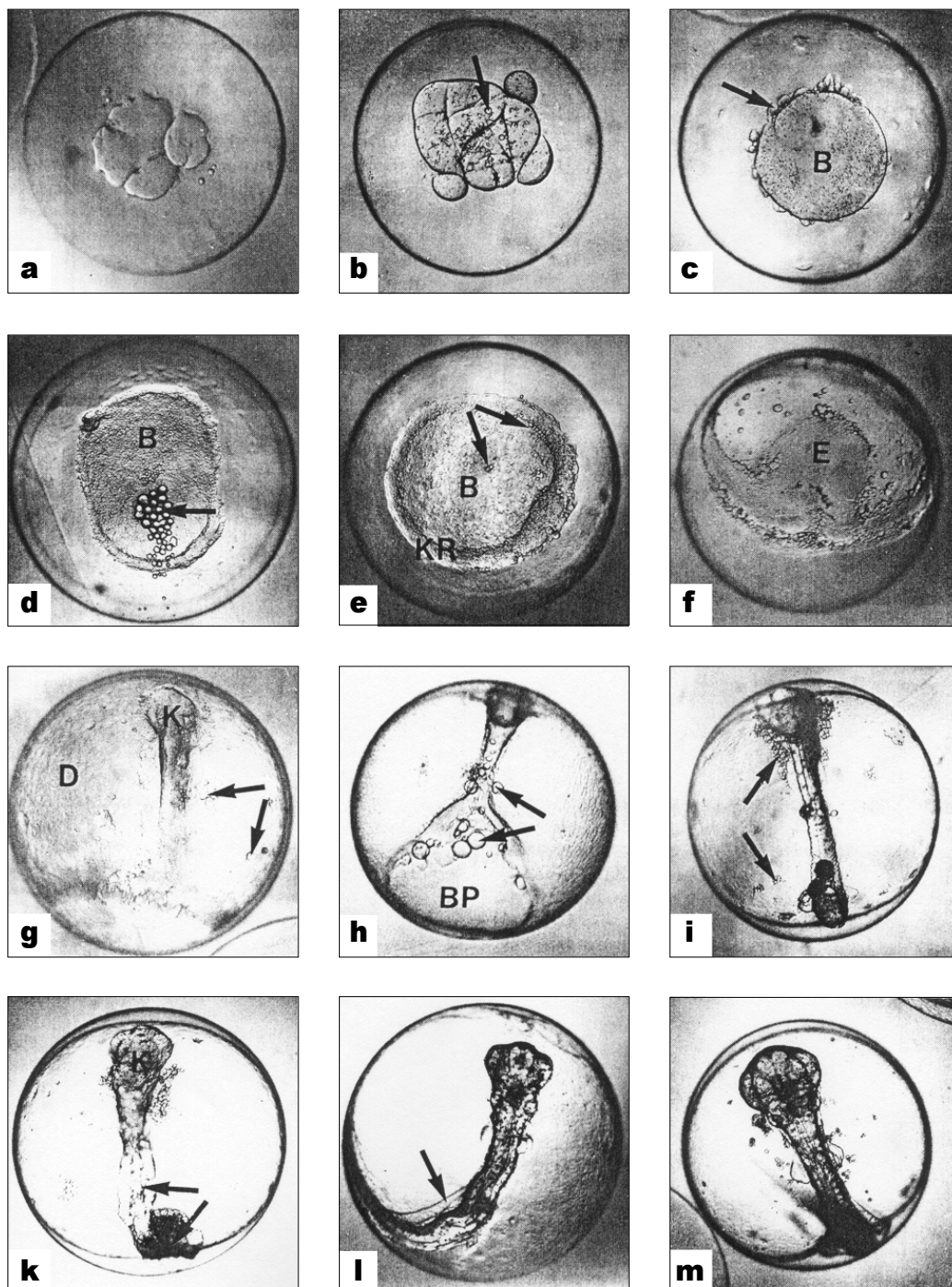


Figure 7. Malformations during embryonic development of pelagic flatfish eggs (from Cameron et al., 1992).
 (a-f) = Malformations during early development:
 (a) Irregular and incomplete cleavage at 4-cell stage with blisters;
 (b) deformation of blastomeres in 16-cell stage with inner building of blisters;
 (c) blastodisc (B) with loose cell aggregates;
 (d) underdeveloped early gastrulation with abnormal blastodisc shape and severe incorporation of blisters;
 (e) gastrulation with blisters on blastodisc and germ ring (KR);
 (f) faulty late gastrula with blister like margins of embryonic shield (E) and germ ring;
 (g-h) = Malformations of the early differentiation processes:
 (g) Severe malformation with blister like buildings on the yolk syncytium (D);
 (h) young embryo with severe blister formation unable to close blastopore (BP);
 (i-m) = Malformations in older embryos:
 (i) Cell proliferation on embryo and yolk especially in the head region;
 (k) faulty differentiation in the head region, proliferation, twisting of the body and crippled tail;
 (l) crippled notochord;
 (m) generation of blisters in further developed fish embryo

Table 3. Optimal temperature and salinity values for the development and survival of marine teleost eggs

Species		Temperature °C	Salinity ‰	Stage showing highest mortality	Reference
<i>Belone belone</i>	garpike	18	15-33		Westernhagen, 1974 Fonds et al., 1974
		17-18	34-37		
<i>Clupea pallasii</i>	Pacific herring	6.5-10.5	10-24	variable; early mortality occurred at highest temperatures and salinities	Alderdice & Velsen, 1971
<i>Engraulis anchoita</i>	Argentine anchovy	10-16	26-50		Ciechomski, 1967(a)
<i>Gadus morhua</i>	Atlantic cod	2-10	28-36	prior to hatching (Stage IV). also high mortalities during Stages I and II	Laurence & Rogers, 1976
<i>Gadus macrocephalus</i>	Pacific cod	3-4.5	17-23		Alderdice & Forrester, 1971
<i>Melanogrammus aeglefinus</i>	haddock	4-10	30-36	gastrula (Stage II)	Laurence & Rogers, 1976
<i>Parophrys vetulus</i>	English sole	8-9	25-28	irregular; high mortality before closure of blastopore	Alderdice & Forrester, 1968
<i>Pseudopleuronectes americanus</i>	winter flounder	3	15-35	high salinities: gastrula low salinities: prior to hatching	Rogers, 1976
		>3	15-25		
<i>Solea solea</i>	sole	10-16	20-40		Fonds, 1979

5.1.4 Oxygen concentration

In the sea, fish egg mortality may be influenced by the complex interaction of factors other than temperature and salinity, including dissolved oxygen. During normal incubation, oxygen uptake in fish eggs increases with development and is dependent on temperature (Rombough, 1988). Demand for oxygen during the early embryonic stages is partly provided by oxygen stores in the yolk and perivitelline fluid. As a result, anoxic external conditions will not inhibit development until gastrulation. Beyond this stage any deviation from normal oxygen consumption will have a negative influence on development and survival. Hempel (1979) described how a deficit of oxygen retards the rate of development, but also causes premature hatching. In addition, an accumulation of lactic acid occurs, possibly coupled with a lack of heartbeat or movement of the embryo. If exposure is short-term, such effects are reversible; mortality and abnormal development will only result from an acute deficiency.

Many studies have estimated the lower lethal levels of dissolved oxygen for freshwater teleost embryos, but very few have attempted to define these for marine species (see review by Rombough, 1988). Despite this, the oxygen concentration of most marine habitats is generally not considered as a limiting factor for the successful production of fish eggs and larvae. The majority of pelagic fish eggs drift in the upper water column where oxygen saturation is sufficient to meet the demands of development. Within normal limits, salinity and temperature appear to have little effect on tolerance

to hypoxia. Alderdice and Forrester (1971) indicated that viable hatch of Pacific cod was largely independent of oxygen, provided experimental levels were above 2-3 mg l⁻¹ and within the optimal ranges of temperature and salinity (Table 3). However, exceptional conditions do occur in marine waters, probably the most noted being found in the Baltic Sea. Here, cod eggs are spawned in deep basins where oxygen and salinity levels vary considerably. Nissling (1994) showed that egg survival declined with decreasing oxygen concentration, but that there was no difference in tolerance between egg stages. At low oxygen concentrations, salinity significantly affected egg survival.

In species that deposit demersal spawn, the mechanisms of gas transfer have been less studied. Some species such as capelin bury their eggs in beach sediments (Frank and Leggett, 1984), while others like herring lay large and sometimes compact masses of eggs. Baxter (1971) calculated that the mortality of herring eggs in the Clyde was less than 6% during the early stages and did not appear to be influenced by the number of layers in the spawn. Evidence suggests that oxygen transport within an egg mass might be facilitated by stirring of the perivitelline fluid as the embryo becomes active (Rombough, 1988). In addition, decreasing levels of oxygen in the perivitelline fluid as development proceeds are thought to increase the diffusion gradient across the egg capsule, ensuring a greater rate of diffusive exchange. However, in thicker masses (i.e. greater than 7 layers), deeper eggs may be threatened with asphyxia as a result of an inadequate oxygen supply (Wood, 1981), or poor water circulation (Taylor, 1971).

5.1.5 Solar and ultraviolet radiation

Early experiments studying the effects of solar radiation on the survival of fish eggs revealed that natural light is not essential to development of the embryo. In some instances, survival to hatching has been found to be less variable when eggs are held in total darkness (Marinero and Bernard, 1966; Ciechomski, 1967(a)). Ultraviolet radiation, specifically UV-B, is the most biologically injurious component of sunlight. Calkins and Thordardottir (1980) stated that in many aquatic organisms, exposure and tolerance to UV radiation are roughly equal. They proposed that there is no large reserve of resistance which could cope with altered exposure without requiring physiological or behavioural modification. In the case of teleost eggs, elevated levels of UV significantly increase the rate of mortality (Marinero and Bernard, 1966; Pommeranz, 1974; Hunter *et al.*, 1979; Steeger *et al.*, 1999). In embryos that survive it retards growth (Hunter *et al.*, 1979; Strähle and Jesuthasan, 1993), reduces buoyancy (Mangor-Jensen and Waiwood, 1995) and alters physiological processes such as heart rate (Steeger *et al.*, 1999).

In their natural environment, fish eggs might rely on passive mechanisms to minimise the effects of radiation. Transparency and opacity in aquatic organisms are both recognised as modifications to protect against deleterious effects of radiation, chiefly in the visible range (Breder, 1962). In transparent embryos, radiation passes through all or nearly all structures without absorption. In pigmented eggs, radiation is blocked, preventing impingement on sensitive organs or systems. In fishes, largely transparent eggs tend to be pelagic and found in places associated with bright illumination, such as the surface and upper layers of the sea. Opaque eggs are normally demersal and deposited in shaded places, strategies that Perlmutter (1961) indicated may have developed in response to radiation effects.

Destructive effects of radiation on teleost eggs in the sea will depend on the wave length and exposure dosage received. These factors will be determined by the amount of light attenuated by different bodies of water in varying weather conditions and patterns of vertical distribution. Water transmits little ultraviolet or infrared emanations (Breder, 1962). However, some pelagic eggs that float close to the sea surface will be vulnerable to some amount of UV radiation, especially in periods of calm. Radiation effects are also likely to differ between species (Hunter *et al.*, 1979; pers. comm. S. Baynes and J. Hallam, CEFAS, Conwy). In laboratory experiments, Baynes and Hallam (*op. cit.*) reported that the yolk-sac larvae of sole were affected by lower ambient levels of UV-B than turbot. Such sensitivities appeared to have some ecological significance; turbot eggs and larvae are found in the plankton in mid-summer, whereas the eggs of sole occur earlier in the year, when UV irradiance is less. Other studies have also indicated a relationship between UV incidence and the time of spawning. In the

North Sea, plaice spawning extends from December to March. During this period, total solar radiation is below the supposed tolerance limits for this species and therefore unlikely to damage the developing eggs (Pommeranz, 1974; Steeger *et al.*, 1999).

Observations on the effects of radiation on stage of embryonic development are few. However, mortality during this period appears to depend on how early exposure to irradiation is started. Steeger *et al.* (1999) reported that plaice eggs exposed to UV-B before gastrulation was finished and stage II reached showed a significantly higher mortality: none survived after five days of irradiation with a daily UV-B dose, compared to 39% survival in control embryos. In contrast, when an identical daily dose was applied at stage II, survival rate in test embryos was no longer significantly different from the controls. A similar, apparently cumulative effect was described by Dethlefsen *et al.* (1996(a)) during a series of tests to simulate irradiance levels with a 40% reduction in atmospheric ozone. High mortalities occurred in the later stages of plaice embryos with pigmented eyes. In contrast, early developmental stages of dab (stage Ia) and plaice (stages II and III), showed no morphological aberrations after 4-18 hours of exposure.

There is growing evidence to suggest that marine organisms may be at risk from the interactive effects of UV radiation and contaminants commonly found in aquatic ecosystems. Under laboratory conditions, aromatic hydrocarbons become toxic or substantially more toxic to a range of freshwater and saltwater species with simultaneous exposure to UV light (Arfsten *et al.*, 1996; Spehar *et al.*, 1999). Unpublished data from studies with the eggs of marine fish is consistent with the findings reported above, namely; that if exposure is started at an early stage of embryonic development, survival during later stages may be seriously impaired (pers. comm., B. Lyons, CEFAS, Lowestoft). However, in most marine environments current levels of UV radiation and pollutants are unlikely to pose a threat to the mortality of fish embryos at different stages of development.

In summary, marine teleost eggs are sensitive to light and elevated UV radiation. In pelagic fish eggs, UV-B reduces survival rates, retards growth, increases abnormalities and reduces buoyancy. Susceptibility to UV exposure depends on a number of factors. Its effects may accumulate with time reducing the survival of later stages. Pelagic marine eggs that are distributed close to the sea surface during prolonged periods of high irradiance and low turbulence are most vulnerable. To date there are no field estimates of fish egg mortality from exposure to UV radiation. However, present ambient levels fall below experimentally determined levels of tolerance are therefore not thought to be of great significance to the mortality rates of embryos at different stages of development.

5.1.6 Mechanical stress

Pelagic fish eggs distributed near the surface in open water may be exposed to the physical effects of mechanical pressure from wave action and sea spray. Early observations of cod eggs suggest that even slight knocks and stress might be enough to rupture the thin membrane surrounding the yolk (Rollefsen, 1930). Osmoregulatory capacity is lost and as a result the embryo sinks rapidly and dies.

Under laboratory conditions, the susceptibility of fish eggs to damage by mechanical pressure has been found to change during development of the embryo (Rollefsen, 1932; Ciechomski, 1967(a); Pommeranz, 1974). Pommeranz (1974) assigned resistance to pressure in North Sea plaice eggs to one of 4 phases:

Stage of egg development	Mechanical resistance	Survival to hatching
First few hours after fertilisation	Extremely low	Low
From ~10hrs post-fertilisation until embryo has surrounded half the yolk	High	Low
From above stage until end of development	High	High
Prior to hatching	Reduced	High

Resistance generally increased with development until just before hatching. However, high mechanical resistance alone does not appear to ensure survival of the embryo through to successful hatching. Comparable studies on the eggs of cod (Rollefsen, 1932), and Argentine anchovy (Ciechomski, 1967(a)), also showed that susceptibility to mechanical pressure is dependent on the stage of development; earlier stages being more vulnerable than older ones. Two stages of development appear to be particularly critical to increased resistance; closure of the blastopore, and envelopment of the yolk by embryonic tissue.

Because the early stages of pelagic teleost eggs appear highly susceptible to application of direct pressure in the laboratory, the forces they might encounter in the sea could be sufficient to increase egg mortality. However, Pommeranz (1974) proposed that there is little evidence to support this in the eggs of plaice. In experiments where eggs were exposed to simulated sea conditions, most survived the effects of spray, bubbling and 'spilling breakers' over short periods. Only prolonged exposure (24 hrs) to sprinkling led to high levels of mortality. Spawning of plaice in the southern North Sea has been observed at a range of depths (Coombs *et al.*, 1990). Depending on factors including wind velocity,

stratification, surface cooling and tidal energy, vertical distribution will vary considerably (Sundby, 1996). In calm conditions, pelagic eggs are predicted to ascend from their spawning depth to reach neutral buoyancy in large numbers near the surface. However, during strong wind-induced mixing, eggs are more evenly distributed throughout the upper layer. This confirms field observations; in both the North Sea (Coombs *et al.*, 1990), and the Irish Sea (Simpson, 1959). Plaice eggs at all stages of development are found throughout the water column in rough weather, so many will avoid the effects of turbulence at the surface.

5.1.7 Pollution

Numerous published reports have demonstrated the potentially toxic effects of pollutants on fish eggs and larvae (see review by Westernhagen, 1988). However, extrapolating laboratory- and mesocosm-based results to field situations is extremely difficult. According to Heath (1992), attempts to provide a direct measurement of pollution mortality in the field are few and have generally proved inconclusive. An alternative approach has been to examine the incidence of abnormalities in developing embryos in relation to possible environmental stressors. Defective early stage embryos are a natural feature of most wild fish populations even in the absence of pollutants (Kjørsvik *et al.*, 1984; Klumpp and Westernhagen, 1995). However, there is strong evidence to suggest that elevated incidences of malformed embryos occur in polluted areas.

Embryos are considered abnormal if stages display any visible morphological and/or chromosomal characteristics that deviate from normal development and differentiation (Westernhagen *et al.*, 1988; Cameron and Berg, 1992; Cameron *et al.*, 1992; Klumpp and Westernhagen, 1995). Gross morphological aberrations, apparent mainly in later stage embryos include missing eyes, bent notochord, twisting of the tail, deformations of the head region and anomalous pigmentation (Figure 7). More subtle abnormalities are identified by irregular cleavages, blister-like outcrops from the body axis and failure of blastopore closure. Detection of cytogenetic defects follows a method determined by Kocan *et al.* (1982), in which numbers of mitotic cells with aberrations at anaphase/telophase are scored to give a relative index. Common malformations include the occurrence of stray chromosomes, attached and free fragments and multi-polar spindles (Cameron and Berg, 1992; Klumpp and Westernhagen, 1995).

The influence of deformation on embryonic survival has been examined in incubation experiments with eggs (cod, plaice and flounder) collected from the western Baltic (Westernhagen *et al.*, 1988). Low hatching success coincided with high malformation rates at respective stations. 85% of embryos that are visibly malformed have been shown to die prior to hatching. In contrast, mortality of normal embryos generally falls

Table 4. Morphological and chromosomal malformation rates in pelagic fish embryos

Area	Species	Year (s)	Mean morphological malformation rate %			Chromosomal aberration rate %	Reference
			f-h	Stage Ia	Stage IV		
Western Baltic	cod	1983-84	18-32	27.9	4.8		Westernhagen <i>et al.</i> , 1988
	plaice		24-28	37.3	1.3		
	flounder		22-44	41.2	8.7		
Southeastern North Sea	dab	1990	6	22.9	1.1	51-63.4 (blastula)	Cameron & Berg, 1992
	plaice		5	6.2	1.9		
	sprat		20	43.2	6.2		
	whiting		24	28.7	6.8		
Southern North Sea	dab: winter	1984-1987	22	44.4	4.9		Cameron <i>et al.</i> , 1992
	summer		8	18.9	5.9		
	flounder		21	41.3	6.8		
	plaice		11	26	1.7		
	Little sole		9	12.5	0		
	turbot		10	22.5	3.1		
Aegean Sea	sole		4				
Aegean Sea	pilchard	1981	11.6				Yannopoulos & Yannopoulos, 1981
	anchovy		9.2				
New York Bight	mackerel		Up to 87 (early stages)			Up to 86	Longwell <i>et al.</i> , 1984
Central & eastern	cod	1979-1982	36				Graumann, 1986
Baltic	sprat		25				
Queensland coast	fish eggs					4.5	Klumpp & Westernhagen, 1995
Norwegian waters	cod		20 (early stages)			6.0-60	Kjorsvik <i>et al.</i> , 1984

below 5% (Cameron *et al.*, 1992). Malformation rates vary widely according to the area, species and developmental stage considered (Table 4). Earliest stages (Ia-II, before closure of the blastopore) show the highest rates of developmental failure compared with more advanced stages, suggesting they are the most sensitive. Many of the deformed stage Ia embryos die off before reaching a later stage, reducing the rate of visibly affected embryos as development proceeds.

One cause of developmental defects in teleost eggs is thought to be the input of anthropogenic contaminants into the marine environment. First reports of unusual mortality of pelagic fish eggs in polluted waters came from the investigations of Dannevig (1895) in the Oslofjord. More recently, sources have reported on malformations in embryos from other marine areas. For instance, in the New York Bight early stage mackerel eggs showed elevated rates of morphological abnormalities up to 87% and similar levels of cytogenetic aberrations, all of which were attributed to pollution of the sea surface waters (Longwell and Hughes, 1981; Longwell *et al.*, 1984). For the period 1979-1982, Graumann (1986) discovered severe anomalies in advanced embryos of cod (36%) and sprat (25%) in the central and eastern Baltic. Oil pollution was discussed as a potential causative agent in this case.

In spring 1983 and 1984 a survey of pelagic fish eggs was conducted by Westernhagen *et al.* (1988) in the western Baltic. A large proportion of embryos of all species displayed aberrant development, reaching maxima of 44% in flounder, 32% in cod and 28% in plaice. In contrast, studies of malformations in fish embryos from 'pristine' environments, e.g. the waters off the Great Barrier Reef in Australia (Klumpp and Westernhagen, 1995), reveal levels of defective embryos to be less than 10%. Besides pollution, fish egg malformation can also be caused by other conditions such as low water temperature (Westernhagen and Dethlefsen, 1996), and changing levels of salinity and oxygen (Alderdice and Forrester, 1971). As examined in Sections 5.1.1 to 5.1.4, these factors are not normally considered critical to egg survival in the sea. However, changes in the levels of these factors might affect the expression of the impact of pollutants in fish eggs (Longwell and Hughes, 1981).

The relationship between incidence of embryo malformations and human activity in the North Sea (generally considered as some of the most highly polluted waters) has been reported extensively. Here, investigations of the health of pelagic fish embryos were initiated in 1984 and have continued to be monitored at intervals since (Cameron and Berg, 1992; Cameron *et*

al., 1992; Dethlefsen *et al.*, 1996(b); Cameron and Westernhagen, 1997). Malformation rates have consistently reached their greatest levels in near-coastal waters known to receive high pollution loads. Rates then decrease with distance from the shore. Particular geographical 'hotspots' are frequently identified in waters off plumes of rivers and estuaries. These include the German Bight (in the plume of the Elbe River), the Rhine and Thames, and other sites along the English coast (Cameron and Westernhagen, 1997).

Seasonal differences are known to occur between embryos from the summer and winter plankton, with overall malformation rates being higher in winter samples (Cameron *et al.*, 1992). Species-specific 'sensitivities' are also evident. For example, abnormalities in whiting were consistently higher than most other species, while the eggs of plaice and other flatfish tend to exhibit overall rates at the lowest end of the scale. In some areas such as off the Wash, no eggs were caught in winter samples and the highest rates were recorded here in summer (77%). Cameron and Westernhagen (1997) suggested that such regions are so heavily polluted that eggs would have a very limited chance of survival.

The main types of pollutants likely to produce effects in the early stages of fish (either experimentally or in the field) are heavy metals, petroleum hydrocarbons and chlorinated hydrocarbons (Westernhagen, 1988). Large quantities of anthropogenic pollutants enter the North Sea by atmospheric deposition, riverine input and ocean dumping (Hardy and Cleary, 1992). Cameron *et al.* (1992) reported that the rivers Rhine and Elbe were the main sources of organochlorine pollution in parts of the southern North Sea and that highest levels of chlorinated hydrocarbons are found in the German Bight. Values of pollutants in the water column decline from estuaries to offshore areas by one or two orders of magnitude. This is as the result of dilution, as well as binding to the sediments.

Pollutants may act on embryos in three ways, either; impairment through the contamination of parental tissue, or via the incubating medium, or both of these in combination. On their way through the food web chlorinated hydrocarbons in tissues become enriched, especially in fatty tissue, and because of their persistence become more concentrated with age. During egg production, the stored substances may be transported with the lipid reserves from the liver or other tissue to the developing gonads (Cameron *et al.*, 1992). The correlation between residues of contaminants in adult reproductive organs and the viability of the eggs produced has been described for flounder, cod and herring from the Baltic, and for North Sea whiting (Westernhagen *et al.*, 1981; Hansen *et al.*, 1985; Cameron *et al.*, 1986; Westernhagen *et al.*, 1987b; Westernhagen *et al.*, 1989). In incubation studies, ovaries with high levels of chlorinated hydrocarbons (particularly polychlorinated biphenyls (PCBs)),

reduced the hatching success and viability of the eggs compared to embryos from less contaminated females.

The sea-surface microlayer (upper 50 μm of the water column) accumulates a range of anthropogenic materials that are potentially toxic to the resident biota (Hardy, 1982; Hardy and Cleary, 1992; Karbe, 1992; Cleary *et al.*, 1993). Substances within the microlayer reduce total and viable hatch in eggs of marine teleosts (Kocan *et al.*, 1987; Westernhagen *et al.*, 1987(a)). The microlayer can retain substances such as heavy metals and pesticides for varying periods of time. Concentrations are sometimes orders of magnitude greater than in subsurface waters (Cleary *et al.*, 1993). Heavy metals have been shown to have a varying effect on incubation times. For instance, hatching is delayed in cod eggs exposed to copper (Swedmark and Granmo, 1981), while in herring eggs exposure results in early hatching (Westernhagen *et al.*, 1987(b)). As with malformation rates, the eggs of test species display different patterns of contamination and vulnerability to toxicants.

Anthropogenic contaminants in the sea impair the development of teleost eggs. Development failure is most apparent in the earliest stages (Ia-II).

Differentiation may be retarded or closure of the blastopore disturbed. In incubation experiments, 85% of registered malformations were lethal within 5 days, while in normal embryos mortality was below 5% (Cameron *et al.*, 1992).

5.1.8 Summary

Changes in exogenous factors, such as increases in temperature and salinity, sufficient to kill large numbers of teleost eggs are probably rare under natural conditions (Hunter, 1984). Marine fish eggs appear to be relatively well protected against damage caused by wave action (Pommeranz, 1974). Meanwhile, impairment from UV radiation seems to require exposure at the sea-surface during a prolonged period of high irradiance; a situation unlikely at current levels, particularly in well-mixed waters. Different species exhibit different abilities to tolerate changes. The sensitivity of a particular species seems to reflect the levels found within its normal habitat. For all species, the earliest stages of development are generally most vulnerable, especially during the gastrula and blastula stages. However, a period of high vulnerability just prior to hatching has also been identified under certain conditions. In limited instances (i.e. pollutants and elevated UV), sublethal effects may be cumulative and lead to a higher mortality in older eggs. However, field data does not support this yet. Changes in the conditions encountered by teleost eggs might influence overall rates during embryonic development, and in turn the total mortality suffered from fertilisation to hatching. However, such fluctuations are not considered of a high enough magnitude to significantly alter the rates of mortality between stages.

5.2 Predation

Little of the natural mortality of fish eggs appears to be caused by the exogenous factors discussed, so alternative sources have been examined. Houde (1987) identified several important causes of mortality in the early life stages of fishes, namely; (i) predation, (ii) starvation or other dietary deficiencies and, (iii) deleterious oceanographic conditions that may transport eggs and larvae into unfavourable conditions for survival. However, only one of these factors is likely to have any significant effect on mortality during the egg phase. Before the mouth, gut and eyes of newly-hatched larvae become functional, developing embryos are sustained nutritionally by yolk reserves. As a result starvation does not normally become a limiting factor until the yolk has been fully utilised (Hewitt *et al.*, 1985; Turner *et al.*, 1985; Houde, 1987). Unusual patterns of oceanic drift and dispersal will, in most cases, similarly affect only the larval stages because individuals risk being transported to regions of low food density (Jones and Hall, 1974). In addition, the duration of larval life usually exceeds that of egg incubation. This reduces the distance over which the eggs are transported compared to larvae, thereby limiting the range of environmental variables to which they may be exposed (Govoni and Olney, 1991). For these reasons predation is widely accepted as the most important cause of mortality during the egg stage (Hunter, 1984; Bailey and Houde, 1989).

Consumption of marine fish eggs and larvae was first documented from incidental observations of their occurrence in the stomachs of field-caught adult fish, e.g. the 'spawny haddock' noted by Bowman (1922). Since then, methods for assessing the impact of predation have largely been determined by the type of predator under scrutiny and the feasibility of large-scale studies. The main approaches used have been:

- i. Analysis of stomach contents to identify predators and estimate frequency and occurrence of eggs in their diets. These are usually coupled with plankton and trawl surveys to establish the relative distributions and frequencies of predator and prey. This approach has most often been used in field situations to examine the feeding of planktivorous fish (Hunter and Kimbrell, 1980; Garrod and Harding, 1981; Daan *et al.*, 1985) and gelatinous zooplankton (Burrell and Van Engel, 1976; Larson, 1991).
- ii. Laboratory-based container studies. These permit direct observation of predatory feeding behaviour including rates of encounter and attack. Estimates can be made of digestion times and the proportion of natural egg mortality attributable to predation. This approach has been used extensively to study predation on eggs and larvae by gelatinous invertebrates (Reeve *et al.*, 1978; Arai and Hay, 1982; Monteleone and Duguay, 1988) and smaller zooplankton (Lillelund and Lasker, 1971; Kuhlmann, 1977; Bailey and Yen, 1983; Brewer *et al.*, 1984).

- iii. Experiments using *in situ* mesocosms, i.e. enclosures large enough to stock fish eggs and their predators close to natural abundance levels. In fish egg mortality studies, mesocosms have been used almost exclusively to assess the impact of gelatinous zooplankton (Cowan *et al.*, 1992; Houde *et al.*, 1994; Purcell *et al.*, 1994).

Laboratory and mesocosm studies have often concentrated on predation mortality of larval stages of fishes, even though field validation of results should be easier to achieve with eggs. Eggs occur in higher numbers than larvae and are presumed to experience higher rates of predation because their distribution is often more patchy, they are smaller and they are unable to evade predators (McGurk, 1986; McGurk, 1987; Ellis and Nash, 1997). In addition, the capsule of a fish egg is relatively resistant to digestion compared with delicate larval tissue which means the consumption of eggs can be more readily identifiable (Bailey and Houde, 1989).

Despite this, the processes that affect fish egg predation are poorly understood. Identification of the major predators from a sizeable range of potential species presents a number of sampling problems, especially if eggs appear only incidentally in their diets. Results can be biased by the type of gear used to collect predators. For instance, voiding of gut contents by trawl and net-caught specimens may take place in unknown quantities in the codend. This would lead to inaccurate calculation of feeding rates, and underestimation of the intensity of predation (Hunter, 1984). In laboratory studies, changes in behavioural patterns brought about by the size of container and/or the stress induced by capture may also influence predation rates and make extrapolation to the field erroneous (Monteleone and Duguay, 1988). Nevertheless, laboratory investigations are recognised as essential for confirming apparent predator-prey relationships and for providing estimates of digestion rates (Brewer *et al.*, 1984). Knowledge of the spatial and temporal distribution of fish eggs and their predators introduces a further confounding factor. Predation is often inferred from an inverse abundance of predator and prey, but presence or absence may actually reflect spatial patchiness (McGurk, 1986), or isolation created by differences in behavioural pattern or vertical distribution, rather than removal by predation (Govoni and Olney, 1991).

Eggs and yolk-sac larvae of marine teleost fish are vulnerable to a great range of predators from small invertebrates to fishes, and even birds (Hunter, 1984). Ideas on the role of egg size regarding natural mortality appear to be conflicting. Bailey and Houde (1989) suggested that a larger diameter of egg confers a survival advantage over eggs of smaller dimensions. In terms of producing larger larvae (which increases chances of survival during this stage) this may hold true. But in laboratory experiments, Ellis and Nash (1997) found that larger plaice eggs were preferred as food to smaller non-plaice eggs by herring and sprat. If offered a

range of particle sizes, Leggett and DeBlois (1994) proposed that predators will select the largest prey item as a strategy to maximise energy intake. This means that if fish do select prey on this basis, then plaice eggs would always be expected to suffer higher rates of predation mortality than smaller eggs. However, this does not appear to be the case. Rijnsdorp and Jaworski (1990) showed that the total mortality of cod eggs was higher than that of larger, sympatric plaice eggs. The authors point out that total mortality rates are the cumulative effect of all predators. Therefore, different size classes of prey will be vulnerable to different size classes of predator. Size strategy will depend not only upon numbers and size-structure of the predator-prey populations, but also the feeding activity of different size classes of predator. For example, in the study by Ellis and Nash (1997), plaice eggs had refuge from sprat which were smaller than 80 mm in length. Since smaller clupeoids are likely to be more numerous than larger ones (Daan *et al.*, 1985), smaller eggs could be expected to be under higher predation pressure than the larger plaice eggs (Rijnsdorp and Jaworski, 1990). Larger egg size may also increase protection from predation by small invertebrate zooplankton. Fish eggs are large relative to the size of food taken by most planktonic invertebrates and have a resilient chorion, making them difficult to grasp and ingest (Bailey and Yen, 1983; Turner *et al.*, 1985). In contrast, rates of consumption of fish eggs by gelatinous predators are independent of egg size (Purcell, 1985).

In addition to size, other passive mechanisms may provide some protection against predation. Immobility ensures that eggs are relatively safe from attack by certain groups of predators which detect prey items from their vibrations or movements (Kuhlmann, 1977). Transparency of pelagic eggs may also reduce vulnerability to visual predators. Ellis and Nash (1997) proposed that because the later stages of plaice eggs are pigmented, they may become more visible to predators such as clupeoids. To demonstrate this the author compared differences in the mortality rates of plaice eggs (determined by Harding *et al.*, 1978), which showed that the mortality of eggs between the older stages (IV and V) is appreciable higher than between stages II and III. Brownell (1987) also reported that eggs and yolk-sac larvae of Cape anchovy, *Engraulis capensis*, were less vulnerable to cannibalism due to transparency than older, eyed larvae. Bailey and Houde (1989) concluded that marine teleost eggs are predated by cruising gelatinous predators, filter-feeding and raptorial fishes, and through random encounters with cruising-raptorial predators.

Rates of predation on fish eggs may also be altered by other factors (see review by Bailey and Houde, 1989). Among these are the numbers of predators relative to prey and the degree to which they overlap temporally and spatially; rates of encounter and digestion; and handling times. In addition, predation rate is also partly determined by the length of time taken before a predator

becomes satiated. Predation by fishes may have a stronger dependence on prey density compared to small invertebrates that satiate rapidly and exhibit relative low rates of attack. Lastly, different water types at different times of the day may affect visibility of fish eggs, making them more or less visible to predators (Hunter, 1984).

Marine fish eggs are preyed upon by a range of aquatic organisms, from dinoflagellates to fishes. Marine birds will also feed on demersally-spawned eggs if they are exposed by low tides (Bailey and Houde, 1989). The main predators can be divided into three functional groups; (a) gelatinous zooplankton, (b) soft-bodied and crustacean zooplankton and (c) planktivorous fish. Small invertebrate zooplankters, such as copepods, are noted to select mostly for small, similar-sized prey items and they often detect prey using non-visual means (e.g. mechanoreception). In contrast, many vertebrate predators are visually oriented towards their prey, are generally much larger and have faster swimming speeds.

5.2.1 Gelatinous zooplankters

Gelatinous zooplankton often prey upon the early life history stages of marine fishes. Much of the earliest information on consumption of pelagic fish eggs has been accumulated incidentally from diet studies and recent research has tended to centre on predation of fish larvae. However, a summary of results from some of these observations is shown in Table 5.

Reeve and Walter (1978), and Reeve *et al.* (1978) showed that pelagic ctenophores have the potential to consume large quantities of copepods and proposed this might also apply to fish eggs. The medusoid stage of many cnidarians also have high daily consumption rates (Purcell, 1985; Fancett and Jenkins, 1988), and are considered as potentially important predators of ichthyoplankton and zooplankton alike. Ctenophores and cnidarians may be particularly effective predators of fish eggs and other relatively immobile zooplankton because they do not reach satiation at high prey densities (Reeve and Walter, 1978). In addition, they feed during both day and night (Purcell, 1989), and ingestion is not inhibited by egg size. Pelagic ctenophore and cnidarian populations can exhibit rapid growth rates (Reeve *et al.*, 1978). Such vigorous growth often results in the sudden appearance of dense swarms of jellyfish which, if they occur at the same time as high numbers of plankton, could lead to significant predatory impact (Purcell, 1985; Fancett and Jenkins, 1988).

Purcell (1985) first reported that fish eggs formed a small percentage of the prey found in the gastrovascular cavities of a number of pelagic cnidarians and ctenophores. Subsequent studies however, have recorded more variability in consumption ranging from as little as 0.1% (*Stomolophus meleagris*) to just over 90% (*Chrysaora quinquecirrha*) (Table 5).

Table 5. Pelagic cnidarian and ctenophore predators of fish eggs (adapted from Purcell, 1985)

Predator		Prey	Consumption	Methods	Location	Reference
Cnidaria						
Scyphozoa						
Rhizostomae	<i>Phyllorhiza punctata</i>	NI	incidental	dip, guts	Puerto Rico	Purcell, 1985*
		<i>Rhopilema verrili</i>	NI	dip, guts	Delaware Bay, USA	Purcell, 1985*
	<i>Stomolophus meleagris</i>	Various	<1% of tot contents	dip, guts, lab	Gulf of Mexico	Larson, 1991
		Sciaenidae	1.40%	dip, guts	Gulf of Mexico	Purcell, 1985*
	<i>Pseudorhiza haeckeli</i>	NI - eggs & ys	2-69.5% (mean 41 %)	dip, guts	Port Phillip Bay, Australia	Fancett, 1988
		NI - eggs & ys		lab		Fancett & Jenkins, 1988
	Semaestomeae <i>Aurelia aurita</i>	NI	5-10%	dip, guts	Puerto Rico	Purcell, 1985*
		Sciaenidae	1%	dip, guts	Gulf of Mexico	Purcell, 1985*
	<i>Chrysaora quinquecirrha</i>	bay anchovy	mean 21.4%. per medusa; 7.6-261.8 eggs	dip, guts	Chesapeake Bay, USA	Purcell <i>et al.</i> , 1994
	<i>Cyanea capillata</i>	NI - eggs & ys	1.6-62.9%. Mean 14%	dip, guts	Port Phillip Bay, Australia	Fancett, 1988
		mainly flounder - eggs & ys		lab		Fancett & Jenkins, 1988
	<i>Pelagia noctiluca</i>	NI	av. 2.5 per medusa	dip, guts	Puerto Rico	Purcell, 1985*
Hydrozoa						
Chondrophora	<i>Velella lata</i>	jack mackerel	48%	net & dip, guts	California, USA	Purcell, 1985*
Hydroida	<i>Aequorea victoria</i>	Pleuronectidae	3%	dip, guts	British Columbia, Canada	Purcell, 1985*
	<i>Liriope tetraphylla</i>	NI	in 40% of medusae	net, guts	Belize	Purcell, 1985*
	<i>Phialidium</i> sp.	hake	4 of 5 eggs available	lab	Washington, USA	Bailey & Yen, 1983
	<i>Sarsia</i> sp.	hake	3 of 5 eggs available	lab	Washington, USA	Bailey & Yen, 1983
Ctenophora						
Tentaculata						
Cydippida	<i>Pleurobrachia bachei</i>	NI	0.13%	net, guts	California, USA	Purcell, 1985*
	<i>Pleurobrachia pileus</i>	plaice	>6 in 33 specimens	net, guts	English Channel	Purcell, 1985*
		NI	0-1.0%	net, guts	Scottish North Sea	Fraser, 1970
	<i>Pleurobrachia</i> sp.	hake	4 of 5 eggs available	lab	Washington, USA	Bailey & Yen, 1983
Lobata	<i>Mnemiopsis leidyi</i>	NI	1%	net, guts	Chesapeake Bay, USA	Burrell & Engel, 1976
		bay anchovy	10-65% eggs d ⁻¹	lab	New York, USA	Monteleone & Duguay, 1988
		bay anchovy	0-3 per medusa	dip, guts	Chesapeake Bay, USA	Purcell <i>et al.</i> , 1994

NI; not identified

ys; yolk-sac larvae

Pelagic cnidarians and ctenophores do not detect prey using vision but, unlike other non-visual predators (see Section 5.2.2), they possess no alternative strategy to perceive an item of prey before contact. Their ability to capture and consume fish eggs is determined by encounter rate and mode of feeding (Bailey and Houde, 1989). Some species, e.g. certain ctenophores such as *Pleurobrachia*, and all siphonophores (with the exception of *Physalia*), feed passively while drifting through the water with their tentacles spread to form a large net (Purcell, 1985). Lobate ctenophores, along with cubomedusae, most scyphomedusae and many hydromedusae feed while actively swimming through the water. In the case of lobate ctenophores, water is drawn through mucus- and tentacle-lined lobes by ciliary current. Such a mechanism is regarded as highly suited for the capture of fish eggs (Reeve *et al.*, 1978).

Predation rates of ctenophores and cnidarians are usually expressed as the volume of water an individual is able to search or 'clear' in a given period of time. Estimates of clearance rates were initially derived from laboratory container studies, but rates can be greatly influenced by the size of container used (Monteleone and Duguay, 1988). To overcome this, floating mesocosms that more closely reflect natural conditions have been devised. Results from these studies suggest that clearance rates tend to be independent of prey density but increase significantly with predator size (Fancett and Jenkins, 1988; Purcell *et al.*, 1993; Purcell *et al.*, 1994). The magnitude of predation mortality of fish eggs will thus depend mainly on the number and sizes of gelatinous predators present.

The predatory impact of two scyphomedusae on the early stages of flounder was assessed by Fancett and Jenkins (1988) in Port Philip Bay, Australia. Using the maximum rate of daily mortality observed (2.4%), the authors calculated that *Cyanea capillata* could remove nearly 20% of the eggs and yolk-sac larvae during a winter incubation period of 9 days. In summer, *Pseudorhiza haeckeli* was estimated to consume a similar proportion (18%) over a corresponding development time of 5 days. Mean values averaged over the whole bay were substantially lower (less than 2%) but both species exhibited significant positive selection for flounder eggs and yolk-sac larvae. This suggested that in areas where scyphomedusae coincided with high ichthyoplankton abundance predation could cause considerable mortality of these early stages.

Predation on the eggs of bay anchovy, *Anchoa mitchilli*, by gelatinous invertebrates has been thoroughly investigated. Purcell *et al.* (1994) reported that the natural mortality of anchovy eggs in Chesapeake Bay was determined by the abundance of gelatinous predators, mainly *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*. Increasing prey density caused a linear increase in the rates of ingestion but did not affect water clearance rates. Clearance rates were also directly related to predator size, confirming laboratory observations of Monteleone and Duguay (1988) and Larson (1991). Monteleone and Duguay (1988) estimated that *M. leidyi* was capable of consuming between 10 and 65% of pelagic fish eggs per day in coastal areas. Meanwhile, total predation mortality of anchovy eggs was calculated by Purcell *et al.* (1994) to range from 3 to 52%. In a comparable study, Houde *et al.* (1994) predicted that this value would be about 22%. Using *in situ* mesocosms as part of the same study, total mortality of anchovy eggs over the 21 hour period between spawning and hatching was estimated to be 78%, equivalent to a mean instantaneous mortality rate of 0.073 h⁻¹. Results inferred that *M. leidyi* and *C. quinquecirrha* were responsible for almost a fifth of this rate.

Govoni and Olney (1991) also studied the predator-prey relationship between *M. leidyi* and *A. mitchilli* in Chesapeake Bay and found small-scale temporal and spatial distributions to be critical to levels of consumption. Predation was heaviest when waters remained mixed allowing fish eggs and gelatinous predators to overlap than during periods of stratification which separated predator and prey in the water column.

Experimentally-derived clearance rates suggest that gelatinous invertebrates can be important predators of pelagic fish eggs. Pelagic ctenophores and cnidarians are potentially responsible for a considerable proportion of the total natural mortality of fish eggs, and an even higher percentage of the predation mortality. For example, the combined influence of *M. leidyi* and *C. quinquecirrha* accounts for virtually all (72-100%) of the predation mortality of bay anchovy eggs in

Chesapeake Bay (Purcell *et al.*, 1994). Predation by large gelatinous zooplankters may be sporadic and will only be critical on the largely undetermined number of occasions when they occur together with fish eggs in high numbers (Blaxter and Hunter, 1982). Evidence suggests that all stages of embryonic development will be equally susceptible to predation by gelatinous invertebrates. They possess no means of detecting prey before contact, so feeding is largely determined by rates of encounter, rather than by any selective process. Consumption rates are unaffected by egg density, and satiation is unlikely to occur at natural prey levels. As a result, ctenophores and cnidarians will tend to consume any particle that is captured on its tentacles.

5.2.2 Other invertebrate predators

Few small invertebrate predators appear capable of effectively feeding on marine fish eggs. In laboratory studies, neither species of cyclopoid copepod (Brewer *et al.*, 1984), calanoid copepod (Lillelund and Lasker, 1971; Bailey and Yen, 1983; Turner *et al.*, 1985; Yen, 1987), chaetognath (Kuhlmann, 1977), euphausiid, nor larvae of crab and shrimp (Bailey and Yen, 1983), consumed fish eggs, even though most were able to feed on fish larvae. Bailey and Yen (1983) reported that, in a series beaker experiments, the only crustacean to feed significantly on the eggs of hake was the amphipod, *Calliopius* sp.

Many copepods are thought to use vision and/or mechanoreception to detect potential food items. Species examined include *Euchaeta* sp., (Bailey and Yen, 1983; Yen, 1987), and *Corycaeus anglicus* (Brewer *et al.*, 1984). Lillelund and Lasker (1971) reported that fish larvae attract copepod predators via the vibrations created by their tail-beat. Individual *Labidocera* react by biting or capturing the larvae but will ignore motionless larvae or floating eggs. *Sagitta* sp. (chaetognaths) also detect prey using non-visual perception. Although showing a clear preference for copepod prey, *Sagitta* attack larval fish in response to their swimming activity. However, they do not attack eggs, even after being starved for up to 48 hours (Kuhlmann, 1977).

Turner *et al.* (1985) suggested that copepods are not major predators of fish embryos simply because the eggs of many species are too large and smooth. In the laboratory, the authors observed that no eggs of Atlantic menhaden (*Brevoortia tyrannus*), size 1.3-1.65 mm diameter, were eaten by the carnivorous copepods, *Anomalocera ornata* and *Centropages typicus*. *A. ornata*, the larger of the two copepods, could grasp and apparently kill smaller eggs of spot (*Leiostomus xanthurus*), 0.72-0.87 mm, but could not ingest them. In contrast, this species readily captured and consumed yolk-sac and first-feeding larvae.

In addition to their large size, the tendency for fish eggs to float at the surface of seawater in containers may

influence laboratory observations of predation by similar-sized zooplankters. Theilacker and Lasker (1974) noted that feeding by *Euphausia pacifica* on anchovy eggs was restricted because the floating eggs were unavailable to the euphausiid. This may not be a problem in the open ocean, however, where eggs are generally more evenly distributed throughout the upper layers of the water column, although this has yet to be tested.

Immunological techniques that detect yolk protein in the digestive tracts of carnivorous zooplankton have provided a relatively new way of assessing predation by these organisms. Using this method, Bailey *et al.* (1993) determined that pelagic crustacean invertebrates are important predators of the early life stages of walleye pollack. Combined with information on the vertical overlap of predators and prey gathered in the field, gammarid and hyperiid amphipods were identified as the main invertebrate predators of eggs, while yolk-sac larvae were the preferred prey of euphausiids. In 1989, gammarid amphipods (all identified as *Cyphocaris challengerii*) alone were calculated to have consumed roughly 14% of the standing stock of walleye pollack eggs for that year. Estimates of overall consumption of eggs by crustacean invertebrates varied with predator abundances, increasing from 11.06% ($0.8\% \text{ d}^{-1}$) in 1988, to 17.44% ($1.2\% \text{ d}^{-1}$) in 1989.

In a similar immunoassay study, Brodeur *et al.* (1996) identified seven taxa of invertebrate zooplankton showing evidence of predation upon walleye pollack eggs. Hyperiid amphipods and euphausiid shrimps were determined as the dominant consumers of fish eggs. But, in contrast to the results of other studies, gammarid amphipods were not considered as major predators for any cruise or gear type. However, this was thought simply to reflect a decrease in relative abundance of gammarid amphipods in some years.

Walleye pollack eggs are estimated to suffer a high and variable natural mortality (Kim and Gunderson, 1989). In the analysis of Brodeur *et al.* (1996), the percentage of available eggs consumed daily by invertebrates fluctuated from <0.1 to $7.4\% \text{ d}^{-1}$. Therefore, the author concluded that variations in predation rate are the most probable cause of differences in the magnitude of daily egg mortality. In addition, the impact of invertebrate predation is likely to be affected by the extent to which the vertical distribution of predators and prey overlap. Walleye pollack eggs are spawned in concentrated patches at depths exceeding 150 m. Bailey *et al.* (1993) found that euphausiids were distributed mainly in the upper 150 m of the water column and so showed minimal overlap with the eggs. In contrast, gammarid and hyperiid amphipods were found at similar depths to the eggs, resulting in higher rates of consumption.

Noctiluca scintillans appears to be the only known unicellular predator of fish eggs. Japanese investigators

have concluded that this dinoflagellate can be a significant predator of eggs of Japanese anchovy. Hattori (1962) reported that eggs were regularly engulfed by *Noctiluca* in the southwestern waters off Japan. In areas with high *Noctiluca* densities, about 13% of the anchovy eggs in the water at the time of sampling were consumed, but the rate for all stations combined was estimated to be around 2%. Similarly, Enomoto (1956) estimated that in areas around the Goto and Koshiki Islands in April, that 7-8% of anchovy eggs were found inside *Noctiluca*. Hattori (1962) suggested predation mortality is potentially very high because the seasonal blooms of *Noctiluca* closely coincide with the main anchovy spawning period. However, Enomoto (1956) reasoned that dinoflagellate blooms are episodic and short-lived in relation to the spawning duration of the Japanese anchovy. So, when the whole spawning season was considered, estimates of the proportion of eggs within *Noctiluca* decreased to 0.4%.

To date, only a few species of pelagic marine amphipod, and the dinoflagellate *Noctiluca*, have been identified as potentially important invertebrate consumers of teleost eggs. However, it must be noted that the predatory impact of only a small number of the soft-bodied and crustacean constituents of the zooplankton have so far been considered (Hunter, 1984). In addition, and as with gelatinous invertebrates, predation on fish eggs by other invertebrate organisms in the plankton is unlikely to significantly affect mortality rates between stages because size appears to be the only factor governing consumption.

5.2.3 Planktivorous fish

Planktivorous fish such as herring, sprat, pilchard, mackerel and others, typically consume copepods and euphausiids as their main prey items (Hunter, 1984; Daan *et al.*, 1985). They are generally filter-feeders, either continuously filtering water through an open mouth (Colin, 1976), or employing a gulping motion to draw in and expel water via their gills. Small zooplankton are retained on the gill rakers during this process (Bailey and Houde, 1989). Because of their size and low avoidance capability, pelagic fish eggs and yolk-sac larvae are likely to be ingested in the same way. Most pelagic embryos should be vulnerable to retention by filter-feeding fishes, providing that rates of encounter are random and the space between each gill raker is small enough to prevent the eggs from passing straight through (Schabetsberger *et al.*, 1999). The impact of planktivorous fish on fish egg mortality could be substantial. For instance, in a cod spawning area in the western Atlantic, approximately 2 to 4 million tons of zooplankton is consumed annually by Atlantic herring, and a further 4 to 28 million tons by mackerel (Edwards and Bowman, 1979). Given their mode of feeding, a proportion of that amount is almost certain to consist of fish eggs and larvae, although no attempt has been made to quantify this.

For the North Sea area, predation on teleost eggs by juvenile and adult fish has been reasonably well documented. Analysis of the stomachs of 27 species from the west-central North Sea in 1976 showed that all of the plankton-feeding fish examined were capable of consuming a wide variety of food organisms including fish eggs (Garrod and Harding, 1981). Anchovy, sprat and sandeel were the main predators of plaice eggs and were also the most abundant in trawl samples. Fish eggs were also found in the guts of herring, whiting, lump sucker, juvenile catfish, gurnard and dab. In the southern North Sea average numbers of fish eggs in the stomachs of clupeoids reached a maximum of 14 in herring, but less than 1 in sprat (Pommeranz, 1981). The eggs were identified as mostly gadoid (whiting and cod) and to a lesser extent pleuronectid (plaice and flounder).

A similar study in the Irish Sea revealed that plaice eggs occurred in 36-97% of stomachs of herring and sprat (Ellis and Nash, 1997). Although plaice eggs formed an important volumetric component in the diet of both species, overall numbers were greatest in sprat. Based on comparison of stomach contents with available prey, plaice eggs appeared to be positively selected compared to the eggs of other species. In addition, ingested embryos were mainly in the later stages of development (III-V), even though they occurred in lower frequencies than stages I and II in plankton samples. In general, the heavy feeding on plaice and other fish eggs recorded in this spawning area was assumed to reflect high densities of eggs in the plankton.

Although there are many accounts of fish egg consumption by planktivorous fish, the proportion of mortality attributable to predation has rarely been determined. Daan *et al.* (1985) estimated that, during the three-year period examined, North Sea herring consumed up to 1.9% of the initial numbers of eggs produced by plaice and from 0.04 to 0.19% of the annual egg production of cod. By number, fish eggs formed a small fraction of the total number of food items (which were mainly copepods), but by weight eggs formed up to 10% of the total consumption. Fish eggs were consumed predominantly by younger herring because older age-groups tended to be found further away from the spawning grounds.

5.2.4 Cannibalism

Cannibalism of fish eggs by pelagic spawners, particularly clupeoids, has been widely reported. Egg cannibalism has been recorded in, amongst others, Argentinian anchovy, *Engraulis anchoita* (Ciechomski, 1967(b)); Japanese anchovy, *E. japonica* (Hayasi, 1967); northern anchovy, *E. mordax* (Loukashkin, 1970), and Peruvian anchovy, *E. ringens* (Blaxter and Hunter, 1982). However, until rates of egg production were established, estimates of the impact of cannibalism on fish eggs remained largely incalculable. In 1980, Hunter and Kimbrell (1980) estimated that about 17% of

the daily egg production of northern anchovy was cannibalised by a single school of adult fish in one day. Using an estimate of natural mortality of around 53% d⁻¹, the authors calculated that roughly 32% of the natural mortality of northern anchovy was due to cannibalism. A subsequent revision of this figure by MacCall (1980), using a new value of Z equal to 0.39, put this value at 28%. Data from the analysis of gut contents showed that frequencies of anchovy eggs in stomachs were highly skewed. In addition, mean numbers of eggs per anchovy increased exponentially in relation to egg abundance in the sea suggesting a non-random consumption of eggs (Hunter and Kimbrell, 1980). During plankton sampling about 90% of the eggs were taken in roughly 20% of the net hauls containing eggs indicating a patchy distribution. Thus, non-random feeding may increase as patchiness of the eggs increases. Schools of fish may aggregate on patches of eggs rather than taking them incidentally when feeding on other zooplankton. In reviewing the evidence available to them, Blaxter and Hunter (1982) found that anchovies in tanks tended to deviated from their normal swimming pattern in response to an extract of anchovy eggs. In addition, in the laboratory active filter-feeding appeared to be stimulated when the water contained egg densities of between 1-5 eggs litre⁻¹.

Egg cannibalism has been found to account for around a fifth of the total egg mortality of Peruvian anchovy (*E. ringens*) during two months in 1981 (Alheit, 1987). In South Africa, consumption of eggs by adult *E. capensis* was estimated to have caused an average of 70% of the total egg mortality (Valdés *et al.*, 1987) and was found to be density-dependent. From laboratory observations Brownell (1985) established that larvae of Cape anchovy longer than about 15 mm will cannibalise eggs and smaller larvae. Under natural conditions, spawning duration of this species is extended and densities of eggs and larvae can be high. As a result, eggs and larvae of varying stages will come into contact with each other, providing numerous opportunities for cannibalism to occur. Predation efficiency increases with predator size and tends to decrease with increasing prey size, presumably due to an improved escape response.

Cannibalistic behaviour in walleye pollack (*Theragra chalcogramma*) in the western Gulf of Alaska has also been the subject of fairly extensive research. Adults of this species form large spawning aggregations and release extensive patches of eggs at depths of between 150 and 200 m (Schabetsberger *et al.*, 1999). As a result eggs occur at higher densities relative to most other pelagic spawning teleosts (Brodeur *et al.*, 1991). Instantaneous mortality of eggs can also be high, reaching up to 0.40 d⁻¹ prior to peak spawning (Kim and Gunderson, 1989). Eggs are apparently ingested inadvertently by the adults during normal gill ventilation. Over a period of five years, mean numbers of eggs per stomach examined ranged from less than 1 up to 47 (Brodeur *et al.*, 1991). In most years, pollack

eggs were found in at least half of the stomachs containing food. The vast majority (86%) of ingested eggs were assigned to the early stages of development. This was linked knowledge of the vertical distribution of eggs and adults, i.e. they are both found in the deepest layers and at the highest densities (Brodeur *et al.*, 1996). Male pollack consume on average 3 times more eggs than females, probably because they spend more time in high egg densities. Alternatively, they may be more active than females during this period thereby increasing rates of gill ventilation (Schabetsberger *et al.*, 1999). Total egg consumption was calculated to be less than 3% of the egg production, even in years of peak adult abundance (Brodeur *et al.*, 1991). Egg cannibalism accounts for only a small proportion of the high natural mortality of this species.

More recently, attempts have been made to quantify the impact of cannibalism in cod and sprat as part of a wider examination of the biological interactions between upper trophic levels in the Central Baltic Sea (Köster and Möllmann, 2000). Results in respect of cannibalism in the cod stock have yet to be published. But for sprat, preliminary studies revealed that predation pressure by sprat on their own eggs appeared to be high. The authors recorded average numbers of sprat eggs ranging from 0 to 50 per stomach, with maximum values tending to occur around the time of peak spawning. In terms of individual daily ration, sprat were estimated to consume up to 189 eggs per fish. The intensity of sprat egg cannibalism varied widely between years. In 1990 to 1992 more than 60% of the seasonal production was estimated to be consumed. After 1993, however, cannibalism rates were significantly lower (<15%). Such differences were caused by a combination of changes in vertical overlap between predator and prey, changes in abundance of sprat, and variations in food availability.

There is some evidence to suggest that planktivorous fish, particularly clupeoids, positively select their prey because they are more highly visible. This would explain why the pigmented, later embryonic stages of plaice were consumed by sprat and herring at higher rates than earlier stages (Ellis and Nash, 1997). Cannibalism of fish eggs appears to have a varying effect on stage-specific mortality depending on the length of the spawning period and the vertical distributions of adults and eggs. However, such interactions have yet to be determined empirically.

5.2.5 Predation on benthic fish eggs

The eggs of demersal spawners normally occur in dense aggregations and are known to attract high densities of fishes and other predatory animals. Eggs are generally fixed to available substrate or buried in the sediment and parental care is lacking. As a result mortality due to predation is expected to be high (Frank and Leggett, 1981; DeBlois and Leggett, 1993(a)). Patches of eggs are immobile compared to pelagic marine eggs and demersal

egg deposition tends to occur in shallower waters, so field observations of egg biomass and predation are relatively easy to obtain. Methods have included the use of SCUBA (Tibbo *et al.*, 1963; Frank and Leggett, 1984), sampling by grabs (Rankine and Morrison, 1989), epibenthic sleds and quadrats (DeBlois and Leggett, 1993b), and coring (Frank and Leggett, 1984).

Accounts of fish predation on the eggs of herring (*Clupea harengus*) in particular are numerous. Consumption of herring eggs by haddock, cod and saithe has been frequently observed (Bowman, 1922; Hempel and Hempel, 1971; Dragesund and Nakken, 1973; Johannessen, 1980; Toresen, 1991). In addition, herring eggs may be inadvertently ingested by sand-eels (*Ammodytes marinus*) as they feed on newly-hatched larvae (Rankine and Morrison, 1989). Species of flounder will also consume benthic eggs, i.e. herring (Tibbo *et al.*, 1963) and capelin (Frank and Leggett, 1984).

Estimates of the proportion of eggs removed by fish predators vary. In some cases up to 40 or 50% of the total annual egg deposition can be consumed (Dragesund and Nakken, 1973; Johannessen, 1980). Tibbo *et al.* (1963) speculated that from the beginning of spawning to the end of hatching, the mortality of herring eggs due to predation by winter flounder, *Pseudopleuronectes americanus*, exceeded 7% and may reach much higher. The stomachs of individual fish contained as many as 16,582 eggs. Sculpins (*Myoxocephalus* sp.), skate (*Raja* sp.) and smelt (*Osmerus mordax*) were also identified as predators of the herring eggs.

Predation on the eggs of spring-spawned herring on the west coast of Norway by cod, haddock and saithe has been described by Toresen (1991). Haddock were established to be the main predator on eggs in this area consuming just over 4% of the total egg production of herring over a period of 50 days. However, the author concluded that this level of predation by haddock was too low to significantly impact survival rates of the eggs before hatching.

Exploitation of the eggs of species that bury them in beach sediments are interesting examples of fish predation on demersal spawn because detection must take place by means other than vision. Frank and Leggett (1984) estimated that egg consumption of capelin (*Mallotus villosus*) eggs by winter flounder reached a maximum of 6% of the total annual egg deposition during the years 1978-80. Larger fish (>34 cm) contained a greater proportion of eggs in their diet than smaller individuals (59% dry weight compared with 22%).

Studies of inshore spawning sites have generally produced estimates of egg mortality substantially lower than many of the offshore examples previously cited. This is suggested to reflect a greater abundance of fish predators

offshore and their larger size (Frank and Leggett, 1984). Demersal eggs are also consumed by marine invertebrates. In coastal regions of Newfoundland, Canada, the gammaridean amphipod *Calliopius laevisculus*, was calculated to remove about 16% of the total capelin egg deposition in 1988 (DeBlois and Leggett, 1993(a)). Allowing for interannual variations in predator/prey abundances the author predicted that predation mortality could reach 30%. Consumption of capelin eggs supports the energetic requirements of *C. laevisculus* to the extent that it may account for roughly half of the total production of the amphipod. Biomass of *C. laevisculus* closely tracks that of capelin eggs suggesting populations may be maintained by the annual reoccurrence of egg deposits at selected intertidal sites (DeBlois and Leggett, 1993(b)).

Only one other study appears to have quantified the intensity of invertebrate predation on the benthic eggs of marine fish. Pálsson (1984) cited in Bailey and Houde (1989), reported herring losses of 10% as a consequence of predation by the amphipod *Anisogammarus pugetensis*. Ducks and gulls were also identified as important predators of herring eggs, accounting for up to half of the estimated total daily predation mortality (17-52%).

5.2.6 Summary

Predation is generally thought to be the main cause of mortality in fish eggs but it is poorly understood in the field in terms of the major predators and their impacts. Extrapolating laboratory data is problematic because of container effects, whilst in the field, gut content analysis is complicated by variable digestion rates, gut voiding, and feeding during net capture (Bailey *et al.*, 1993). Difficulties in the quantitative assessment of egg predation arise because of the incidental nature of eggs in the diets of predators, the role of alternative prey and the patchiness of eggs in the plankton. Feeding behaviour of predators needs to be measured throughout the spawning season, as consumption rates may increase non-linearly with egg abundance (Hunter, 1984).

Studies concluding that predation causes significant egg mortality have often been inconsistent, probably because the parameters on which they are based are so highly variable. For instance, although it can be shown that North Sea plaice eggs are predated by herring (van der Veer *et al.*, 1990), this explains only part of the observed decline in egg abundance. The eggs of cod and plaice are likely to encounter the same types of predator, but cod egg mortality was higher than that of plaice. Predation by herring was estimated to account for about 10% of the mortality in plaice and less than 1% of the mortality in cod. This supports evidence examined by Heessen and Rijnsdorp (1989) indicating that even though herring consume a small proportion of cod and plaice eggs, the main predators (not identified) are likely to be organisms that prefer smaller prey sizes.

The validity of the assumption that predation is the major source of egg mortality in marine teleost fishes has been questioned by Leggett and DeBlois (1994), because it appears to be based upon little conclusive data. Inferences made by Ellertsen *et al.* (1989) regarding the high mortality of cod eggs in the Vestfjord, Norway, are fairly typical. The authors were unable to establish the exact causes of mortality, but suggest they may have included a considerable impact from herring. Likewise, in studies on bay anchovy, predicted rates of egg mortality were lower than measured rates, leaving a significant proportion of the daily mortality (18-28%) unaccounted for (Leake and Houde, 1987). This was presumed to be due to predation by the ctenophore, *Mnemiopsis mccradyi*, and cannibalism by juveniles and adults. However, no predators were actually identified.

Hunter (1984) stated that the high mortality rate of cod eggs is associated with high levels of predation, although the identity of the predators was unclear. Planktivorous fish eat cod eggs, but are unlikely to account for all losses. Gelatinous zooplankters may also consume significant quantities, but predation rates observed in the laboratory are probably seldom realised at sea because of the relatively low densities of fish eggs and the presence of alternative prey items. Laurence (1990) also found that predation effects on the pre-recruit mortality of fish on the Georges Bank were hard to detect and measure. At the time of publication, no important predators of eggs or larvae had yet been identified, nor the magnitude of predation mortality quantified, but predation was still concluded to be significant. In general it would seem that, given certain conditions (for example, high simultaneous numbers of fish eggs and known predators), the levels of fish egg mortality caused by predation can be critical. However, it is perhaps due to the lack of evidence regarding any other significant source of mortality that predation is thought to be the major cause (Heath, 1992).

5.3 Endogenous factors

Egg quality and parental condition are endogenous factors considered to influence embryonic development and survival, but very few studies have been published on the natural level of egg viability in the sea. In the majority of investigations, egg quality is determined from rates of fertilisation and hatching during laboratory incubation. Other criteria sometimes used include egg size, gross morphology, chemical content and evidence of chromosomal abnormality (Kjørsvik *et al.*, 1990). In general, embryos deemed to be of poor quality exhibit reduced buoyancy, a softer chorion, increased susceptibility to contamination by bacteria and higher incidences of chromosomal aberrations compared to those of good quality. The problem with such studies is that most are undertaken with the specific aim of establishing rearing regimes for the successful mass production of fish fry. As a consequence, details of stage-specific mortalities

throughout the incubation period are not readily available. Furthermore, the impact of egg quality on the survival with age of wild fish eggs, especially marine species, has received little attention.

Egg quality will in part be the product of characteristics inherited from the parent fishes. However, experimental evidence suggests that other parental factors may be important in limiting embryonic development and survival. For example, maternal temperature experience prior to spawning has been shown to have a significant effect on the thermal limits of eggs of *Menidia audens* (silverside) incubated in the laboratory (Hubbs and Bryan, 1974). Similarly, the initial buoyancy of pelagic fish eggs may be determined by the salinity profiles to which the parent female is exposed, e.g. flounder (Solemdal, 1973). However, in the sea eggs are likely to encounter environmental conditions approximating those of their parents. Even in fishes that migrate from seawater into brackish water to spawn, survival of the eggs may not be affected. Westernhagen (1974) suggested that the unfertilised eggs in the ovaries of garpike undergo a process of slow adaptation to lower salinities as the parent fishes migrate from the North Sea into the Baltic Sea. This enables them to withstand lower salinities than normal. In contrast, development failure significantly increases in eggs spawned by fish with high pollution loads (see Section 5.1.7).

Age of the spawning female is another factor which plays an important role in egg viability. In gadoids and flounder, survival of fertilised eggs during incubation has been shown experimentally to depend upon their protein and fat content (Kjørsvik *et al.*, 1990). Levels of these substances vary with the age of the parental female, with greatest survival occurring in eggs from the middle-aged groups. Buoyancy of an embryo is also influenced by maternal age or, more specifically, by changes occurring between consecutive spawnings in the same individual. Solemdal (1997) proposed that a larger variation in specific gravity of eggs produced by a repeat spawner leads to greater dispersal throughout the water column. In laboratory experiments with cod eggs, mortality decreased significantly in eggs from the same female, from first to subsequent spawnings:

	Total egg mortality %	Egg diameter (mm)
First-time spawners	57	1.22
Second-time spawners	33	1.32
Third-time spawners	35	1.29

(after Solemdal *et al.*, 1995)

In the sea, morphological and chromosomal abnormalities are the main indicators used to describe egg viability. These are discussed in Section 5.1.7 in relation to the deleterious effects of pollutants. However, a proportion of abnormal development is almost certainly due to natural mutations. Kjørsvik *et al.* (1984) noted that as many as

20% of cod eggs from unpolluted areas showed morphological aberrations. At present, the extent to which endogenous factors impact egg mortality, including varying rates between stages, are little known. Heath (1992) concluded that their influence is almost impossible to measure with any accuracy. Therefore they are usually ignored in estimates of egg mortality.

6. CONCLUSION

Correction of egg numbers for mortality remains a major uncertainty in the annual egg production method. For the 1995 Irish Sea study, applying a variable mortality curve, as opposed to the exponential function, reduces the estimated spawning stock biomass by around 30% (C. Fox, CEFAS, Lowestoft, unpublished data). Non-exponential decline appears to be seen in several studies. However, the problem remains that it is unclear how egg mortality is generated in the sea and how it varies both spatially and temporally. Furthermore, studies into egg mortality in the field are complicated by a lack of resolution in egg age determination. This leads to difficulties in discriminating between mortality functions. In view of this, the development of improved egg ageing techniques should be a priority. Of the causes of mortality considered in this review, predation appears to be the principal factor with the potential to generate reduced instantaneous rates during the earliest egg stages. More specifically, increased predation by visual predators due to enhanced visibility of eggs in later developmental stages could be a possible mechanism. Such selectivity should be further investigated in laboratory or mesocosm studies.

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