

# Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness

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**ABSTRACT:** Daily instantaneous natural mortality rates of marine pelagic fish eggs and larvae are higher than expected from the trend of mortality rate with dry weight in the sea. The difference between observed mortality rates and those predicted from the trend of mortality with dry weight is directly and positively correlated with the patchiness of their spatial distribution, which suggests that it is caused by the feeding of predators on patches of eggs and larvae. The product of weight-dependent mortality,  $5.26 \times 10^{-3} W^{-0.25}$ , and 1 + Lloyd's patchiness index predicts mortality rates close to those that have been measured from the field by other workers. Mechanisms that control the spatial patchiness of eggs and larvae may control early life history survival and thereby influence relative year-class strength of adult fish stocks.

## INTRODUCTION

Mathematical models of mortality rate in marine pelagic organisms have been based mainly on size-dependent predation (Ürsin 1967, Ware 1975, Peterson & Wroblewski 1984). The inherent assumption of these models is that predation occurs everywhere at the same rate, but this is not a realistic assumption because predation in a real aquatic ecosystem depends on the spatial distribution of both predators and prey. The act of predation includes search time as well as feeding time, which implies that the spatial distribution of prey influences both the fraction of the total time spent by a predator searching for prey, and the intensity of feeding (number of attacks per unit time spent feeding) once a predator has located prey.

The maximum effect of spatial distribution on mortality rate occurs in the limiting case where the time required by a predator to handle (capture and consume) a prey item is very much smaller than the total time. In this case a predator's feeding rate is not limited by handling time and it can attack every prey item it encounters. In such a situation the mortality rate inflicted on a prey population by a predator population is mainly controlled by 2 correlated variables: the time available for feeding, and the density of the prey

patches. The variables are correlated because they are different aspects of a single phenomenon: spatial patchiness. The fraction of the total time that is spent searching for prey is directly proportional to the fraction of the total area that is empty of prey, and the density of prey in the remaining area is directly proportional to the fraction of the total area that is empty of prey.

The situation of negligible handling time occurs in nature for at least one group of prey: pelagic fish eggs and larvae. Fish eggs and newly-hatched larvae have poorly developed sensory systems, skeleton, and musculature. The eggs cannot evade capture once a predator has fixed its attention on them, and newly-hatched larvae have only a marginally improved evasion capability. However, once fish larvae begin to school, if they are a pelagic species, or migrate to the ocean floor, if they are a demersal species, the situation of negligible handling time may no longer apply. At this age and size a fish develops predator avoidance behaviour and the handling time of its predator increases towards the level where the natural mortality rate of the fish and its spatial distribution become uncoupled.

Fish eggs and larvae are known to be patchily distributed in space (Smith 1973, Hewitt 1981, Houde & Lóvdal 1985, Koslow et al. 1985, McGurk 1986). This implies that natural mortality rates of fish eggs and larvae are higher than would be expected from the

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general trend of mortality with weight in the sea, because predators have a higher feeding rate on patches of prey than on a uniform or randomly distributed prey. Peterson & Wroblewski (1984) noted that mortality rates of some species of fish larvae with a mean dry weight between  $1 \times 10^{-4}$  and  $1 \times 10^{-2}$  g were higher than expected from the overall trend of mortality rate with dry weight for fish.

This paper describes a model of mortality rate in marine pelagic fish eggs and larvae that combines the weight-dependence of previous models with an index of the spatial patchiness of the eggs and larvae. First, the model and its assumptions are described. Second, a large body of published data is used to demonstrate that mortality rates of marine pelagic fish eggs and larvae are 5 to 10 times higher than rates expected from their dry weight. Third, it is shown that this difference in mortality rates can be explained as the result of the reaction of predators to the spatial patchiness of the eggs and larvae. Finally, the implications of this patchiness-mortality interaction for the study of the population dynamics of fish eggs and larvae, and for the general theory of fishing, are discussed.

#### MODEL OF MORTALITY-PATCHINESS INTERACTION

The exponential rate of natural mortality for fish eggs and larvae is assumed to be the product of the expression for the weight-dependence of mortality,  $M_w$  ( $d^{-1}$ ), and a function of patchiness,  $H(p)$ ,

$$\frac{1}{N} \frac{dN}{dt} = -M_w \cdot H(p), \quad (1)$$

where  $N$  = the number of eggs and larvae;  $t$  = time (d).  $M_w$  is assumed to decrease with increasing body weight of the prey in the pelagic ecosystem according to Peterson & Wroblewski's (1984) model,

$$M_w = 5.26 \times 10^{-3} W^{-0.25}, \quad (2)$$

where  $W$  = dry body weight (g). This model was based on a combination of biomass spectrum theory and bioenergetics principles. It is not a regression model. It was found to describe well the trend of decreasing mortality rate with increasing size for juvenile and adult fishes.

A simple and appropriate index of spatial patchiness is Lloyd's index (Lloyd 1967, Pielou 1977),

$$p = 1 + (\sigma^2 \bar{x}^{-1} - 1) \bar{x}^{-1}, \quad (3)$$

where  $\bar{x}$  = the mean density of eggs or larvae for a cruise;  $\sigma^2$  = the variance of  $x$ . This index measures the

actual crowding of an individual, relative to the average crowding expected in a randomly dispersed population. In a randomly distributed population each individual occupies its own individual space. If the distribution becomes more non-random each individual comes to share its space with 'crowders'. Lloyd's index is equal to the number of 'crowders' per personal space. It is probably the best index of spatial patchiness because it has some biological meaning, it is independent of density, and it is theoretically independent of the scale of sampling. Pielou (1977) presented a mathematical argument based on the Poisson distribution that demonstrated the latter point. However, the empirical relation between Lloyd's index and sampling scale for ichthyoplankton is unknown.

Predators of fish eggs and larvae move through spaces that are empty of prey as well as spaces that contain prey. Therefore, any hypothesis that links predation mortality with spatial patchiness must be tested with data that contains both zero counts and non-zero counts. An examination of the effect of including zero counts on patchiness reveals a simple empirical law: patchiness calculated from data including zero counts,  $p_1$ , is always higher than patchiness calculated from data excluding zero counts,  $p$ , and the fractional change in patchiness is exactly equal to the fraction of zero counts among the total samples,  $\frac{n_1}{n}$ , i.e.

$$1 - \frac{p}{p_1} = \frac{n_1}{n}. \quad (4)$$

Rearranging Eqn (4) for  $p_1$  gives

$$p_1 = p \left( 1 - \frac{n_1}{n} \right)^{-1}. \quad (5)$$

The ratio  $\frac{n_1}{n}$  in Eqn (5) is equal to that fraction of the total time that is spent searching for food in empty space. Therefore,  $1 - \frac{n_1}{n}$  is equal to the fraction of the total time that is spent feeding in a patch, and  $p_1$  is the ratio of the relative number of prey 'crowders' ingested to the fraction of total time that is spent feeding in a patch.  $p_1$  is, in fact, the ratio of the 2 correlated variables discussed above that are thought to control the rate of predation in the case where handling time is negligible. It is an index of the intensity of predation; as the ratio  $\frac{n_1}{n}$  increases, a predator spends more time searching empty space, but when it encounters a patch it feeds more rapidly and efficiently than it would if the prey were distributed more randomly in space.

The hypothesis proposed in this paper is that  $H(p)$  varies directly with  $1 + p_1$ , one for the occupant of a personal space plus the number of 'crowders' that share its space. Therefore, the complete model is

$$\frac{1}{N} \frac{dN}{dt} = -5.26 \times 10^{-3} W^{-0.25} (1 + p_1). \quad (6)$$

## SOURCES OF DATA

Lists of data sources used in this paper are given in Table 1 and the Appendix. Table 1 lists mortality rates for populations of fish eggs and larvae with accompanying patchiness values. All other mortality rates are included in the Appendix. The total mortality rates

of fish eggs, larvae, and juveniles, and of pelagic invertebrates were estimated as the slopes of the right-hand limbs of the catch curves ( $\log_e$  density on age; Ricker 1975). The catch curves of larval fishes spanned the first-feeding stage. The natural mortality rates of adult fishes and whales were calculated from several methods: catch curves of virgin populations; Beverton

Table 1. Natural mortality rates, M, dry weights, W, and spatial patchiness of marine pelagic fish eggs and larvae. Mortality rates for fish eggs and larvae that are not accompanied by estimates of patchiness are listed in the Appendix. V: average volume of water filtered in one plankton-net tow; A: total area surveyed during one cruise; N: number of sampling stations occupied during the cruise; a: area per sampling station. The mean patchiness is the geometric mean weighted by the number of samples taken on each cruise; n: number of cruises or number of ages for which patchiness was reported. Dashes: missing data

Species	Area	M (d <sup>-1</sup> )	W (g)	V (m <sup>3</sup> )	A (km <sup>2</sup> )	N	a (km <sup>2</sup> )	Patchiness			Source
								$\bar{x}$	SD	n	
<b>Fish eggs</b>											
<i>Chrysophrys auratus</i>	Hauraki Gulf, New Zealand	1.01	$8.4 \times 10^{-5}$	50–300	$4.5 \times 10^3$	42	$1.07 \times 10^2$	6.75	1.84	7	Crossland (1980)
<i>Melanogrammus aeglefinus</i>	Browns Bank, Nova Scotia	0.38 <sup>a</sup>	$3.2 \times 10^{-4}$	–	$9.4 \times 10^3$	27	$3.48 \times 10^2$	3.32 <sup>b</sup>	1.31	8	Koslow et al. (1985)
<i>Pleuronectes platessa</i>	English Channel	0.08	$8.4 \times 10^{-4}$	–	$1.3 \times 10^4$	–	–	1.00	–	–	Harding & Talbot (1973), Talbot (1977)
<i>Sardinops sagax</i>	S California coast	0.31	$5.2 \times 10^{-4}$	500	$6.1 \times 10^5$	202	$3.02 \times 10^3$	22.42 <sup>b</sup>	1.98	16	Ahlstrom (1966), Smith (1973)
<i>Scomber scombrus</i>	NE Atlantic coast, USA	0.13	$1.4 \times 10^{-4}$	850	$6.8 \times 10^4$	33	$2.05 \times 10^3$	6.32	1.31	7	Sette (1943)
	NE Atlantic coast, USA	0.88	$1.4 \times 10^{-4}$	–	$1.3 \times 10^5$	191	$6.95 \times 10^2$	12.74	1.28	5	Berrien et al. (1981)
<b>Fish larvae</b>											
<i>Archosargus rhomboidalis</i>	Terminos Lagoon, SE Mexico	0.43	$9.2 \times 10^{-5}$	–	$1.6 \times 10^3$	17	$9.24 \times 10$	9.80	1.69	7	Stepien (1976), Chavance et al. (1984)
<i>Clupea harengus pallasii</i>	Barkley Sound, Vancouver Is.	0.09	$1.6 \times 10^{-3}$	207	$4.16 \times 10$	9	4.51	1.86	1.48	4	McGurk (1986)
		0.09	$1.6 \times 10^{-3}$	207	$4.16 \times 10$	9	4.51	2.13	1.57	22	
		0.06	$1.6 \times 10^{-3}$	207	$4.16 \times 10$	9	4.51	1.86	1.48	13	
		0.31	$1.6 \times 10^{-3}$	207	$4.16 \times 10$	9	4.51	1.77	1.64	13	
<i>Engraulis mordax</i>	S California coast	0.22 <sup>c</sup>	$7.0 \times 10^{-4}$	500	$6.1 \times 10^5$	202	$3.0 \times 10^3$	16.79 <sup>b,d</sup>	1.34	13	Ahlstrom (1966), Zweifel & Lasker (1976), Hewitt (1981), Zweifel & Smith (1981), Hewitt & Methot (1982)
<i>Pleuronectes platessa</i>	English Channel	0.08 <sup>e</sup>	$7.5 \times 10^{-4}$	–	$1.3 \times 10^4$	–	–	1.00	–	–	Harding & Talbot (1973), Talbot (1977)
<i>Sardinella aurita</i>	Senegal-Gambia coast	0.45	$3.6 \times 10^{-4}$	–	$7.1 \times 10^4$	46	$1.5 \times 10^3$	11.39	1.76	11	Conand & Fagetti (1971), Zweifel & Lasker (1976), Conand (1977)
<i>Scomber scombrus</i>	NE Atlantic coast USA	0.35	$3.0 \times 10^{-4}$	850	$6.8 \times 10^4$	33	$2.1 \times 10^3$	5.38	1.26	9	Sette (1943), Kendall & Gordon (1981), Ware & Lambert (1985)
<i>Sebastes</i> spp.	Flemish Cap, NW Atlantic	0.05	$3.8 \times 10^{-3}$	–	$5.8 \times 10^4$	42	$1.4 \times 10^3$	3.53	1.51	3	Anderson (1984)
		0.05	$3.8 \times 10^{-3}$	–	$5.8 \times 10^4$	42	$1.4 \times 10^3$	2.43	1.09	3	
		0.07	$3.8 \times 10^{-3}$	–	$5.8 \times 10^4$	42	$1.4 \times 10^3$	1.05	1.55	4	
<i>Trachurus symmetricus</i>	S California coast	0.78 <sup>f</sup>	$4.0 \times 10^{-4}$	500	$6.10 \times 10^5$	202	$3.02 \times 10^3$	15.83 <sup>b,d</sup>	1.41	9	Ahlstrom (1966), Hewitt (1981), Hewitt et al. (1985)

<sup>a</sup> Mean of 6 estimates of M

<sup>b</sup> Weighted geometric mean patchiness-at-age over the age range over which natural mortality was measured

<sup>c</sup> Mean of 79 quarterly estimates of mortality rate taken from Zweifel & Smith (1981), and 2 annual estimates for 1978–79 taken from Hewitt & Methot (1982). The former were calculated assuming that average linear rate of growth in length was  $0.4 \text{ mm d}^{-1}$  over the 3 to 15 mm length range

<sup>d</sup> Patchiness for data including zero counts,  $p_1$ , was calculated by combining patchiness for data excluding zero counts,  $p$ , and data on the proportion of zero counts to total sample size,  $n_1/n^{-1}$ , (both variables taken from Hewitt [1981]) with the identity:  $p_1 = p(1 - n_1/n^{-1})^{-1}$

<sup>e</sup> Mean of 4 annual estimates

<sup>f</sup> Mortality rate at age 12.5 d, the midpoint of the age range 1 to 25 d. Mortality rate fell from  $1.38 \text{ d}^{-1}$  at hatching to  $0.18 \text{ d}^{-1}$  at age 30 d

& Holt's (1957), Pauli's (1963), and Joseph & Calkin's (1969) tag-recovery methods; regressions of total mortality on fishing effort to find the intercept when fishing effort was zero; and Beverton & Holt's (1956) method of calculating mortality rates from the parameters of the growth equation and the average length of the catch. No distinction was made between pelagic or demersal adult fish.

Dry weight was assumed to be 20% of wet weight. Some universal assumption had to be made because the proximate compositions of many aquatic organisms are not available in the literature. The same assumption was used by Peterson & Wroblewski (1984) and others.

Wet weight was calculated from the midpoint of the length range that spanned the time period over which the mortality rate was measured using a weight-length equation for that species. An equation for a closely related species was employed if a weight-length equation was not available. This procedure is acceptable as long as the body shapes of the 2 species are similar, e.g. early post-yolk-sac clupeid larvae.

The average length was calculated as the definite integral of the length-age equation,  $g(t)$ , from time  $t_1$  to time  $t_2$ , divided by  $t_2 - t_1$ , i.e.

$$\bar{L} = (t_2 - t_1)^{-1} \int_{t_1}^{t_2} g(t) dt.$$

The midpoint of the length range was used for species for which there were no available growth curves.

Egg wet weight was taken from the equation for the volume of a sphere,

$$W = \frac{4}{3} \pi r^3 \rho,$$

where  $r$  = the average radius of the egg (cm);  $\rho$  = the specific gravity of the eggs ( $1 \text{ g cm}^{-3}$ ). Egg radii were taken from the author or from Bagenal (1971), Russell (1976), and Theilacker & Dorsey (1980).

Estimates of Lloyd's patchiness index came from 3 sources: (1) values reported by the authors, e.g. Smith (1973), Hewitt (1981), Koslow et al. (1985), and McGurk (1986); (2) values calculated from densities-at-station data reported by the authors, e.g. Sette (1943), Conand & Fagetti (1971), Crossland (1980), Berrien et al. (1981), Anderson (1984), and Chavance et al. (1984), or (3) values calculated from catch statistics such as the coefficient of variation of the catches reported by Harding & Talbot (1973). All estimates of patchiness were extracted from the same body of data that were used to calculate mortality rates. The patchiness or density-at-station data were reported for either a series of sampling cruises (Sette 1943, Conand & Fagetti 1971, Harding & Talbot 1973, Crossland 1980, Berrien et al. 1981, Anderson 1984, Chavance et al. 1984, McGurk 1986), or for a range of ages of the eggs or larvae (Smith 1973, Hewitt 1981, Koslow et al. 1985). The calculation of patchiness for density-at-station data was as follows: (1) a mean density, a variance, and a single patchiness index were calculated for each cruise; (2) each value of patchiness was  $\log_e$ -transformed, because patchiness is log-normally distributed for many of the species for which it has been measured, and was then weighted by the total number of samples used to estimate it, because the accuracy of a statistic increases with the number of samples used to calculate it; and (3) a mean ( $\pm 1$  SD) patchiness value was calculated from the weighted  $\log_e$  (patchiness) values for the series of cruises. The patchiness values reported for a range of ages had to be adjusted so that they were

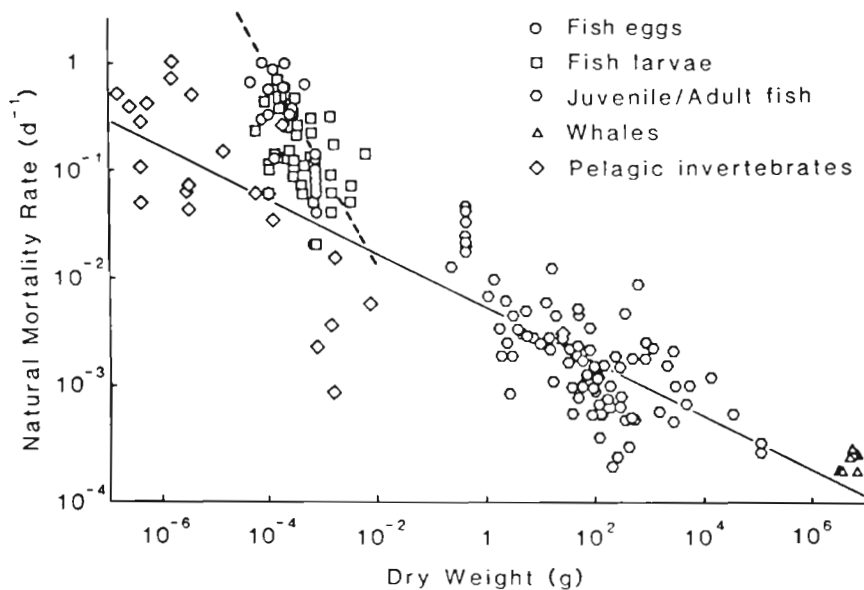


Fig. 1. Plot of instantaneous daily natural mortality rates on dry weight for marine organisms. See Table 1 and Appendix 1 for sources of data. Solid line is the mortality rate predicted by Peterson & Wroblewski's (1984) model:  $M_w = 5.26 \times 10^{-3} W^{-0.25}$ . Broken line is the linear regression of  $\log_e M$  on  $\log_e W$  for fish eggs and larvae:  $M = 2.2 \times 10^{-4} W^{-0.85}$  ( $n = 74$ ,  $r = 0.58$ ,  $P < 0.001$ ,  $SE_e = 0.08$ ).

comparable to those calculated directly from density-at-station data. This was done by: (1) using the reported mortality rates to calculate the relative number of eggs or larvae that were present at each age; (2) weighting each  $\log_e$ -transformed value of patchiness-at-age by the relative number of individuals at that age; and (3) calculating a mean ( $\pm 1$  SD) patchiness value from the weighted log (patchiness-at-age) values. This procedure gives patchiness values that are correlated to some small degree with the observed field mortality rates. Therefore, caution was exercised in employing these data.

Sampling scale was measured with 2 variables: (1) the average volume of water filtered by one tow of the plankton net; and (2) the average area surrounded by a single sampling station. This latter variable corresponds to Lloyd's (1967) definition of a quadrat. I assumed that all surveys were performed over a uniform grid of stations. The total survey area was estimated from maps reported by the authors and then divided by the total number of sampling stations to give the average area of the quadrat surrounding a single station.

All linear regressions reported in this paper are of the functional, rather than predictive, type because of all the variables were measured with error. In such cases the functional regression provides the best estimate of the central tendency of the relation (Ricker 1973).

## RESULTS

### Natural mortality and dry weight

The plot of natural mortality rates on dry weight (Fig. 1) shows that the mortality rates predicted by Peterson & Wroblewski's (1984) model provide an excellent overall fit to the data for pelagic invertebrates, juvenile and adult fish, and whales, over a weight range of 14 orders of magnitude. The plot also shows that: (1) their model consistently underestimates the mortality rates within the fish eggs and larvae group; (2) these rates are 5 to 10 times higher than those predicted from their dry weight; and (3) the weight exponent of the mortality rate for fish eggs and larvae is more than 3 times higher than  $-\frac{1}{4}$ . The relation estimated by the linear regression of  $\log_e M$  on  $\log_e W$  for fish eggs and larvae is

$$M = 2.2 \times 10^{-4} W^{-0.85}; n = 74; r = 0.58; P < 0.001; SE_v = 0.08, \quad (7)$$

where  $SE_v$  = the standard error of the slope,  $v$ . These 3 observations suggest that a variable additional to dry weight is involved in determining the natural mortality

rates of marine pelagic fish eggs and larvae. The hidden variable,  $H$ , must be equal to the ratio of the observed mortality rate as summarized by Eqn (7) to that predicted by Eqn (2), or

$$H = 4.18 \times 10^{-2} W^{-0.60}. \quad (8)$$

### Patchiness of fish eggs and larvae

The patchiness of marine pelagic fish eggs and larvae is generally log-normally distributed within a species (Fig. 2). Therefore, the geometric mean is the appropriate statistic of the central tendency of patchiness (Table 1). A plot of mean patchiness on dry weight (Fig. 3) demonstrates that patchiness is an excellent

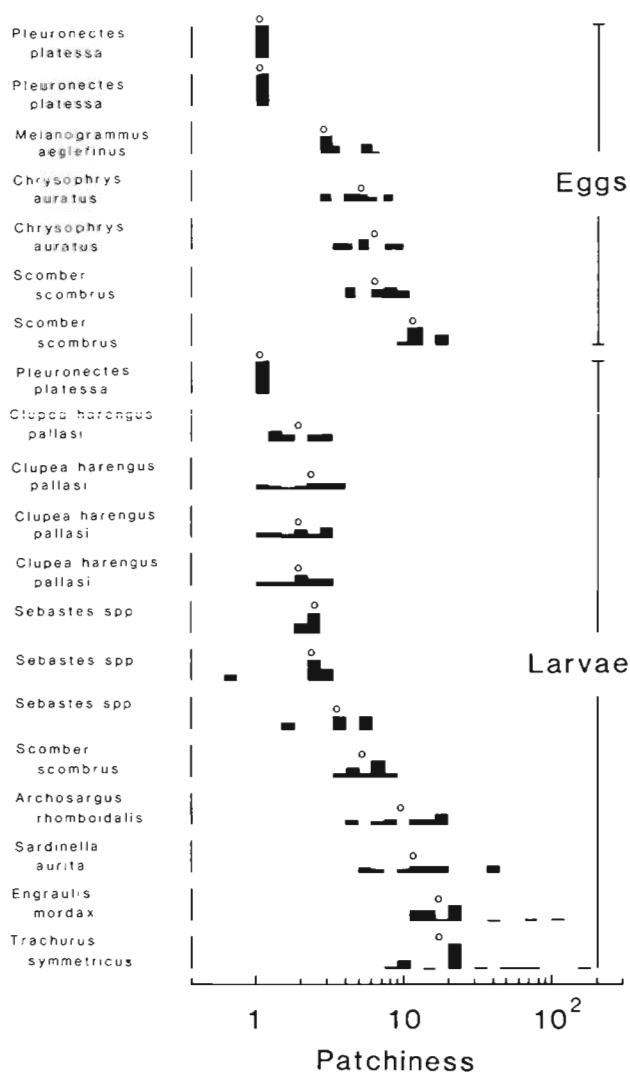


Fig. 2. Frequency distribution of sample-weighted  $\log_e$ -transformed Lloyd's patchiness index for 10 species of marine pelagic fish eggs and larvae. Vertical axes range from 0.0 to 1.0. Empty circles indicate mean  $\log_e$  (patchiness)

candidate for the hidden variable,  $H$ ; the mean patchiness values of the eggs of 5 species of fish and the larvae of 8 species of fish fall symmetrically about the line described by Eqn (8). The linear regression of  $\log_e$  (mean patchiness) on  $\log_e W$  has a slope ( $\pm 1$  SE) of  $-0.79$  ( $\pm 0.15$ ); the slope ( $\pm 1$  SE) for the regression using only patchiness-cruise data is  $-0.71$  ( $\pm 0.14$ ). Although both the slopes and the intercepts are higher than those of Eqn (8), the fit of the patchiness data is good considering the error involved in measuring both patchiness and dry weight.

In order to determine if the scale of sampling has an effect on patchiness 2 indices of sampling scale were

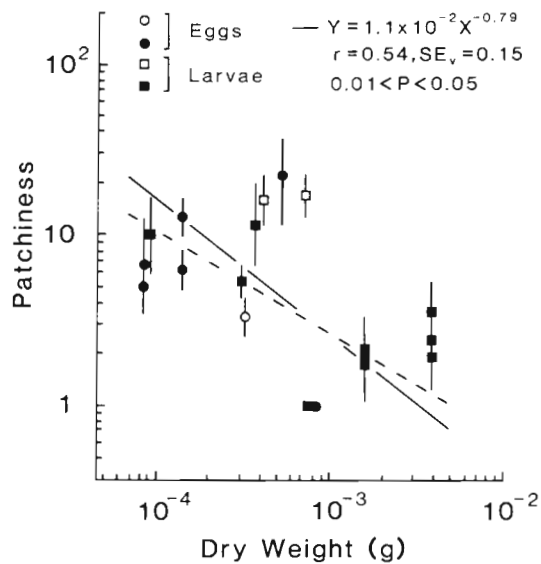


Fig. 3. Linear regression of mean  $\log_e$  (patchiness) on  $\log_e$  (dry weight) for marine pelagic fish eggs and larvae. Vertical bars indicate  $\pm 1$  standard deviation of mean  $\log_e$  (patchiness). Broken line is the predicted line for the hidden variable,  $H$ . Open symbols are patchiness values from patchiness-at-age data; closed symbols are values from patchiness-cruise data

devised: (1) the average volume of water filtered in one plankton-net tow; and (2) the average area per sampling station. Unfortunately, the volume of water filtered was reported for only 7 of the 13 species listed in Table 1. In the other 6 species it was replaced with numbers of eggs or larvae  $m^{-2}$  surface area or numbers  $m^{-2} d^{-1}$ . The information required to convert one set of numbers to another was not reported. Therefore, the residuals of the patchiness-weight regression were plotted on area per station. They were positively and significantly ( $0.001 < P < 0.005$ ) correlated with area per station but this correlation depended totally on the area per station of the 3 species sampled by the CalCOFI ichthyoplankton survey grid off southern California (Ahlstrom 1966): *Sardinops sagax* eggs, and *Engraulis mordax* and *Trachurus symmetricus* larvae.

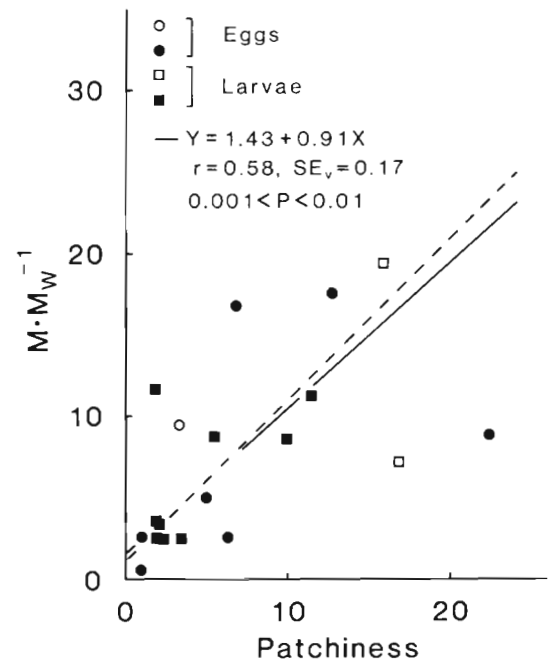


Fig. 4. Linear regression of the ratio of observed mortality,  $M$ , to the rate predicted by Peterson & Wroblewski's (1984) model,  $M_w$ , on Lloyd's patchiness index. Broken line is predicted from Eqn (6):  $M \cdot M_w = 1 + p_i$ . Open symbols are patchiness values calculated from patchiness-at-age data; closed symbols from patchiness-cruise data

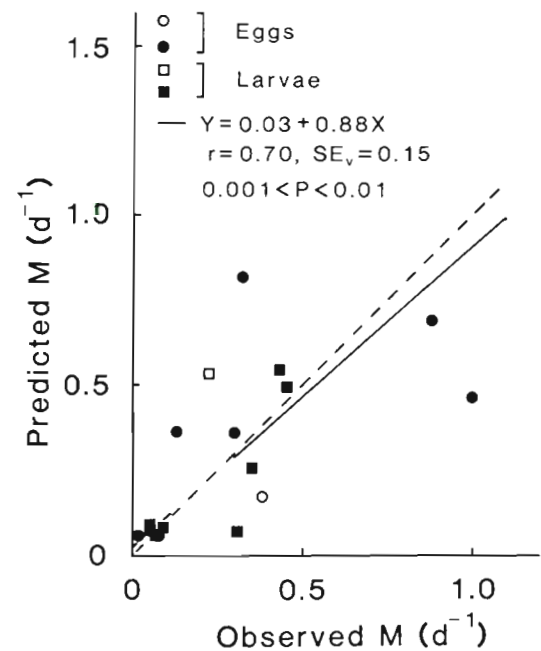


Fig. 5. Linear regression of mortality rates predicted by the mortality-patchiness model,  $M = 5.26 \times 10^{-3} W^{-0.25} (1 + p_i)$ , on observed field mortality rates. Broken line is the line of equality between predicted and observed. Open symbols are patchiness values calculated from patchiness-at-age data; closed symbols are values from patchiness-cruise data

When these species were removed the correlation was not significant ( $P > 0.05$ ). Since: (1) two of these 3 CalCOFI data points were derived from patchiness-at-age data, which is considered less trustworthy than patchiness-cruise data; (2) there was no relation between the residuals and area per station over the range 0 to 2050 km<sup>2</sup>; and (3) there is no other evidence to support the hypothesis that patchiness increases with increasing quadrat size, but theoretical arguments that support the opposite, patchiness was not corrected for the effects of sampling scale.

### Patchiness-mortality interaction

A plot of the ratio of the observed field mortality rates to that predicted by Eqn (2) on mean patchiness shows that the 2 variables are highly correlated (Fig. 4). This correlation remains after the 3 patchiness-at-age data points are removed, although the level of significance falls to  $0.01 < P < 0.05$ . The slope and the intercept of the regression are indistinguishable from 1.0, which supports the theoretical arguments that the hidden variable is equal to  $1 + \text{patchiness}$ . When the mortality rate predicted by Eqn (6) is plotted against the observed field mortality rates (Fig. 5), the data points fall symmetrically about the line of equality. A linear regression of predicted on observed mortality rate has a slope that is within 1 standard error of the line of equality and an intercept that is indistinguishable from zero. These results are unchanged when the 3 patchiness-at-age data points are removed. In summary, the evidence supports the hypothesis that the mortality rates of marine pelagic fish eggs and larvae vary directly with their spatial patchiness as measured by  $1 + \text{Lloyd's patchiness index}$ .

## DISCUSSION

Powerful ideas generate new questions as well as answer old ones. The allometric approach to studying ecosystem processes has produced a simple model of the weight-dependence of mortality rate in the pelagic ecosystem. It has also generated a new question: why are the mortality rates of marine pelagic fish eggs and larvae so much higher than those predicted by this general trend line? This observation is what Schmidt-Nielsen (1984) calls a 'secondary signal'. I propose one possible answer: the mortality rate for this group of animals is directly proportional to their spatial patchiness. This hypothesis has biological meaning that is rooted in the idea that fish embryos and early stage larvae are more vulnerable to predators than they would otherwise be on the basis of their body weight.

Their vulnerability implies that the feeding rate of their predators is limited more by the time required to locate them than by the time required to capture and consume them. Thus the spatial distribution of fish eggs and larvae determines how often a predator encounters a patch of eggs or larvae and how intense is the predation mortality on a patch.

Peterson & Wroblewski's (1984) premise, that natural mortality rate scales as the  $-0.25$  power of dry weight, was derived from data on juvenile and adult fish only, but it also happens to describe well the overall trend of mortality rate with dry weight for organisms other than adult fish. It also happens to be the exponent for the weight-dependence of specific metabolic rate (metabolic rate per unit weight). Therefore, it was used in this paper as a convenient description of the first-order scaling of natural mortality rate. In this argument, patchiness is considered to be a second-order scaling. I recognize that the weight exponent of mortality rate may be quite different from  $-0.25$  for groups other than fishes. It is possible that the profound differences in the mass exponent and scaling coefficient of the production/biomass (P/B) ratios between invertebrates, fishes, and mammals that were demonstrated by Banse & Mosher (1980) have counterparts in the weight exponents of natural mortality rate. In a steady-state system the P/B ratio is equivalent to natural mortality rate because it is that fraction of the production which is excess to the requirements of maintaining a steady-state biomass and which is lost to predation. The question of the correct numerical weight exponent of mortality rates is still an open one; it can be answered by: (1) evaluating the parameters of Peterson & Wroblewski's Eqn (6),  $M_w = ckW^{-x}$ , for organisms other than fish; (2) by filling the gaps in the mortality-weight plot, particularly the gap between  $10^{-2}$  and 1 g and the very large gap between  $10^{-10}$  and  $10^{-6}$  g; and (3) by devising and testing second-order ecological hypotheses to account for any between-group differences in the weight exponent. However, even if it can be demonstrated that the overall weight exponent is not  $-0.25$ , this does not affect the core of the mortality-patchiness hypothesis. There is a real correlation between natural mortality and spatial patchiness in pelagic fish eggs and larvae and there are logical arguments to support the idea that this correlation is causal in nature.

The mortality-patchiness hypothesis is a significant improvement over Peterson & Wroblewski's (1984) model; it reduces the deviation between model and observation from a factor of +5 to 10 to a factor of  $\pm 1$ . The fit of the field mortality rates to the model is excellent for those species whose eggs and larvae experience mortality rates less than  $0.1 \text{ d}^{-1}$ : *Pleuronectes platessa* eggs and larvae, *Clupea harengus*

*pallasi* larvae, and *Sebastes* spp. larvae. The fit is less good for those with higher mortality rates. One reason for the relatively poor fit of the latter group is real variation in time and space of both mortality and patchiness.

In this analysis natural mortality rates are assumed to be constant over the egg and larval stages even though it is obvious that over longer time periods mortality must decrease in order to approach the lower values that have been measured for juvenile and adult fish. The assumption of constant mortality rate has been commonly used in larval fish ecology and it is supported by the fact that the catch curves of most fish eggs and larvae are relatively straight (May 1974, Dahlberg 1979). This assumption is probably reasonable for those species which fall on the low mortality/low patchiness end of the mortality-patchiness continuum, but it is probably not an accurate assumption for those species in the high mortality/high patchiness group. An example of the former is Pacific herring *Clupea harengus pallasi*; the larvae lose 2.5 patchiness points over a 25 d period before they begin to school (McGurk 1986). According to the mortality-patchiness hypothesis this implies a 2.5-fold decrease in larval mortality rate over this period, a decrease which is probably within the range of observational error; the catch curves measured for all populations of larval Pacific herring have been straight (McGurk 1984, 1986). An example of the latter group is the jack mackerel *Trachurus symmetricus*, which loses 12 patchiness points in 4 d of early larval life (Hewitt 1981). Hewitt et al. (1985) reported that the mortality rate of larval jack mackerel off southern California decreases from  $1.37 \text{ d}^{-1}$  at hatch to  $0.18 \text{ d}^{-1}$  30 d later (Table 1), a 7.6-fold decrease. The eggs of the Pacific sardine *Sardinops sagax* lose about 50 patchiness points in 3 d (Smith 1973), indicating that the mortality rate should decrease 50-fold during the egg stage. This rapid change in mortality rate may not be measurable with current sampling and egg-aging techniques. At the very least, it suggests that the estimate of  $M = 0.31 \text{ d}^{-1}$  (Table 1) for Pacific sardine eggs is too low.

Mortality rates have been assumed to operate uniformly in space but there is evidence to indicate that mortality varies spatially as well as temporally. Irreversibly starving larvae have been found to be patchily distributed by Shelbourne (1957: *Pleuronectes platessa*), O'Connell (1980: *Engraulis mordax*), Hewitt et al. (1985: *Trachurus symmetricus*), and McGurk (1986: *Clupea harengus pallasi*). The role of irreversible starvation has been ignored in this analysis because there is no agreement on how the instantaneous rate of mortality due to starvation is to be calculated, and therefore, there is no agreement on its relative importance to total mortality. The evidence to date

indicates that starvation occurs in nature but that it is responsible for only 3 to 25 % of total mortality (McGurk 1986). Eqn (6) can be easily modified to accept an additive term for starvation mortality. This subject deserves further investigation.

Spatial patchiness also changes with time and space. It changes with age as eggs disperse from their spawning sites and as larvae develop schooling behaviour (Hewitt 1981, Koslow et al. 1985, McGurk 1986). Therefore, the patchiness indices calculated from ichthyoplankton sample data are influenced by the daily rate of production of eggs and larvae, the daily rate of mortality, and the age structure of the population. Despite theoretical argument to the contrary, it is entirely reasonable to suppose that there is a relationship between patchiness and sampling scale. The nature of the relationship, if it exists, is entirely unknown; it deserves more investigation.

The success of Eqn (6) in predicting the mortality rates of fish eggs and larvae in the sea has implications for the study of reproductive strategies in marine fishes, and for the study of the recruitment process. Those species which release eggs in a highly patchy pattern, e.g. Pacific sardine, experience relatively high egg and larval mortality rates. I speculate that there are advantages to patchy egg release that offset the losses due to predation. One possible advantage is predator avoidance by the spawning adults. A comprehensive theory of reproductive strategies in fishes must combine hypotheses of egg release in space with hypotheses of egg release in time (Lambert & Ware 1984).

The model implies that turbulent mixing of the upper sea due to storms, upwelling events, and tides would promote dispersal of eggs and larvae and thereby decrease predation mortality, while stratification of the water would tend to retard dispersal and so increase predation mortality. Lasker (1985) has proposed that stratification would tend to promote survival in larval fishes by allowing the formation of patches of food organisms with sufficient density to promote successful first-feeding. The optimal environment for larval survival may be a balance between high densities of aggregated food organisms and low densities of well-dispersed larvae. Such an environment occurs whenever dispersing larvae drift into a front between 2 water masses where mixing is vigorous and biological production is high. These fronts are presumed to define and surround larval fish retention zones (Iles & Sinclair 1982).

The patchiness-mortality hypothesis described in this paper can be generalized to any predator-prey system where handling time can be considered a relatively small quantity. One system of obvious practical importance is predation by man on schooling pelagic



fishes. For such fisheries the limiting step is the time required to locate a school, not the time required to handle it. For example, once a purse-seine vessel has located a school of herring and manoevered its gear into the school it can often capture a large proportion of the school. It is reasonable to speculate that the instantaneous rate of fishing mortality is proportional to the spatial patchiness of the herring. Since fishing mortality is equal to the product of the catchability coefficient and fishing effort, this implies that the catchability

coefficient is directly proportional to the spatial patchiness of the fish. It also implies that management policies that involve restricting the areal extent of a fishery may be biasing the catchability of the fleet and the fishing mortality that it exerts on the stock. This generalization of the mortality-patchiness hypothesis and others have yet to be tested.

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**Appendix.** Natural mortality rates and dry weights for marine organisms. Species are listed in alphabetical order within their group. Populations of fish eggs and larvae for which estimates of spatial patchiness were available are listed in Table 1

Species	Area	M (d <sup>-1</sup> )	W (g)	Source
<b>Pelagic invertebrates</b>				
<i>Acartia hudsonii</i>	Narragansett Bay	$6.3 \times 10^{-2}$	$3.1 \times 10^{-6}$	Durbin & Durbin (1981)
<i>Acartia tonsa</i>	Chesapeake Bay	$7.0 \times 10^{-1}$	$1.6 \times 10^{-6}$	Heinle (1966)
		$5.0 \times 10^{-1}$	$3.9 \times 10^{-6}$	
<i>Euphausia pacifica</i>	California coast	$6.1 \times 10^{-2}$	$1.1 \times 10^{-4}$	Brinton (1976), Lindley (1978)
		$1.5 \times 10^{-2}$	$1.9 \times 10^{-3}$	
<i>Eurytemora affinis</i>	Patuxent River, Maryland	$5.0 \times 10^{-2}$	$4.2 \times 10^{-7}$	Heinle & Flemer (1975)
		$1.1 \times 10^{-1}$	$4.2 \times 10^{-7}$	
		$2.8 \times 10^{-1}$	$3.8 \times 10^{-7}$	
		$3.9 \times 10^{-1}$	$2.5 \times 10^{-7}$	
		$4.3 \times 10^{-2}$	$3.3 \times 10^{-6}$	
		$7.4 \times 10^{-2}$	$3.3 \times 10^{-11}$	
		$7.2 \times 10^{-2}$	$3.3 \times 10^{-11}$	
		1.1	$1.6 \times 10^{-6}$	
<i>Illex illecebrosus</i>	Scotian Shelf	$2.9 \times 10^{-3}$	$3.2 \times 10^1$	Amaratunga et al. (1978), Hurley & Mohn (1978)
<i>Paracalanidae</i> spp.	Kaneohe Bay, Hawaii	$5.2 \times 10^{-7}$	$1.5 \times 10^{-7}$	Newbury & Bartholemew (1976)
<i>Pleurobrachia brachei</i>	La Jolla Bight	$2.6 \times 10^{-1}$	$7.0 \times 10^{-4}$	Hirota (1974)
<i>Thysanoessa inermis</i>	North Sea	$1.5 \times 10^{-1}$	$1.5 \times 10^{-5}$	Lindley & Williams (1980), Lindley (1980)
		$2.3 \times 10^{-3}$	$8.1 \times 10^{-4}$	
<i>Thysanoessa longicaudata</i>	North Atlantic	$6.0 \times 10^{-2}$	$8.1 \times 10^{-4}$	Lindley (1978)
<i>Thysanoessa raschi</i>	Gulf of St. Lawrence	$3.4 \times 10^{-2}$	$1.3 \times 10^{-4}$	Berkes (1977)
		$5.7 \times 10^{-3}$	$8.2 \times 10^{-3}$	
	North Sea	$3.6 \times 10^{-3}$	$1.5 \times 10^{-3}$	Lindley (1978, 1980)
	NW Atlantic	$8.6 \times 10^{-4}$	$1.7 \times 10^{-3}$	
<b>Fish eggs</b>				
<i>Engraulis anchoita</i>	N Argentine coast	$6.0 \times 10^{-1}$	$1.1 \times 10^{-4}$	Ciechomski & Capezzani (1973)
<i>Engraulis japonica</i>	Japan coast	$3.3 \times 10^{-1}$	$1.1 \times 10^{-4}$	Hiyashi (1966)
<i>Melanogrammus aeglefinus</i>	Faroe Islands	$1.0 \times 10^{-1}$	$3.2 \times 10^{-4}$	Saville (1956)
<i>Pleuronectes platessa</i>	English Channel	$4.0 \times 10^{-2}$	$8.4 \times 10^{-4}$	Harding et al. (1978)
		$1.4 \times 10^{-1}$	$8.4 \times 10^{-4}$	
		$9.0 \times 10^{-2}$	$8.4 \times 10^{-4}$	
		$7.0 \times 10^{-2}$	$8.4 \times 10^{-4}$	
		$6.0 \times 10^{-2}$	$8.4 \times 10^{-4}$	
		$1.0 \times 10^{-1}$	$8.4 \times 10^{-4}$	
		$1.1 \times 10^{-1}$	$8.4 \times 10^{-4}$	
		$8.0 \times 10^{-2}$	$8.4 \times 10^{-4}$	
		$1.3 \times 10^{-1}$	$8.4 \times 10^{-4}$	
	Irish Sea	$1.0 \times 10^{-1}$	$8.4 \times 10^{-4}$	Harding & Talbot (1973)
<i>Sardinops melanostica</i>	Kyushu Is., Japan	$3.3 \times 10^{-1}$	$2.8 \times 10^{-4}$	Nakai & Hattori (1962)
<i>Scomber scombrus</i>	St. Georges Bay, Nova Scotia	$5.6 \times 10^{-1}$	$1.6 \times 10^{-4}$	Ware & Lambert (1985)
		$4.0 \times 10^{-1}$	$1.6 \times 10^{-4}$	
		$5.2 \times 10^{-1}$	$1.6 \times 10^{-4}$	
		$4.1 \times 10^{-1}$	$1.6 \times 10^{-4}$	
<i>Solea solea</i>	R Blackwater estuary, England	$6.0 \times 10^{-1}$	$2.3 \times 10^{-4}$	Riley (1974)
	E coast England	1.0	$2.3 \times 10^{-4}$	
<i>Tautoglabrus adspersus</i>	Long Is. Sound	$6.7 \times 10^{-1}$	$5.0 \times 10^{-5}$	Williams & Williams (1973)
<i>Trachurus symmetricus</i>	S California coast	$5.8 \times 10^{-1}$	$1.4 \times 10^{-4}$	Farris (1961)

## Appendix (continued)

Species	Area	M (d <sup>-1</sup> )	W (g)	Source
<b>Fish larvae</b>				
<i>Clupea harengus harengus</i>	Bay of Fundy, Nova Scotia	1.0 × 10 <sup>-1</sup>	1.1 × 10 <sup>-4</sup>	Das (1968), Laurence (1979)
		6.0 × 10 <sup>-2</sup>	1.1 × 10 <sup>-4</sup>	
		1.1 × 10 <sup>-1</sup>	1.1 × 10 <sup>-4</sup>	
	Norwegian coast	1.4 × 10 <sup>-1</sup>	1.4 × 10 <sup>-4</sup>	Dragesund & Nakken (1971a), Laurence (1979)
		4.6 × 10 <sup>-1</sup>	1.4 × 10 <sup>-4</sup>	
Georges Bank	4.0 × 10 <sup>-2</sup>	1.6 × 10 <sup>-3</sup>	Laurence (1979), Lough et al. (1981)	
R Blackwater estuary, England	6.0 × 10 <sup>-2</sup>	4.6 × 10 <sup>-4</sup>	Henderson et al. (1984), Laurence (1979)	
	7.0 × 10 <sup>-2</sup>	4.6 × 10 <sup>-4</sup>	Stevenson (1962), McGurk (1986)	
<i>Clupea harengus pallasii</i>	Barkley Sound, British Columbia	4.1 × 10 <sup>-1</sup>	3.0 × 10 <sup>-4</sup>	lizuka (1966), McGurk (1986)
	Queen Cove, Vancouver Is.	2.5 × 10 <sup>-1</sup>	3.0 × 10 <sup>-4</sup>	
	Akkeshi Bay, Japan	9.0 × 10 <sup>-2</sup>	3.3 × 10 <sup>-4</sup>	
<i>Engraulis japonica</i>	W coast Japan	1.2 × 10 <sup>-1</sup>	3.3 × 10 <sup>-4</sup>	Hiyashi (1966), Zweifel & Lasker (1976)
		3.0 × 10 <sup>-1</sup>	7.0 × 10 <sup>-4</sup>	
<i>Etrumeus teres</i>	E Gulf of Mexico	1.3 × 10 <sup>-1</sup>	2.7 × 10 <sup>-4</sup>	Houde (1977a)
		1.3 × 10 <sup>-1</sup>	2.2 × 10 <sup>-4</sup>	
<i>Harengula jaguana</i>	E Gulf of Mexico	2.8 × 10 <sup>-1</sup>	3.0 × 10 <sup>-4</sup>	Houde (1977c)
<i>Melanogrammus aeglefinus</i>	North Sea	1.1 × 10 <sup>-1</sup>	4.9 × 10 <sup>-4</sup>	Jones (1973), Laurence (1979)
<i>Micromesistius poutassou</i>	Rockall Bank, NE Atlantic	1.5 × 10 <sup>-1</sup>	2.7 × 10 <sup>-4</sup>	Bailey (1974), Laurence (1979)
<i>Opisthonema oglinum</i>	E Gulf of Mexico	2.1 × 10 <sup>-1</sup>	3.7 × 10 <sup>-4</sup>	Houde (1977b)
		2.6 × 10 <sup>-1</sup>	3.7 × 10 <sup>-4</sup>	
<i>Pleuronectes platessa</i>	English Channel	6.0 × 10 <sup>-2</sup>	7.5 × 10 <sup>-4</sup>	Bannister et al. (1974), Ryland (1966)
		2.0 × 10 <sup>-2</sup>	7.5 × 10 <sup>-4</sup>	
<i>Pseudopleuronectes americanus</i>	Mystic R, Connecticut	2.3 × 10 <sup>-1</sup>	6.0 × 10 <sup>-5</sup>	Pearcy (1962a, b)
<i>Sardinops melanostica</i>	S Japan coast	1.3 × 10 <sup>-1</sup>	7.0 × 10 <sup>-4</sup>	Nakai & Hattori (1962), Zweifel & Lasker (1976)
		1.0 × 10 <sup>-1</sup>	1.8 × 10 <sup>-3</sup>	
<i>Sardinops sagax</i>	S California coast	1.0 × 10 <sup>-1</sup>	1.8 × 10 <sup>-3</sup>	Lenarz (1973), Zweifel & Lasker (1976)
<i>Scomber japonicus</i>	Japan coast	1.4 × 10 <sup>-1</sup>	7.0 × 10 <sup>-3</sup>	Watanabe (1970), Ware & Lambert (1985)
<i>Scomber scombrus</i>	St. Georges Bay, Nova Scotia	3.8 × 10 <sup>-1</sup>	1.7 × 10 <sup>-4</sup>	Ware & Lambert (1985)
		6.9 × 10 <sup>-1</sup>	1.7 × 10 <sup>-4</sup>	
		4.8 × 10 <sup>-1</sup>	1.7 × 10 <sup>-4</sup>	
<b>Juvenile and adult fishes</b>				
<i>Ammodytes tobianus</i>	SE English coast	3.3 × 10 <sup>-3</sup>	1.9	Reay (1973)
<i>Argentina silus</i>	Nova Scotia banks	7.7 × 10 <sup>-3</sup>	5.0 × 10 <sup>1</sup>	Zukowski (1972)
<i>Argyrosomus argentatus</i>	E China and Yellow Seas	1.9 × 10 <sup>-3</sup>	5.1 × 10 <sup>1</sup>	Mako (1961)
<i>Blennius pholis</i>	Menai Straits, Wales	2.5 × 10 <sup>-3</sup>	2.6	Qasim (1957)
<i>Brevoortia tyrannus</i>	Chesapeake Bay	1.0 × 10 <sup>-3</sup>	7.5 × 10 <sup>1</sup>	Schaaf & Huntsman (1972)
<i>Cephalopholis fulva</i>	S Jamaican Shelf	1.5 × 10 <sup>-4</sup>	1.1 × 10 <sup>2</sup>	Thompson & Munro (1978)
<i>Cetengraulis mysticetus</i>	Gulf of Panama	5.8 × 10 <sup>-3</sup>	1.4 × 10 <sup>1</sup>	Bayliff (1966)
<i>Cheilodactylus macropterus</i>	Chatham Is., New Zealand	2.2 × 10 <sup>-3</sup>	2.6 × 10 <sup>2</sup>	Vooren (1977)
<i>Clupea harengus harengus</i>	Celtic Sea	5.5 × 10 <sup>-4</sup>	4.2 × 10 <sup>1</sup>	Burd & Bracken (1965)
	S North Sea	5.5 × 10 <sup>-4</sup>	4.0 × 10 <sup>1</sup>	Cushing & Bridger (1966)
	Lusterfjord, Norway	2.1 × 10 <sup>-3</sup>	1.6 × 10 <sup>1</sup>	Aasen (1952)
<i>Colabis saira</i>	N Norway Sea	9.4 × 10 <sup>-3</sup>	1.5	Dragesund (1970)
		4.4 × 10 <sup>-3</sup>	2.1 × 10 <sup>1</sup>	
<i>Cynoscion nebulosus</i>	NE Pacific	4.4 × 10 <sup>-3</sup>	2.1 × 10 <sup>1</sup>	Hughes (1974)
<i>Cynoscion nobilis</i>	SW Florida coast	1.2 × 10 <sup>-3</sup>	9.1 × 10 <sup>1</sup>	Iverson & Moffet (1962)
<i>Eopsetta jordani</i>	California coast	8.3 × 10 <sup>-4</sup>	2.9 × 10 <sup>3</sup>	Thomas (1968)
		6.9 × 10 <sup>-4</sup>	4.9 × 10 <sup>3</sup>	
<i>Epinephelus guttatus</i>	British Columbia coast	5.5 × 10 <sup>-4</sup>	3.6 × 10 <sup>4</sup>	Ketchen & Forrester (1966)
		1.9 × 10 <sup>-3</sup>	2.6 × 10 <sup>2</sup>	
<i>Epinephelus striatus</i>	S Jamaican Shelf	5.8 × 10 <sup>-4</sup>	1.5 × 10 <sup>3</sup>	Thompson & Munro (1978)
<i>Etrumeus micropus</i>	W Sea of Kyushu	1.9 × 10 <sup>-3</sup>	3.3	Chullasorn et al. (1977)
<i>Fundulus heteroclitus</i>	Delaware Bay, USA	1.9 × 10 <sup>-3</sup>	2.1	Meredith & Lotrich (1979)
<i>Gadus macrocephalus</i>	Hecate Strait, British Columbia	2.5 × 10 <sup>-3</sup>	9.4 × 10 <sup>2</sup>	Ketchen (1964)
<i>Gadus minutus</i>	English Channel	3.0 × 10 <sup>-3</sup>	5.1	Menon (1950)
		2.5 × 10 <sup>-3</sup>	1.1 × 10 <sup>1</sup>	

## Appendix (continued)

Species	Area	M (d <sup>-1</sup> )	W (g)	Source
<i>Gadus morhua</i>	Labrador coast	$4.9 \times 10^{-4}$	$5.5 \times 10^2$	Pinhorn (1975)
	Faroe Islands	$4.7 \times 10^{-4}$	$2.8 \times 10^3$	Jones (1966)
	Gulf of St. Lawrence	$2.7 \times 10^{-4}$	$4.2 \times 10^2$	Dickie (1964)
	W Baltic Sea	$9.6 \times 10^{-4}$	$4.1 \times 10^1$	Jensen (1959), Bagge (1974)
	S Gulf of St. Lawrence	$5.2 \times 10^{-4}$	$4.8 \times 10^2$	Paloheimo & Kohler (1968), Kohler et al. (1970)
<i>Galeorhinus australis</i>	NE Gulf of St. Lawrence	$4.8 \times 10^{-4}$	$3.9 \times 10^2$	Minet (1978)
	SE Australian coast	$2.4 \times 10^{-4}$	$1.1 \times 10^5$	Grant et al. (1979)
<i>Glyptocephalus cynoglossus</i>	SW Newfoundland	$3.0 \times 10^{-4}$	$1.1 \times 10^5$	Kohler et al. (1970), Bowering (1977)
		$5.5 \times 10^{-4}$	$1.3 \times 10^2$	
<i>Hippoglossoides platessoides</i>	Grand Banks	$6.9 \times 10^{-4}$	$1.4 \times 10^2$	Pitt (1973), Kohler et al. (1970)
		$6.3 \times 10^{-4}$	$3.0 \times 10^2$	
<i>Katsuwonus pelamis</i>	E Pacific	$4.7 \times 10^{-3}$	$3.9 \times 10^2$	Hennemuth (1959), Joseph & Calkins (1969)
<i>Leiognathus splendens</i>	Borneo coast	$4.9 \times 10^{-3}$	6.0	Pauly (1980)
<i>Lethrinus enigmatus</i>	S Indian Ocean	$6.3 \times 10^{-4}$	$1.9 \times 10^2$	Lebeau & Cuff (1975)
<i>Merluccius angustimanus</i>	Gulf of California	$2.2 \times 10^{-3}$	$3.8 \times 10^1$	Matthews (1975)
<i>Merluccius productus</i>	NE Pacific	$1.5 \times 10^{-3}$	$1.6 \times 10^2$	Nelson & Larkins (1970)
<i>Micropogonias undulatus</i>	N Gulf of Mexico	$8.6 \times 10^{-3}$	$6.9 \times 10^2$	White & Chittenden (1977)
<i>Mugil cephalus</i>	N Gulf of Mexico	$1.7 \times 10^{-3}$	$6.5 \times 10^1$	Broadhead (1953), Broadhead & Mefford (1956)
<i>Neothunnus macropterus</i>	E Pacific	$2.1 \times 10^{-3}$	$3.0 \times 10^3$	Hennemuth (1961)
<i>Nemipterus marginatus</i>	S China Sea	$6.0 \times 10^{-3}$	$1.3 \times 10^1$	Pauly & Martosuboro (1980)
<i>Notothenia neglecta</i>	S Orkney Islands	$9.9 \times 10^{-4}$	$2.1 \times 10^2$	Everson (1970)
<i>Notothenia rossi</i>	S Georgia, Antarctica	$2.1 \times 10^{-3}$	$8.9 \times 10^1$	Burchett & Ricketts (1984)
<i>Pagrus pagrus</i>	Caroline coast, USA	$1.5 \times 10^{-3}$	$3.0 \times 10^2$	Manooch & Huntsmann (1977)
<i>Paralabrax clathrus</i>	California coast	$7.9 \times 10^{-4}$	$3.3 \times 10^2$	Young (1963)
<i>Parophrys vetulus</i>	Puget Sound, USA	$1.8 \times 10^{-3}$	$5.0 \times 10^2$	Holland (1969)
	N Hecate Strait, British Columbi	$1.5 \times 10^{-3}$	$2.2 \times 10^3$	Ketchen (1947), Holland (1969)
<i>Pleuronectes platessa</i>	Wadden Sea	$1.8 \times 10^{-3}$	$9.2 \times 10^2$	
		$9.9 \times 10^{-4}$	$3.0 \times 10^3$	
		$6.8 \times 10^{-3}$	1.2	
		$2.1 \times 10^{-2}$	$5.0 \times 10^{-1}$	
		$4.1 \times 10^{-3}$	$5.0 \times 10^{-1}$	
	Filey Bay, England	$1.9 \times 10^{-2}$	$5.0 \times 10^{-1}$	Kuipers (1977), Lockwood (1980)
		$1.7 \times 10^{-2}$	$5.0 \times 10^{-1}$	
		$4.4 \times 10^{-2}$	$5.0 \times 10^{-1}$	
		$3.2 \times 10^{-2}$	$5.0 \times 10^{-1}$	
		$2.3 \times 10^{-2}$	$5.0 \times 10^{-1}$	
Firemore Bay, Scotland	$4.6 \times 10^{-2}$	$5.0 \times 10^{-1}$	Macer (1967), Kuipers (1977)	
	$1.7 \times 10^{-2}$	$5.0 \times 10^{-1}$		
	$2.7 \times 10^{-4}$	$1.2 \times 10^2$		
Port Erin Bay, Ireland	$1.2 \times 10^2$	$1.2 \times 10^2$	Beverton & Holt (1957)	
	$1.7 \times 10^{-2}$	$5.0 \times 10^{-1}$		
<i>Pseudopeneus maculatus</i>	Red Wharf Bay, N Wales	$4.6 \times 10^{-2}$	$5.0 \times 10^{-1}$	Munro (1976)
	North Sea	$2.7 \times 10^{-4}$	$1.2 \times 10^2$	
<i>Pseudopleuronectes americanus</i>	S Jamaican Shelf	$5.2 \times 10^{-3}$	$5.4 \times 10^1$	Pearcy (1962b)
	Mystic R, Connecticut	$1.2 \times 10^{-2}$	$3.0 \times 10^{-1}$	
	St. Mary's Bay, Nova Scotia	$2.8 \times 10^{-3}$	8.4	Dickie & McCracken (1955)
		$9.9 \times 10^{-4}$	$2.0 \times 10^2$	
	Massachusetts coast	$7.5 \times 10^{-4}$	$1.8 \times 10^2$	Lux (1969), Howe & Coates (1975)
		$2.3 \times 10^{-3}$	$1.2 \times 10^3$	
<i>Pseudosciaena diacanthus</i>	E Indian Ocean	$2.7 \times 10^{-3}$	$1.6 \times 10^1$	Rao (1966, 1968)
<i>Pseudosciaena manchurica</i>	E China and Yellow Seas	$1.2 \times 10^{-2}$	$1.8 \times 10^1$	Mako (1961)
<i>Rastrelliger kanagurta</i>	Java Sea	$1.7 \times 10^{-3}$	$1.9 \times 10^1$	Sudjastani (1974)
<i>Rastrelliger neglectus</i>	Gulf of Thailand	$1.6 \times 10^{-3}$	$3.5 \times 10^1$	Hongskul (1974)
<i>Rhombosolea plebeia</i>	Canterbury, New Zealand	$3.4 \times 10^{-3}$	$9.1 \times 10^1$	Webb (1972), Colman (1978)
<i>Sardinops ocellatus</i>	Walvis Bay, S Africa	$1.2 \times 10^{-3}$	$1.3 \times 10^2$	Newman (1970)
<i>Saurida tumbil</i>	E China and Yellow Seas	$1.2 \times 10^{-3}$	$1.3 \times 10^2$	Mako (1961)
<i>Scomber scombrus</i>	New England coast	$9.6 \times 10^{-4}$	$9.7 \times 10^1$	Paciorkowski et al. (1973)
		$9.0 \times 10^{-4}$	$1.1 \times 10^2$	
<i>Sebastes alutus</i>	NE Pacific	$6.4 \times 10^{-4}$	$2.0 \times 10^2$	Westrheim & Snytko (1974), Gunderson (1977)
		$1.8 \times 10^{-4}$	$2.1 \times 10^2$	
		$5.3 \times 10^{-4}$	$9.4 \times 10^1$	
	Queen Charlotte Sound	$1.2 \times 10^{-3}$	$1.2 \times 10^2$	Westrheim & Snytko (1974), Chikuni (1975)
	Gulf of Alaska	$5.0 \times 10^{-4}$	$4.7 \times 10^2$	
<i>Sphyræna argentea</i>	California coast	$5.0 \times 10^{-4}$	$4.7 \times 10^2$	Pinkas (1966)

## Appendix (continued)

Species	Area	M (d <sup>-1</sup> )	W (g)	Source
<i>Sprattus sprattus</i>	Skagerak, Sweden	$2.9 \times 10^{-3}$	6.4	Johnson (1970), Lindquist (1978)
	North Sea	$3.3 \times 10^{-3}$	4.3	Bailey (1980)
<i>Stenotomus chrysops</i>	E Long Is. Sound	$4.4 \times 10^{-3}$	$5.7 \times 10^1$	Briggs (1968), Finkelstein (1971)
<i>Taius tumifrons</i>	E China Sea	$5.5 \times 10^{-4}$	$1.4 \times 10^2$	Shindo (1960)
<i>Thunnus obesus</i>	Central Atlantic	$1.2 \times 10^{-3}$	$1.5 \times 10^4$	Lenarz (1974), Kume (1977)
	Pacific Ocean	$9.9 \times 10^{-4}$	$5.7 \times 10^3$	Silliman (1966), Suda & Kume (1967)
<i>Trachurus japonicus</i>	E China Sea	$2.7 \times 10^{-3}$	$2.8 \times 10^1$	Mitani & Shojima (1966)
<i>Trichiurus lepturus</i>	E China and Yellow Seas	$9.9 \times 10^{-4}$	$6.1 \times 10^1$	Misu (1964)
<i>Trisopterus esmarkii</i>	N North Sea	$4.4 \times 10^{-3}$	3.4	Raitt (1968)
<i>Urolophus paucimaculatus</i>	Victoria State, Australia	$1.2 \times 10^{-3}$	$7.8 \times 10^1$	Edwards (1980)
<i>Urophycis chuss</i>	Georges Bank	$2.3 \times 10^{-3}$	$5.1 \times 10^1$	Kohler et al. (1970), Rikhter (1974)
<b>Whales</b>				
<i>Balaenopterus borealis</i>	S Africa coast	$1.6 \times 10^{-4}$	$3.6 \times 10^6$	Lockyer (1977a, b)
<i>Eschrichtius robustus</i>	E Pacific Ocean	$2.2 \times 10^{-4}$	$5.0 \times 10^6$	Rice & Wolman (1971)
		$2.6 \times 10^{-4}$	$5.8 \times 10^6$	
<i>Megaptera novaeangliae</i>	Antarctic Ocean	$2.4 \times 10^{-4}$	$5.8 \times 10^6$	Chittleborough (1965), Lockyer (1976)
		$2.4 \times 10^{-4}$	$6.6 \times 10^6$	
<i>Physeter catodon</i>	S Africa coast	$1.6 \times 10^{-4}$	$6.6 \times 10^6$	Gambell (1974), Allen & Kirkwood (1977)
		$1.6 \times 10^{-4}$	$3.1 \times 10^6$	

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