PRODUCTION AND MORTALITY OF EARLY LIFE STAGES OF FLATFISHES

Thesis submitted in accordance with the requirements of the University of Liverpool
for the degree of Doctor in Philosophy by

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ABSTRACT

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Plankton sampling established the presence of a plaice spawning ground off the west coast of the Isle of Man in the Irish Sea. The total production of stage I plaice eggs from this spawning ground in 1993 was estimated at 7.6×10^9. Theoretically this spawning ground could supply the local nurseries with plaice larvae. Spawning was most intense in March, before the peak in the plankton bloom in the Irish Sea.

Predation on plaice eggs by clupeids was studied in March in an area of high plaice egg density to the east of the Isle of Man. Fish eggs formed the bulk of the stomach contents of sprat and herring due to the lack of alternative zooplankton food at this time of year. The later developmental stages of plaice eggs were more vulnerable to predation. This was thought to be due to the increase in pigmentation with embryonic development increasing the contrast between the egg and the water to predators that detect prey visually. Sprat and herring >80 mm showed a strong selection for plaice eggs over smaller pelagic fish eggs. However, the large eggs of plaice had a refuge in size from predation by sprat <80 mm. Smaller clupeids were feeding more actively than larger clupeids, as indicated by stomach fullness and the total number of fish eggs in stomachs. Stomach content data was combined with published biomass estimates and the daily instantaneous mortality rate of plaice eggs due to predation was estimated at 0.023 for sprat and 0.001 for herring. Sprat were therefore an important predator of plaice eggs in the Irish sea, whereas herring seemed of limited significance.

Predation by fishes on 0-group flatfishes was studied on a Scottish nursery ground by stomach content analysis. Fish predation was shown to be a significant source of mortality and I-group grey gurnards and gadoids were the major predators. Flounder suffered higher predation rates than plaice or dab due to the smaller size at settlement. Predation on plaice and dab was size-selective, concentrated on the smaller individuals. Smaller flatfishes were vulnerable to a greater size range and greater taxonomic range of predators. Predation by 0-group cod on 0-group dab was limited by the sizes of predator and prey. It was hypothesised that the times of recruitment of flatfishes and their predators to nurseries, and relative growth rates, would affect predation and hence mortality.

The handling time of 0-group flatfishes by 0-group cod in laboratory experiments was positively related to flatfish size and negatively related to cod size. The handling time of plaice was longer than for dab of a similar size due to the difference in body shape. Profitability of flatfishes (wet weight gained per unit handling time) decreased monotonically with flatfish size over the range of prey and predator sizes used. It was therefore predicted that when 0-group cod forage in the field the smallest 0-group flatfishes would be the most profitable and would be behaviourally selected for. However, the selection of prey by cod was suggested to be determined by both behavioural and physical processes. There was evidence that behavioural selection of prey occurred at the ingestion stage of feeding.

The current evidence for density-dependent processes in the juvenile stage of plaice was reviewed. Both the data in support of, and the processes thought to cause, density-dependent mortality in the juvenile phase were equivocal. It was hypothesised that density-dependent mortality occurs in the early egg stages of plaice and evidence, and the rationale for a potential predatory process resulting in such mortality, were presented.

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CONTENTS

CHAPTER 1:

GENERAL INTRODUCTION:

THE IMPORTANCE OF PREDATION IN DETERMINING THE YEAR-CLASS STRENGTH OF PLAICE.

The number of fish that can be removed from a population by fishing will depend upon the size of the stock. A fish population, spawning over limited periods, must be considered as composed of discrete year-classes (cohorts) which together make up the fished stock. In temperate latitudes exploited fish species are generally long lived (e.g., plaice *Pleuronectes platessa* L. ≥20 years, WIMPENNY, 1953) and stocks are composed of several year-classes (e.g., Figure 1.1). It is the number of individuals in, and the weights of, the year-classes which determine stock size (see Figure 1.1 a+b). Year-class strength varies between years (see Figure 1.2 for Irish Sea). Often a single strong year-class can make a considerable contribution to the total biomass of a stock, and some fisheries may be sustained by strong cohorts.

The factors affecting year-class strength and ultimately the level of recruitment to the exploited population have been, and still are, of major concern for fisheries research. Plaice have been used as a case study species in European fisheries research for several reasons.

1. Plaice are an important food fish. Plaice were the most important demersal fish species landed by U.K. vessels in the Irish Sea (ICES area VIIa) in 1990 by weight (20% total landings), and the third most important by value (15% total landings) (BOON, 1992).
2. Plaice are common, as reflected in landings.
3. Interest in the population dynamics of plaice stems back a long way (Petersen, 1894: cited in CUSHING, 1976) and plaice are relatively easy to age using otoliths (see WIMPENNY, 1953).
4. Plaice eggs are easily identified (SIMPSON, 1959b).
5. Juvenile plaice populations are amenable to study (ILES & BEVERTON, 1991).
6. Plaice can be maintained and cultured in the laboratory with relative ease (see SHELBOURNE, 1975).
7. Plaice populations are thought to show strong density-dependence (VAN DER VEER, 1986).

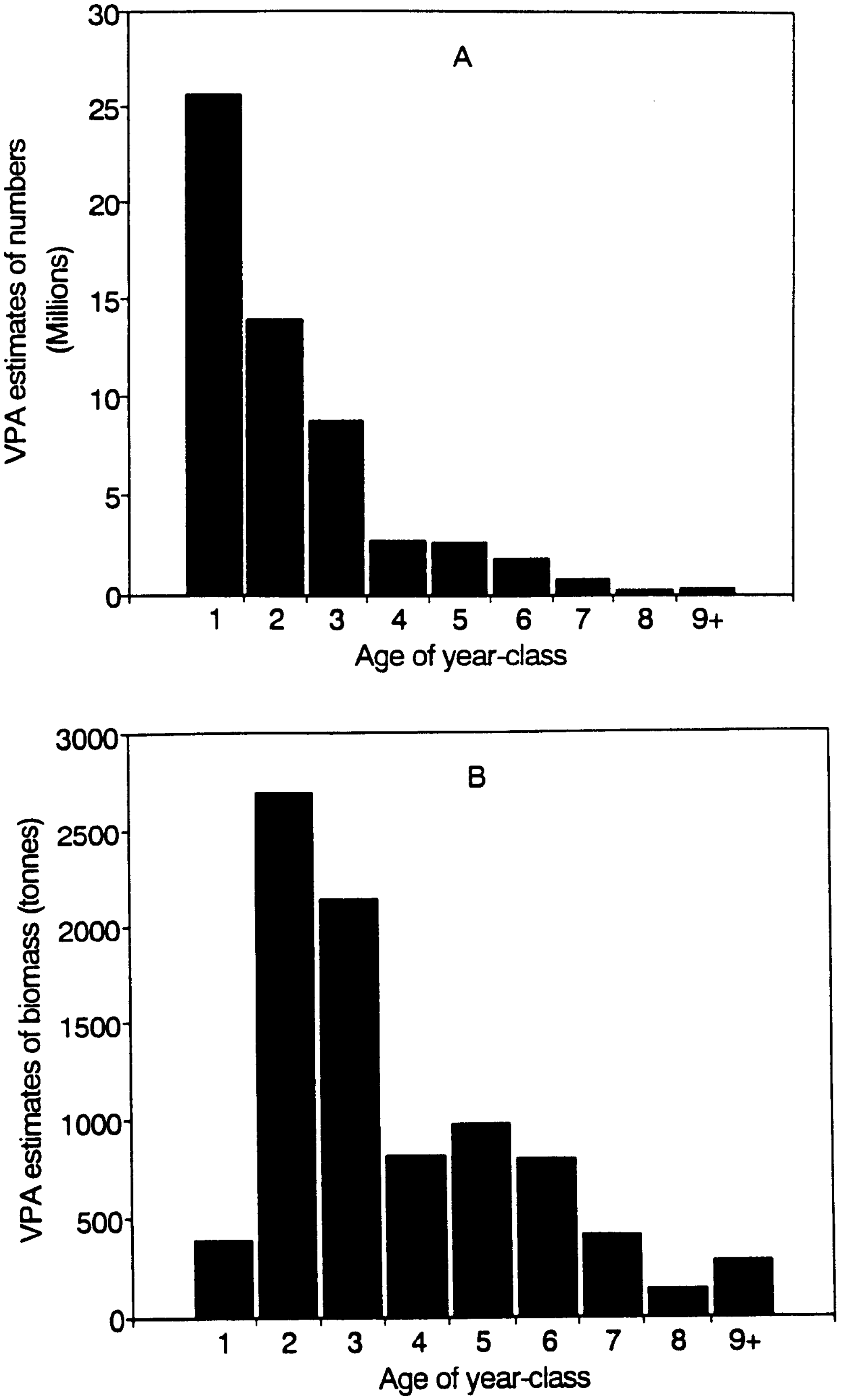


Figure 1.1: Virtual population analysis estimates of numbers (A) and biomass (B) of year-classes forming the Irish Sea plaice stock in 1992. Data from ANON (1993).

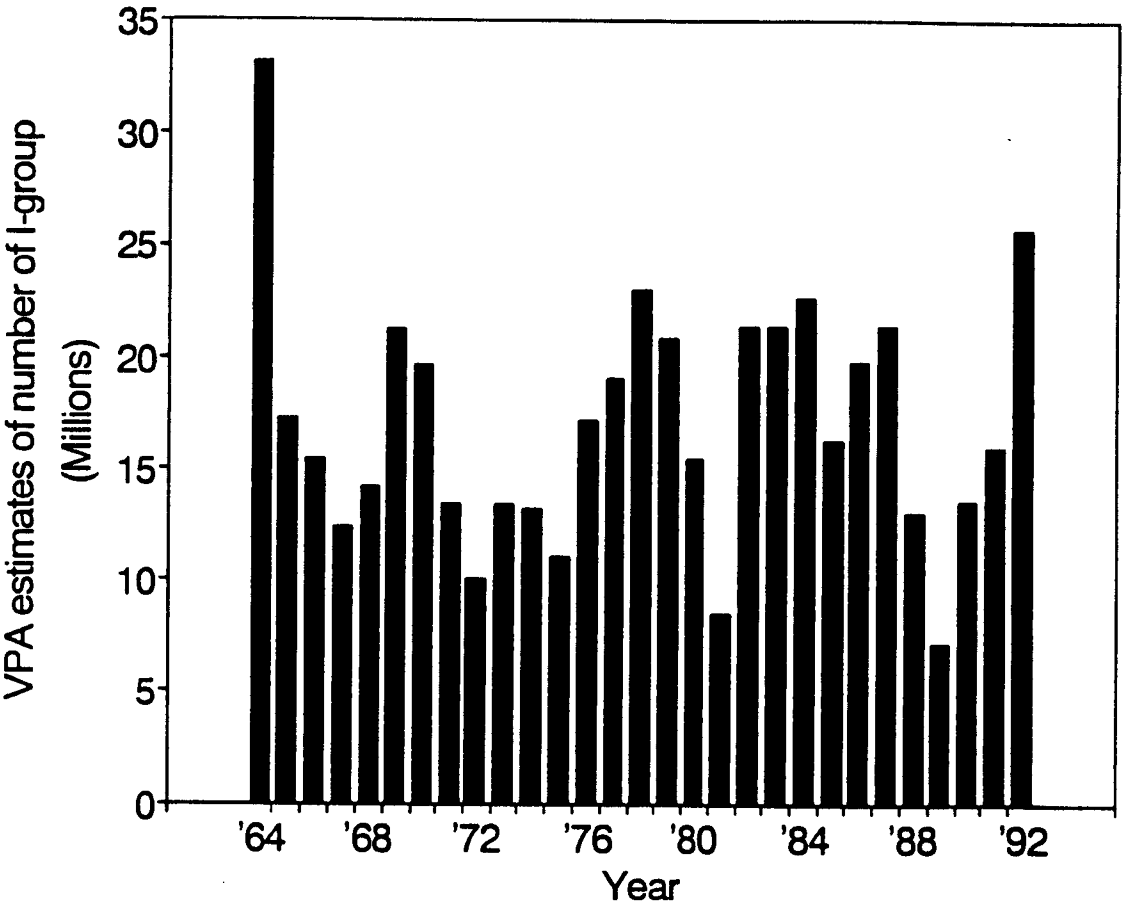


Figure 1.2: Estimates from virtual population analysis of numbers of I-group plaice in Irish Sea in years 1964-1992. Data from ANON. (1993).

The plaice typifies the generalised life cycle of a migratory marine fish species (Figure 1.3, HARDEN JONES, 1968). There is a spatial separation of diffuse feeding grounds, well-defined spawning grounds and restricted nursery grounds. Adult plaice use selective tidal stream transport (HARDEN JONES *et al.*, 1979) to migrate to and from the spawning grounds (SIMPSON, 1959a, 1959b; HARDING *et al.*, 1978) where they spawn large numbers of eggs (10-400 x 10^3 eggs fish^{-1}: HORWOOD, 1990). The eggs and larvae drift passively with the residual currents during development (TALBOT, 1978). The larvae recruit to restricted inshore sandy beach nurseries (RILEY *et al.*, 1981) where they remain for at least the first few months of demersal life (see ILES & BEVERTON, 1991). Juvenile plaice move offshore as they grow and age (MACER, 1967; LOCKWOOD, 1974), leaving the coastal nursery to recruit to the parent stock (LOCKWOOD & LUCASSEN, 1984). Plaice continue to move to deeper water as they grow and age, and the depth distribution with size is known as Heincke's Law (WIMPENNY, 1953). Plaice therefore show a spatial separation of the different stages in the life cycle (adults, eggs, larvae, juveniles).

The factors that affect the year-class strength of plaice can be seen as a consecutive series, each factor determining the number of individuals passing into the next phase of the life cycle (*c.f.* Paulik diagram in ROTHSCHILD *et al.*, 1989).

1. The biomass and age structure will determine the fecundity of the stock.
2. The fertilization rate of ova will determine the number of early stage eggs.
3. The mortality of eggs will determine the number of early stage larvae.
4. The mortality of larvae will determine the number of newly-settled juveniles.
5. The mortality of juveniles will determine the number of recruits to the adult stock.

There seems to be little or no relationship between spawning stock biomass (i.e., the number of ova produced) and subsequent recruitment to the plaice stocks in the North Sea (ZIJLSTRA & WITTE, 1985) or Irish Sea (R.D.M. NASH, *pers. comm.*), over the range of stock sizes recorded. The fertilization rate in natural populations of flatfish is very high, 99.4% recorded in sole *Solea solea* (HOWELL *et al.*, 1991), so the

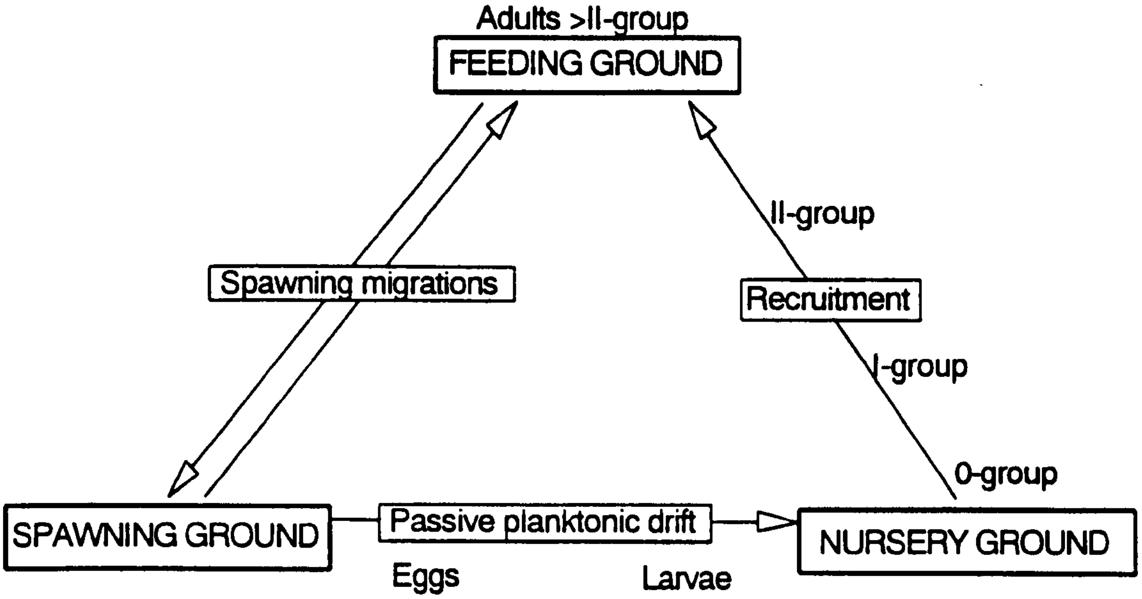


Figure 1.3: Diagrammatic representation of life-cycle of plaice, following the typical cycle of a migratory fish species (after HARDEN JONES, 1968).

possibility of low fertilization rates can be excluded. By inference, it follows that it is the mortality of pre-recruits (eggs, larvae and juveniles) that affects recruitment.

That there must be very high mortality of pre-recruits is shown by the disparity between fecundity and the number needed for replacement. HJORT (1914) first put forward the idea that year-class strength is determined in early life stages, when numbers of individuals are maximal (VAN DER VEER, 1986) and changes in the high mortality rate will affect recruitment (SHEPHERD & CUSHING, 1980).

The potential sources of mortality of pre-recruit plaice are listed in Table 1.1, with an indication as to the evidence for the different causes. It is difficult to show from field sampling of natural populations that many of the factors (e.g. physiological stress, lack of food, parasite and pathogen load) are a direct source of mortality. Affected individuals will be more vulnerable to predation, and will be eaten before the stressors directly cause death (BAILEY & HOUDE, 1989). However, such an assumption presupposes that predation pressure is high, and predation is thought to be the principle cause of mortality of all three pre-recruit stages, that is eggs (POMMERANZ, 1981; HUNTER, 1984; BAILEY & HOUDE, 1989), larvae (HARDING *et al.*, 1978; BAILEY & HOUDE, 1989) and juveniles (MACER, 1967; EDWARDS & STEELE, 1968; VAN DER VEER *et al.*, 1990; BEVERTON & ILES, 1992a). Accepting the hypothesis that predation is the primary source of mortality, reveals the importance of the abundance and feeding behaviour of predators, which must both generate and moderate fluctuations in year-class strength.

Plaice year-class strength is negatively correlated with the sea temperature in the late winter/early spring of the first year of life, both in the North Sea (THOMPSON & HILDEN, 1989) and Irish Sea (R.D.M. NASH, *pers. comm.*). This shows that extrinsic (environmental) rather than intrinsic (genetic) effects are important. Year-class strength appears to be determined in the egg stage, as indicated by the significant positive correlation between the abundance of late stage eggs and subsequent recruits (ZIJLSTRA & WITTE, 1985). Temperature seems to affect the mortality rate, low

Table 1.1: Review of evidence for potential causes of mortality of pre-recruit plaice. Classification of causes of mortality follows HEATH (1992).

CLASSIFICATION OF POTENTIAL FACTORS				Life history stage					
				Eggs		Larvae		Juveniles	
					Ref		Ref		Ref
Endogenous		Genetic and developmental abnormality		++	1	0		0	
Exogenous	Abiotic	Physiological stress	Temperature	+	2	0		++	3
			Salinity	+	2	0		0	
			Oxygen	0		0		0	
			U.V. light	+	4	0		+	3
			Pollution	?	1	0		0	
		Physical damage		+	4	0		0	
		Transport to unsuitable areas		NA		+	5,6	NA	
	Biotic	Food limitation		NA		+	7,8	?	9-11
		Parasitism and disease		+	12	+	12	+	13, 14
		Algal toxins		0		0		0	
		Predation		++	15-22	++	20-24	++	25-30

KEY:
++ : Field evidence as source of mortality
\+ : Laboratory evidence as source of mortality or suspected in field
0 : No evidence found in literature
N.A.: Not applicable to life history stage
? : Literature unconvincing.

REFERENCES:
1: CAMERON *et al.*, 1992
2: WESTERHAGEN, 1970
3. BERGHAHN *et al.*, 1993
4: POMMERANZ, 1973
5: TALBOT, 1978
6: PIHL, 1990
7: SHELBOURNE, 1957
8: HOVENKAMP, 1989 & 1990
9: see ZIJLSTA & WITTE, 1985
10: see BERGMAN *et al.*, 1988
11: VAN DER VEER & WITTE, 1993
12: SHELBOURNE, 1975
13: MACKENZIE, 1968
14: Kioe, cited in THÉODORIDÈS, 1989
15: HANSEN, 1955
16: DAAN, 1976
17: POMMERANZ, 1981
18: DAAN *et al.*, 1985
19: LAST, 1989
20: LEBOUR, 1923
21: HARDING *et al.*, 1978
22: GARROD & HARDING, 1981
23: VAN DER VEER, 1985
24: TUNGATE, 1975
25: RILEY & CORLETT, 1966
26: MACER, 1967
27: EDWARDS & STEELE, 1968
28: LOCKWOOD, 1972
29: PIHL, 1982
30: VAN DER VEER & BERGMAN, 1987

temperatures favouring survival of the eggs (ZIJLSTRA & WITTE, 1985). However temperature is not thought to be a direct cause of mortality, but acts by affecting the numbers, distribution and feeding activity of predators (BANNISTER *et al.*, 1974; ZIJLSTRA & WITTE, 1985).

The variability in year class strength of plaice is low compared to other exploited species (BANNISTER *et al.*, 1974). This suggests that density-dependent processes stabilize recruitment (VAN DER VEER, 1986). Density-dependent processes can operate at all stages of the life cycle and are listed below for all fish species (quoted from HEATH, 1992), although mechanisms 2 and 9 will not apply to plaice.

> "1. Variations in the quality and viability of eggs due to density-dependent competition for food in the adult stage.
> 2. For demersal spawning species, density-related egg survival as a result of oxygen starvation in thick egg mats.
> 3. Competition for a limiting food resource between members of a cohort of larvae leading to a reduced growth rate.
> 4. Switching of predators to selective feeding in response to high densities of the target species.
> 5. Aggregation of predators in patches of the target species.
> 6. Cannibalism between larvae.
> 7. Transmission of disease between larvae in close proximity.
> 8. Competition for substratum between metamorphosing flatfish.
> 9. Requirement to encounter other larvae to initiate schooling."

CUSHING (1973) suggested that year-class strength would be modulated by density-dependent mortality rather than fecundity caused by density-dependent growth. Indeed RIJNSDORP *et al.* (1991) found no evidence that density affected the fecundity of plaice. Density-dependent processes therefore occur later in the life-cycle of plaice, either in the pelagic or demersal stage.

For most density-dependent processes (competition and predation) to occur, plaice biomass would have to constitute a major proportion of the community biomass. Plaice would have to consume a large proportion of the available prey, or constitute an important part of the predators diets, to produce density-dependent effects. In addition density-dependent processes are most likely to operate when members of a cohort are concentrated at high densities. This intuitively suggests that density-dependent processes will occur on the spawning and/or nursery grounds when recently spawned eggs and newly settled juveniles are concentrated. Dispersal of eggs and larvae may reduce density-dependent processes in the planktonic phase (ROTHSCHILD *et al.*, 1989).

DAAN (1976) observed that the density of plaice eggs may have to be above a threshold level to promote predation by herring and sprat. Although DAAN (1976) did not seem to realise the importance of his suggestion, prey switching in relation to prey density (4) could produce density-dependent mortality in the egg stage.

There is evidence (SHELBOURNE, 1957; HOVENKAMP, 1989, 1990) of food limitation affecting the growth of plaice larvae. Density-dependent competition for a limiting food resource between members of a cohort could lead to a reduced growth rate (3). If vulnerability to predation is size-dependent, then cumulative mortality will be density-dependent (SHEPHERD & CUSHING, 1980). However there is no evidence from field studies of density-dependent growth of plaice larvae.

VAN DER VEER (1985) suggested that strong year classes, associated with extended development times, would suffer a higher mortality in the late larval phase due to coelenterate predation. He wrongly suggested this process as density-dependent. His predictions of predatory impact will have a compensatory effect on mortality, but this will be due to the timing of larval recruitment rather than density.

The concentration of juvenile plaice in restricted inshore nurseries suggests that it is in this phase of the life history that density-dependent processes are most likely (BERGMAN *et al.*, 1988). VAN DER VEER (1986) noted that for North Sea plaice populations, the coefficient of variation in abundance between years was high for pelagic larvae (62%) and newly settled plaice (62%). However it was lower later in the season (35%), at a level similar to the variation in recruitment of 2 year old plaice (35%), and in the abundance of newly fertilized eggs (40%). This suggests that stochastic density-independent factors in the pelagic phase generate variation in year-class strength, but density-dependent processes operating in the nursery reduce the variation. VAN DER VEER (1986) and BEVERTON & ILES (1992b) produced evidence that mortality rate in the nursery phase was density-dependent. VAN DER VEER (1986) and BERGMAN *et al.* (1988) suggested that density-dependent mortality occurred during and shortly after settlement, and no further compensatory mechanisms operated in later stages.

Density-dependent mortality in the nursery could occur through pathogens and parasites, competition for food, predation and cannibalism. There is some evidence for density-dependent transmission of parasites in 0-group plaice populations (MACKENZIE, 1968), although there is no data to show this produces density-dependent mortality. If parasite load is density-dependent and affects growth, and if predation is size-selective, then density-dependent mortality could occur.

Density-dependent competition for a limiting food resource between members of a cohort of larvae or juveniles could lead to a reduced growth rate (HEATH, 1992). If vulnerability to predation is size-dependent, then cumulative mortality will be density-dependent (SHEPHERD & CUSHING, 1980). There is evidence that vulnerability to predation is size-dependent (VAN DER VEER & BERGMAN, 1987). However the published evidence suggests that density-dependent growth of juvenile plaice does not occur (ZIJLSTRA & WITTE, 1985; BERGMAN *et al.*, 1988; VAN DER VEER & WITTE, 1993).

For predation to cause density-dependent mortality predators must either show a functional and/or a numerical response to prey density. Both types of predator response to plaice density have been suggested (LOCKWOOD, 1980; VAN DER VEER & BERGMAN, 1987), and are discussed further in Chapter 7.

Intra-cohort cannibalism will produce density-dependent mortality (HEATH, 1992). However, it is most likely to occur in piscivorous flatfish species, where there is great variation in size within a year class (GIBSON, 1994), and has not been recorded in plaice. Cannibalism of 0-group plaice, by I- and II-group plaice, does occur (RILEY & CORLETT, 1966; MACER, 1967). Inter-cohort cannibalism will not, however, result in density-dependent mortality, unless the predators show a numerical or functional response (see Chapter 7) to the density of 0-group plaice.

BERGMAN *et al.* (1988) and PIHL (1990) suggested that in some nurseries inter-annual variation in predation pressure, due to variable predator abundance, would increase the variation in year class strength. VAN DER VEER *et al.* (1990) provided evidence that in these nurseries density-dependent mortality did not occur, and they suggested that fluctuations in predator abundance, and hence mortality rate, would be independent of plaice density.

It is interesting to note that common data were used in these analyses (BERGMAN *et al.*, 1988; VAN DER VEER *et al.*, 1990) and those by LOCKWOOD (1980) and BEVERTON & ILES (1992b) who found evidence for density-dependent mortality in nurseries where mortality was supposed to be density-independent (VAN DER VEER *et al.*, 1990). The nurseries supplying the Irish Sea plaice stock will have variable numbers of predators, and yet the coefficient of variation in recruitment i.e. 32% (from data in ANON, 1993) is very similar to that of North Sea plaice.

Density-dependent mortality of plaice could occur, independent of predator abundance, if the predators present showed a strong switching response to prey density. That the abundance of predators on the nursery ground does have an important effect on year-class strength is shown by the evidence that very strong year classes can result when predator numbers are markedly reduced by cold winters (PIHL, 1990; VAN DER VEER *et al.*, 1990). Freed from regulatory predation in the nursery, unusually strong year classes can result.

In summary, predation probably determines both the level of recruitment and reduces inter-annual variation. Current evidence suggests that variation in the strength of plaice year-classes is generated in the pelagic phase (probably in the egg phase) through the feeding activity, distribution and/or numbers of predators. The stability in recruitment to plaice stocks is, at present, most convincingly explained by density-dependent predation in the early demersal phase. Predators, their feeding activity and their feeding behaviour are of paramount importance in determining year class strength. To cause density-dependent mortality, predators must aggregate on dense patches of prey, switch prey selection in relation to prey abundance or show selection for smaller prey.

The work presented in this thesis concentrates on mortality in the field, in particular predation, and on the feeding behaviour of predators. The thesis is divided into two parts. The first part concentrates on the egg stage. Distributions of plaice eggs around the Isle of Man are described in Chapter 2, and in Chapter 3 knowledge of the distributions is used to examine predation on plaice eggs. The second part is concerned with the early demersal phase. Population sizes and mortality rates of a plaice population on a nursery ground are assessed in Chapter 4. Chapters 5 and 6 examine predation by fishes on 0-group plaice and other flatfishes sharing the nurseries. Chapter 7 describes a laboratory study of predator behaviour and includes a discussion of predator behaviour in relation to density-dependent mortality. The major findings are summarised in the general discussion (Chapter 8) and the evidence for density-dependent mortality of plaice on the nursery ground is reviewed. It is proposed that evidence for density-dependent predation should be sought in the early egg stages. The effects of size and timing to predation, and the importance of such life history traits are discussed.

The pelagic phase

Chapter 2:

The distribution of stage I plaice eggs around the south and west of the Isle of Man

Introduction

Plaice, like many other marine fish species, have well defined spawning grounds, the locations of which are relatively constant over many years (HARDING *et al.*, 1978). Plaice eggs and larvae are pelagic and develop in the plankton, drifting with the residual currents (TALBOT, 1978). Plaice also have well defined nursery grounds. If the spawning products are transported by a consistent current system from an invariable spawning ground, then the position of the nursery ground will also be fixed (NORCROSS & SHAW, 1984). CUSHING (1990a) suggested that the duration of the larval phase and the direction of larval drift has been averaged to ensure recruitment to the nursery.

The origin of the plaice larvae recruiting to the Port Erin nursery ground (see Chapter 4), on the west coast of the Isle of Man (IoM), is unknown (COLMAN, 1966). SIMPSON (1959b) showed that plaice eggs are not transported far from the spawning grounds in the Irish Sea and HARDEN JONES (1968) suggested settlement in nurseries near to spawning grounds. Plaice eggs have been recorded to the west of the Isle of Man close to Port Erin Bay (SCOTT, 1913, 1915, 1919; BAL, 1940; SIMPSON, 1959b). However, COLMAN (1966) dismissed the importance of local spawning, and assumed that larvae recruiting to Port Erin originated from one or more of the main spawning grounds in the Irish Sea (see Figure 2.1) described by SIMPSON (1959b). R.D.M. NASH (*pers. comm.*) has shown that it is theoretically possible, on the basis of development times and transport speeds, for Port Erin Bay 0-group plaice to originate from both the spawning grounds to the east of the IoM and off the Great Orme.

Not only is the position of plaice spawning consistent between years, but also the timing of spawning. Peak spawning in the Southern Bight of the North Sea varies very little inter-annually (CUSHING, 1969). The time of spawning and the duration of embryonic stages will be important in relation to larval feeding conditions. The "match-mismatch" hypothesis (CUSHING, 1972; see CUSHING, 1990b for review) suggests

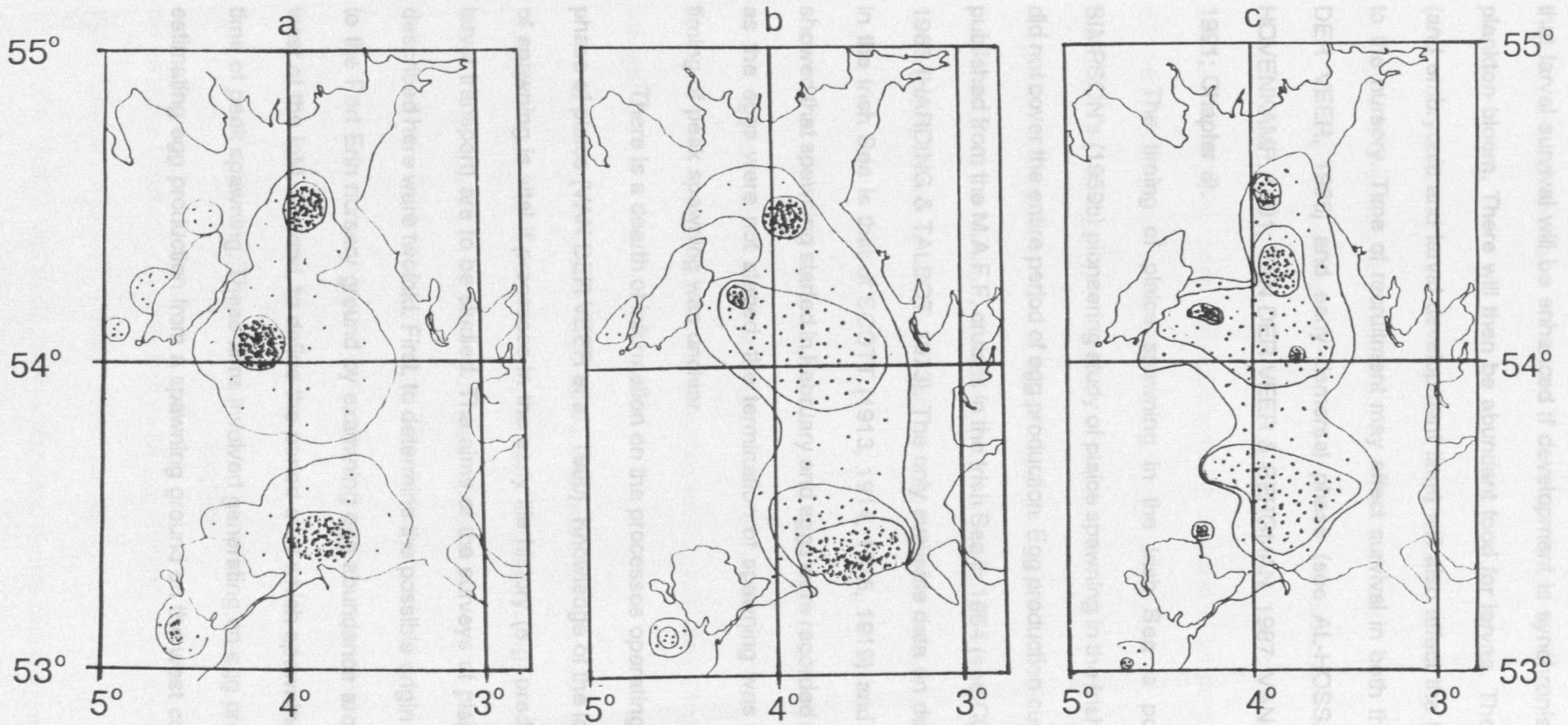


Figure 2.1: Location of plaice spawning grounds in north-east Irish Sea, assessed by ichthyo-plankton surveys. Stippling indicates areas of high plaice egg density. a: redrawn from SIMPSON (1959b); b: redrawn from COLMAN (1966) based on survey 7-14 March 1953 in SIMPSON (1959b); c: redrawn from COLMAN (1966) based on survey 8-11 March 1964.

that larval survival will be enhanced if development is synchronised with the spring plankton bloom. There will then be abundant food for larvae. The time of spawning (and embryonic and larval development time) will also affect the time of recruitment to the nursery. Time of recruitment may affect survival in both the late larval (VAN DER VEER, 1985) and early demersal phase (see AL-HOSSAINI *et al.*, 1989; HOVENKAMP, 1991; VAN DER VEER & BERGMAN, 1987; VAN DER VEER *et al.*, 1991; Chapter 6).

The timing of plaice spawning in the Irish Sea is poorly documented. SIMPSON's (1959b) pioneering study of plaice spawning in the Irish Sea unfortunately did not cover the entire period of egg production. Egg production curves have not been published from the M.A.F.F. cruises in the Irish Sea in 1964 (see COLMAN, 1966) and 1965 (HARDING & TALBOT, 1973). The only available data on duration of spawning in the Irish Sea is that of SCOTT (1913, 1914, 1915, 1919) and BAL (1940). They showed that spawning started in February and eggs were recorded until May. However as the eggs were not staged, the termination of spawning was unknown, and the timing of peak spawning was unclear.

There is a dearth of information on the processes operating during the pelagic phase of plaice (VAN DER VEER *et al.*, 1990). Knowledge of the locations and timing of spawning is vital if processes in the early life history (e.g. predation and egg and larval transport) are to be studied. The aims of the surveys of plaice egg distribution described here were twofold. First, to determine the possible origin of larvae recruiting to the Port Erin nursery ground by examining egg abundance around the south and west of the IoM. Second, to define the period over which spawning occurred and the time of peak spawning. These aims involved generating an egg production curve and estimating egg production from a spawning ground on the west coast of the IoM.

MATERIALS AND METHODS

Stations

The positions of stations sampled are shown in Figure 2.2 and the dates of the surveys and the stations sampled are given in Table 2.1.

In 1991 a broad scale survey was undertaken and stations 1-16 were surveyed. In 1992 more intensive surveys of the west coast of the IoM were made and sampling was extended further north with stations 17-20. Stations 21-23 were added after survey 2 in 1992 in response to the distribution of eggs previously recorded. Station 27 was surveyed on 6 April to compare with SCOTT's (1915) data. In addition, two supplementary stations (25 and 26) off the east coast of the IoM were surveyed. This was in response to the results of 1991 and the difference in the location of the centre of spawning shown by SIMPSON (1959b; see Figure 2.1a) and COLMAN (1966; see Figure 2.1b+c).

In 1993 seven surveys were made off the west coast of the IoM and stations 29 and 28 were added to improve spatial definition. Station 25 off the east coast was sampled twice in conjunction with sampling for clupeids (see Chapter 3).

Sampling

Sampling for plaice eggs was conducted from *R.V. Cuma* in 1991 and *R.V. Roagan* in 1992 and 1993. Plankton samples were taken with a modified, un-encased Gulf III high speed plankton sampler (see LOCKWOOD, 1974b) fitted with a 333 μm mesh (Figure 2.3) towed at 4-5 knots. The conical nose cone was fitted with a General Oceanics flowmeter which was read before and after sampler deployment to estimate the volume (m^3) of water filtered, as below:

$$\text{Volume} = \frac{\text{Difference in flowmeter counts} \times \text{Rotor constant}}{999{,}999} \times \pi r^2$$

where Rotor constant = 26,873, and r = radius of mouth of nose cone, 0.096 m (1991, 1992, 1993 surveys 1-6), 0.099 m (1993 survey 7).

The Gulf III was deployed in a standard double oblique tow, from the surface

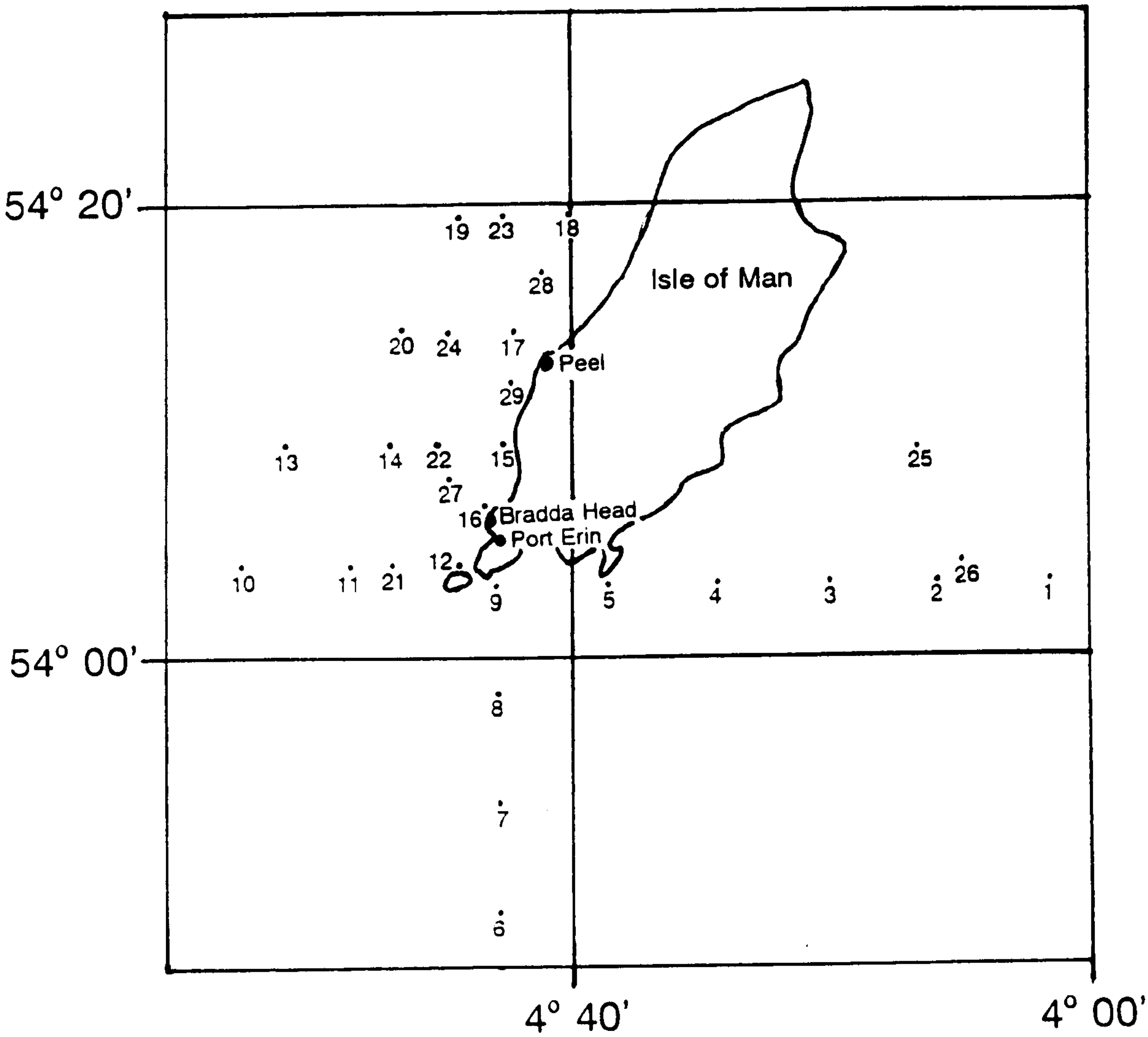


Figure 2.2: Positions of stations sampled in plaice egg distribution surveys, 1991-1993.

Table 2.1: Details of plaice egg distribution surveys around south and west of Isle of Man in 1991, 1992 and 1993. See Figure 2.2 for locations of stations.

Year	Survey	Date	Stations sampled					
1991	1	28/2	1	2	3	4		
		1/3	5	6	7	8		
		6/3	9	10	11	12		
		7/3	13	14	15	16		
1992	1	13/1	11	14	15	12		
		14/1	17	18	19	20		
	2	6/2	11	12	14			
		11/2	15	17	18	19	20	
	3	5/3	21	22	15	16	12	
		16/3	17	18	23	24		
	East coast	24/3	25	26				
	4	3/4	15	17	18	24		
		6/4	12	21	22	27		
1993	1	9/2	24	23	18	28*	17	
		10/2	21	22	29	15	12	
	2	22/2	21	22	29	15	12	
		23/2	24	17	28	18*	23*	
	3	4/3	22	29	15			
		5/3	17	28	18	24		
	4	9/3	15	29	17	28	12*	
		10/3	18	23	24	22		
	East coast	11/3	25					
	East coast	24/3	25					
	5	25/3	18*	28	17	29*	15	12
	6	31/3	18*	28*	17	29*	15	12*
		1/4	23*	24	22	21*		
	7	15/4	12*	18*	28*	17	29	15

*: Only one sample taken at station.

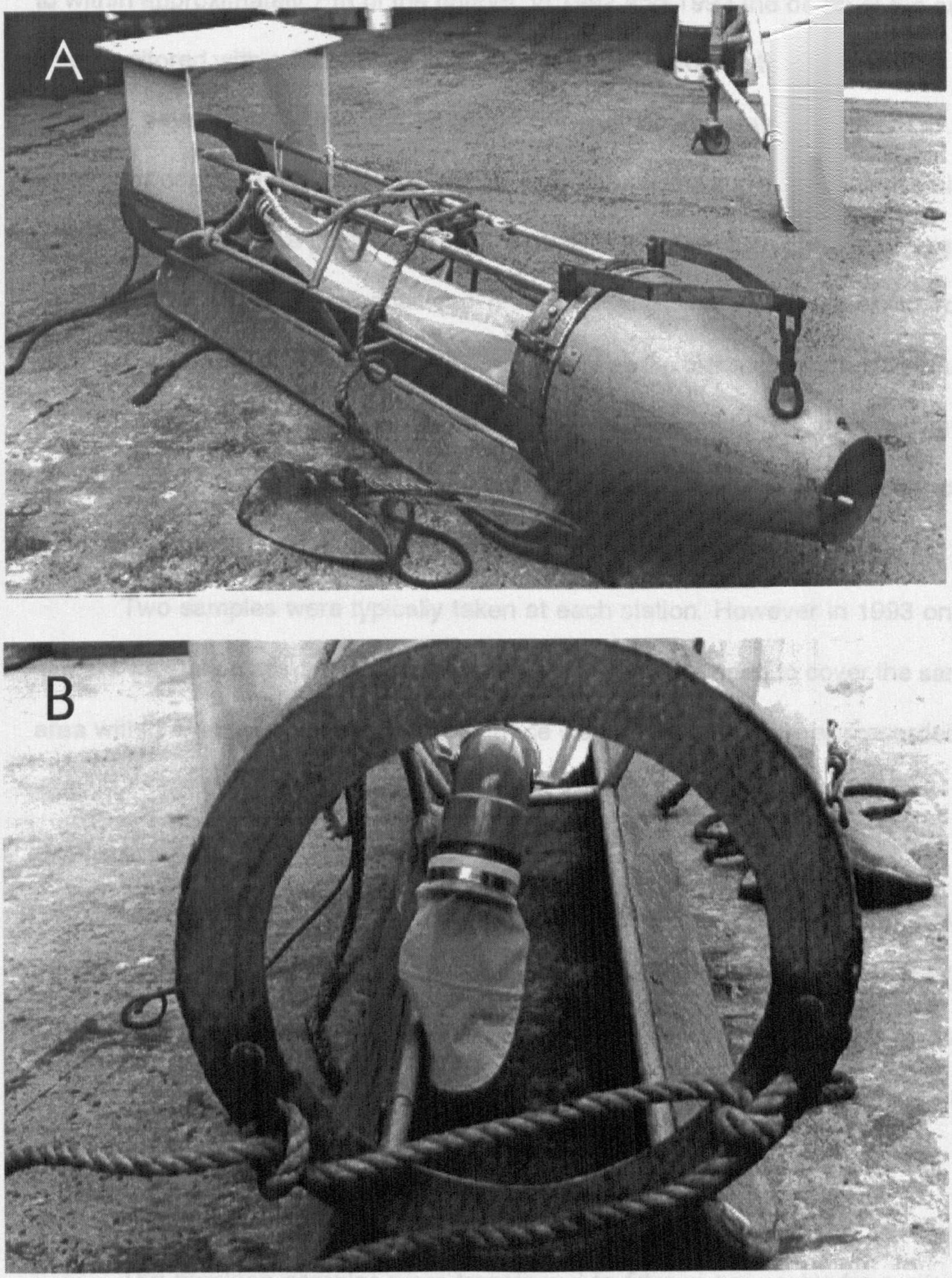


Figure 2.3: Un-encased Gulf III high speed plankton sampler used in plaice egg distribution surveys. The sampler is approximately 2 m long.
A: Lateral view. Note flowmeter mounted in mouth of the nose-cone, and depressor by the side of the sampler.
B: End view. Note detachable cod-end and rope for attachment of drogue.

to within approximately 2 m of the bottom. In 1992 and 1993 the depth of the sampler was monitored with a Furuno net sonde. In 1991 depth was estimated from the length of warp payed out, and a depth gauge attached to the sampler recorded actual maximum depth. The duration of the tow was 20 min, 10 min down and 10 min up.

Plaice eggs are positively buoyant (COOMBS *et al.*, 1990) and may aggregate near the surface in calm conditions (POMMERANZ, 1973). However, in rougher conditions wind induced mixing distributes eggs of all developmental stages throughout the water column (COOMBS *et al.*, 1990). Fishing the sampler for a similar time over all depth strata ensured that an average density of eggs over the whole water column would be recorded.

Two samples were typically taken at each station. However in 1993 only one sample was taken at some stations (Table 2.1), due to the need to cover the sampling area within a restricted time. In 1993 surface water temperatures were recorded at all stations.

Preservation

Upon recovery of the sampler, the net was hosed down with sea water, and the cod end was removed. Plankton samples were preserved in 4% formaldehyde (in sea water in 1991 and 1992, in buffered (pH 7-8) freshwater in 1993). 4% formaldehyde in freshwater is approximately isotonic with sea water (ANON., 1985), and the use of freshwater seemed to eliminate the problem of buckling of eggs.

Sorting

The plankton samples were transferred to filtered sea water for sorting. The samples were placed in a glass dish and set upon a black background marked in 2 cm rows, and sorted under an illuminated magnifying glass. The fish eggs were removed and retained.

Identification of plaice eggs and staging

The following criteria were used for the identification of plaice eggs, based on RUSSELL (1976).

1. Diameter: 1.66-2.17 mm.
2. No large perivitelline space.
3. No oil globule
4. Unsegmented yolk.

Size was the primary identification feature and was measured with a dissecting microscope (fitted with Wild Digital Length-Measuring Units MMS225 and MMS235). RUSSELL (1976) gave the diameter of cod *Gadus morhua* eggs as 1.16-1.89 mm, with the same characteristics as plaice eggs. SIMPSON (1956) gave the diameter of cod eggs as 1.15-1.60, thereby eliminating confusion. SIMPSON (1959b) stated that only long rough dab *Hippoglossoides platessoides* eggs could be confused with plaice eggs on the basis of size. However *H. platessoides* eggs are obviously different due to the large perivitelline space.

Plaice eggs were assigned to one of six developmental stages (Table 2.2, from RYLAND *et al.*, 1975).

Calculation of numbers of plaice eggs m^{-2} sea surface

The average number of plaice eggs m^{-2} at each station was calculated by multiplying the number of eggs m^{-3} (derived from flowmeter calculations) by the water depth at the sampling station.

Plotting of Contours

Contour plots of the number of stage I (A and B) plaice eggs m^{-2} within an area encompassing the survey grid were produced for each survey with the computer package SURFER™, version 4 (Golden Software Inc.). The inshore limit for contouring was set at the 10 m depth contour, and the outer limits were set outside the outer stations at half the distance between stations.

Calculation of total number of stage I eggs in survey grid for 1993 surveys

For each contour plot for the 1993 surveys, the total number of stage I eggs within the survey grid was estimated by gravimetry. A known area of the contour plot was weighed and the areas between successive contours were estimated by weight.

Table 2.2: Developmental stages of plaice eggs.

SIMPSON's (1959a) stage	APSTEIN's (1909) stage
IA	1-3
IB	4-6
II	7-11
III	12-16
IV	17-21
V	22-26

The area between each pair of contours was then multiplied by the average number of eggs in the area (average of levels of inside and outside contour), to estimate the number of eggs between contours. The total number of eggs within the grid was obtained by summation.

Calculation of daily production of stage I eggs during 1993 surveys

To estimate daily egg production, the total number of eggs in each survey was corrected for stage duration (HARDING & TALBOT, 1973), which is temperature-dependent (RYLAND *et al.*, 1975). A weighted average sea surface temperature for each survey was calculated using the numbers of eggs m^{-2}. Stage duration was then calculated from the following equation (from RYLAND *et al.*, 1975).

$$D = k / (t - t_o) + D_o$$

where D= development time (days) to end of stage IB, k= 42.4559, t= observed temperature (°C), t_o=-1.9937 and D_o=-1.2662.

Calculation of total egg production over season

The daily egg production for the seven 1993 surveys was plotted against time in days. A quadratic equation was fitted to the data (MINITAB Inc). The area under the plot, i.e. total egg production, was estimated by integration.

RESULTS AND DISCUSSION

The distributions of stage I plaice eggs recorded in the 1991, 1992 and 1993 surveys are shown as contour plots in Figures 2.4, 2.5 and 2.6 respectively. Insufficient later stage eggs were sampled to merit further discussion, but the numbers are recorded in the Appendix. SIMPSON (1959b) also sampled few later stage eggs in the Irish Sea.

Distribution of Stage I plaice eggs off the east coast of the Isle of Man

The 1991 survey showed fewer stage I plaice eggs at stations 1 and 2, than station 15 (Figure 2.4). This was unexpected because stations 1 and 2 correspond to an inferred spawning area (SIMPSON, 1959b; see Figure 2.1a). The 1992 survey off

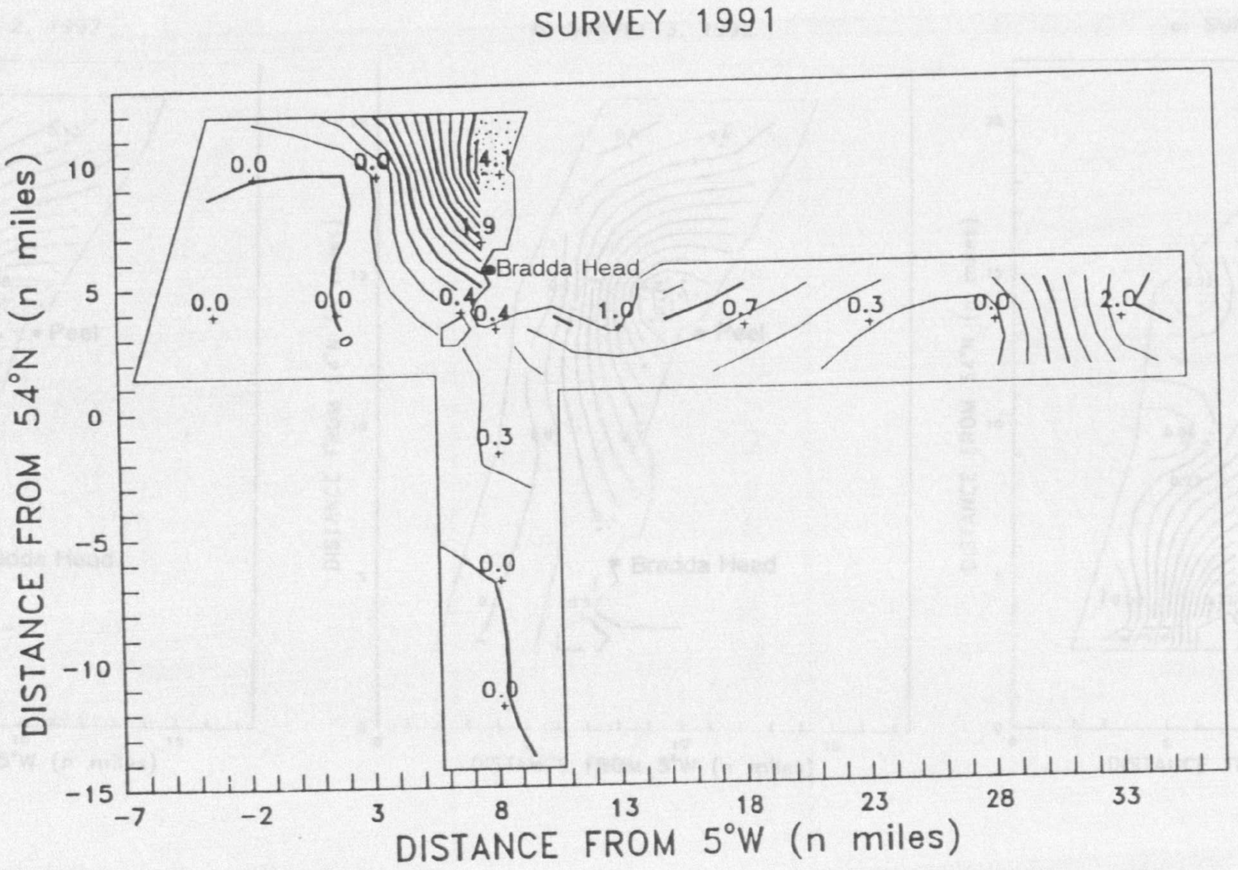


Figure 2.4: Contour plot of numbers of stage I plaice eggs m^{-2} sea surface recorded in 1991 survey (28/2-7/3/91) around the south of the Isle of Man. Sampling stations are indicated by +. Contour interval: 0.25 eggs m^{-2}.

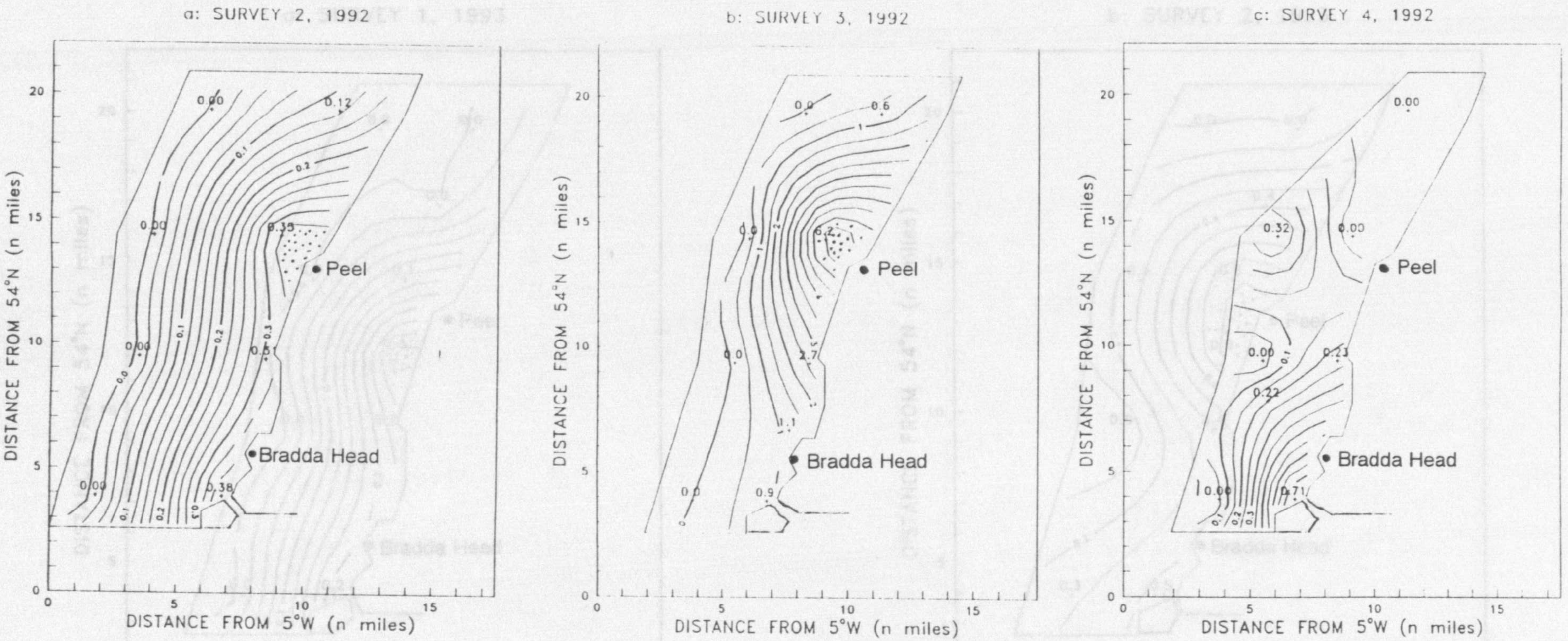


Figure 2.5: Contour plots of numbers of stage I plaice eggs m^{-2} sea surface recorded in 1992 surveys off the west coast of the Isle of Man. a: survey 2 (6-11/2/92); b: survey 3 (5-16/3/92); c: survey 4 (3-6/4/92). Sampling stations are indicated by +. Contour intervals: a: 0.025, b: 0.5, c: 0.05 eggs m^{-2}.

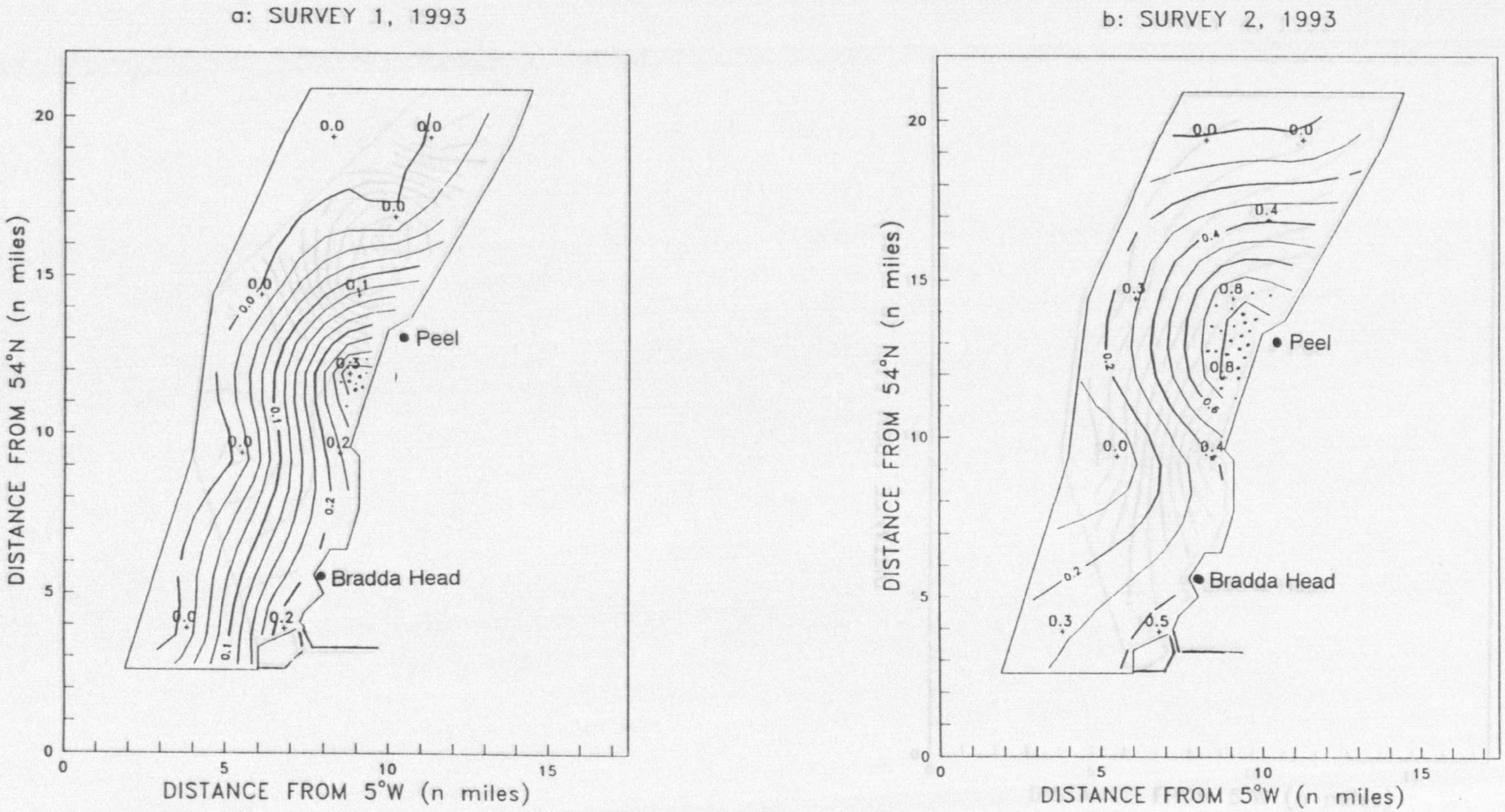


Figure 2.6: Contour plots of numbers of stage I plaice eggs m^{-2} sea surface recorded in 1993 surveys off the west coast of the Isle of Man. a: survey 1 (9-10/2/93); b: survey 2 (22-23/2/93). Sampling stations are indicated by +. Contour intervals: a: 0.025, b: 0.1 eggs m^{-2}.

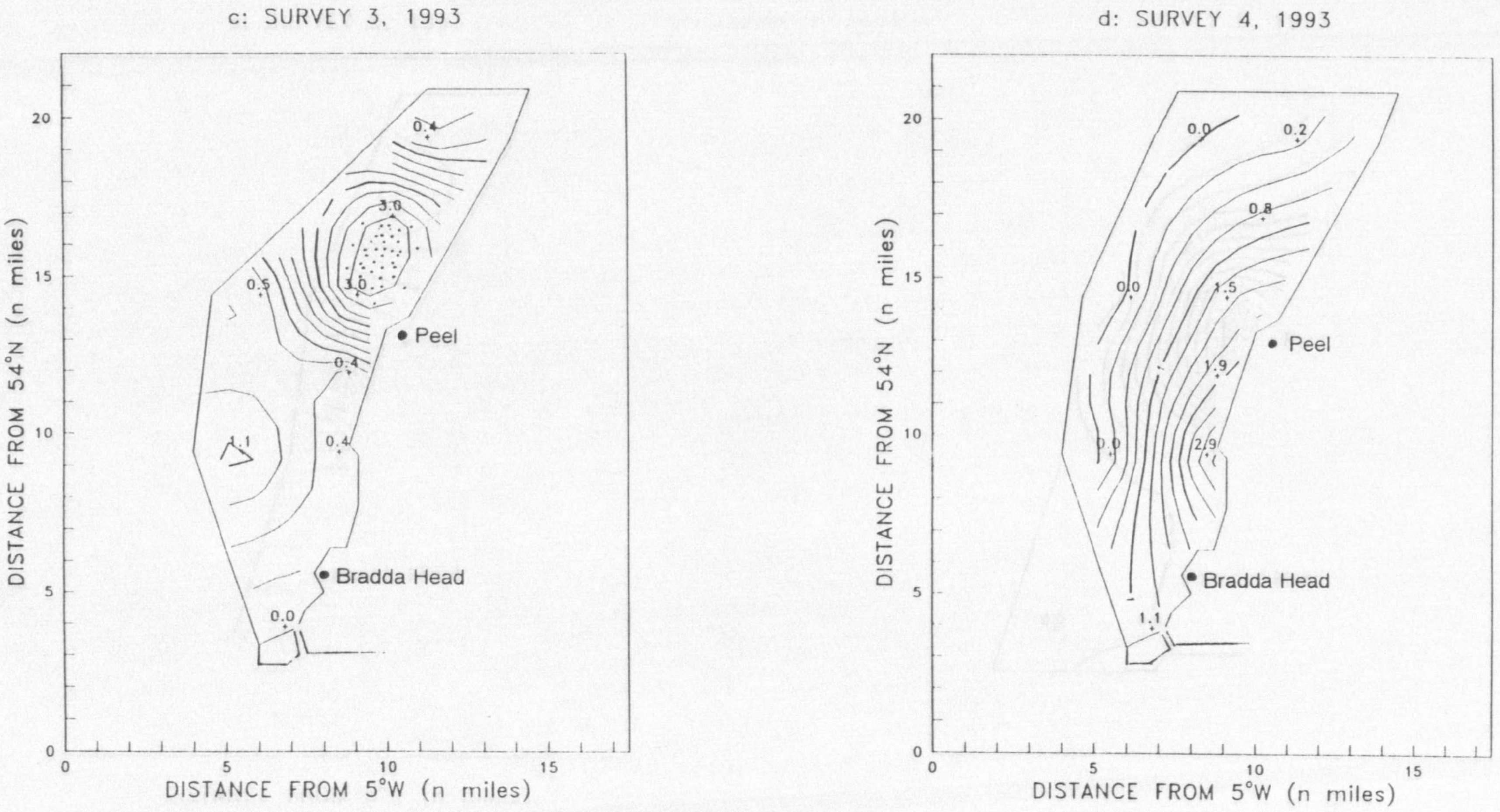


Figure 2.6 (continued): Contour plots of numbers of stage I plaice eggs m^{-2} sea surface recorded in 1993 surveys off the west coast of the Isle of Man. c: survey 3 (4-5/3/93); d: survey 4 (9-10/3/93). Sampling stations are indicated by +. Contour intervals: c: 0.25, d: 0.25 eggs m^{-2}.

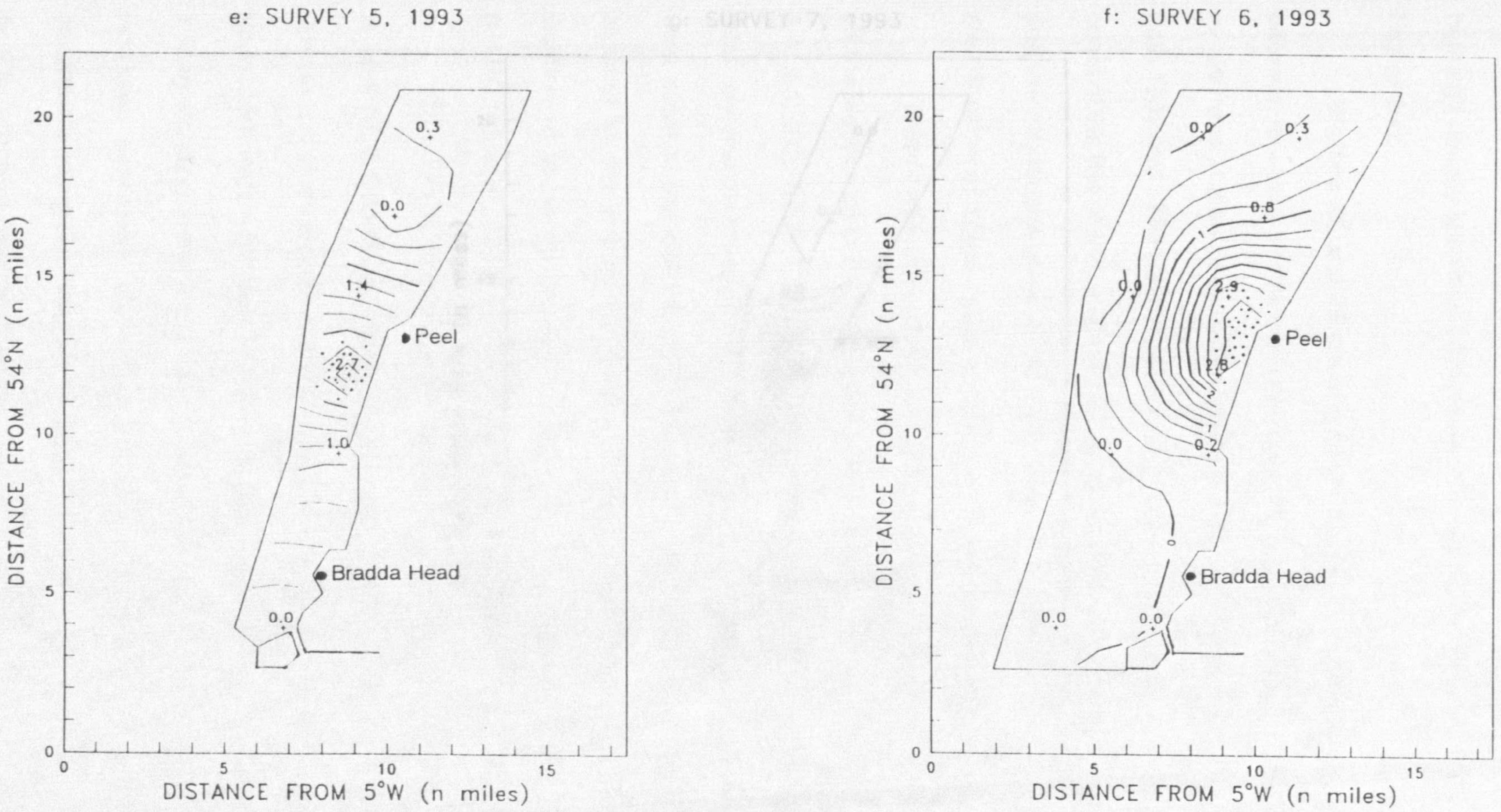


Figure 2.6 (continued): Contour plots of numbers of stage I plaice eggs m^{-2} sea surface recorded in 1993 surveys off the west coast of the Isle of Man. e: survey 5 (25/3/93); f: survey 6 (31/3-1/4/93). Sampling stations are indicated by +. Contour intervals: e: 0.25, f: 0.25 eggs m^{-2}.

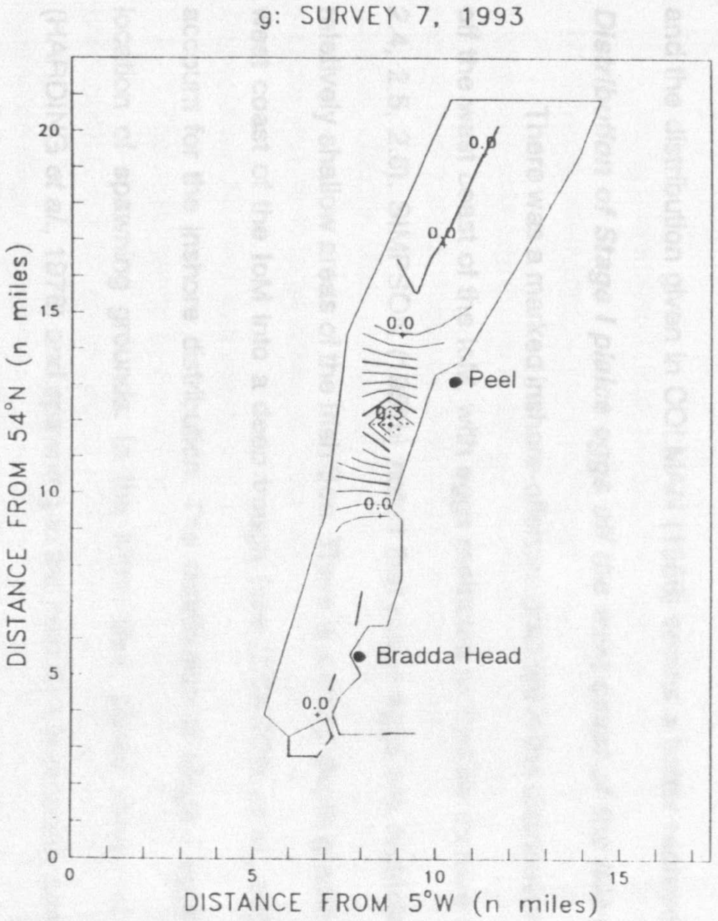

g: SURVEY 7, 1993

Figure 2.6 (continued): Contour plots of numbers of stage I plaice eggs m^{-2} sea surface recorded in 1993 surveys on the west coast of the Isle of Man. g: survey 7 (15/4/93). Sampling stations are indicated by +. Contour interval: g: 0.025 eggs m^{-2}.

the east coast (not contoured) showed far more stage I eggs at station 25 than 26 (9.7 m^{-2} and 0.8 m^{-2}; $t=6.49$; $p<0.05$). Stations 25 and 26 corresponded to the locations of high egg density shown by COLMAN (1966) and SIMPSON (1959b) respectively (see Figure 2.1).

Stations 25 and 26 are separated by only 5 n miles. However the difference between locations seems consistent, as few eggs were recorded at stations 1 and 2 in 1991 and station 26 in 1992 whereas large numbers were recorded at station 25 in both 1992 and 1993 (see Chapter 3). The area of high stage I egg density off the east coast of the Isle of Man is therefore further north than indicated by SIMPSON (1959b), and the distribution given in COLMAN (1966) seems a better representation.

Distribution of Stage I plaice eggs off the west coast of the Isle of Man

There was a marked inshore-offshore gradient in the distribution of stage I eggs off the west coast of the IoM, with eggs restricted to shallow inshore waters (Figures 2.4, 2.5, 2.6). SIMPSON (1959b) noted that plaice eggs are restricted to coastal or relatively shallow areas of the Irish Sea. There is a sharp depth gradient off the south-west coast of the IoM into a deep trough (see DICKSON *et al.*, 1988) which could account for the inshore distribution. The distribution of stage I eggs will reflect the location of spawning grounds. In the North Sea, plaice spawn at depths <50 m (HARDING *et al.*, 1978) and spawning in the Irish Sea is probably similarly restricted.

SCOTT (1915) noted large numbers of plaice eggs 3 miles NW of Bradda Head in April 1914. SIMPSON (1959b) also recorded stage I eggs off the west coast of the IoM. In this study a distinct centre of plaice egg distribution was typically recorded in near-shore waters between stations 15 and 28 (Figures 2.5, 2.6). There is therefore a long-standing spawning ground off the west coast of the Isle of Man. The very restricted near-shore distribution of eggs may have lead to its presence and importance being dismissed by COLMAN (1966).

Egg production from west coast spawning ground

The estimates for the number of stage I eggs within the survey grid and daily stage I egg production, for each of the seven surveys in 1993, are shown in Table 2.3. Daily egg production over time is shown graphically in Figure 2.7. The egg production curve fitted to the data (n = 7; R-sq = 0.77; p = 0.023) was:

$$P=-129.94+14.165D-0.165D^2$$

where P is the number of stage I eggs (in millions) produced day^{-1}, and D is the number of days after 31 January.

This equation integrates to:

$$\int_{10}^{74} P = [c-129.94D+7.083D^2-0.055D^3]_{10}^{74}$$

Using this method, total production over the survey period (day 10 to 74 from 31/1/93) was estimated at 7.6 x 10^9 stage I eggs. This must only be considered as a preliminary estimate due to inaccuracies inherent in the method. The errors include the sampling of heterogeneously distributed organisms, estimation of the volume filtered (Corten, cited in VAN DER LAND, 1991), average age estimates, extrapolation of sample results to large areas, and the estimation of contour areas.

Importance to Irish Sea plaice stock

The significance of the spawning ground can be assessed by comparing egg production (7.6 x 10^9 stage I eggs) with other estimates. HARDING & TALBOT (1973) estimated stage I egg production in 1965 from the Great Orme spawning ground (see Figure 2.1) at 2.75 x 10^{11}. Using data from ANON. (1993), and allowing for atresia (2.7%), R.D.M. NASH (*pers. comm.*) estimated the total fecundity of the Irish Sea plaice stock in 1993 at 5.63 x 10^{11}. Assuming a fertilization rate of 100%, a daily instantaneous mortality rate of 0.095 (HARDING & TALBOT, 1973) and an average age of 1.7 days at 7.0°C (from equation in RYLAND *et al.*, 1975), total stage I egg production in the Irish Sea in 1993 was 4.79 x 10^{11} eggs. The spawning ground described here therefore produces approximately 1.6% of the eggs in the Irish Sea, and is of little significance to the Irish Sea plaice stock.

Table 2.3: Estimates of stage I plaice egg production in 1993 from spawning ground on west coast of IoM.

Survey	Date	Number Stage I eggs[*1] (x 10^6)	Weighted temperature[*2] (°C)	Duration of stage I[*3] (Days)	Average age[*4] (Days)	Production of stage I eggs[*5] (x 10^6 d^{-1})
1	10/2/93	26	7.3	3.3	1.7	15.4
2	23/2/93	107	7.0	3.5	1.7	61.9
3	5/3/93	369	6.4	3.8	1.9	194.6
4	9/3/93	262	6.7	3.6	1.8	144.6
5	25/3/93	291	7.7	3.1	1.6	186.9
6	31/3/93	211	7.2	3.4	1.7	125.6
7	15/4/93	14	7.8	3.1	1.5	9.1

[*1]: Estimate from contour plots of total number of eggs within survey grid.

[*2]: Surface water temperature recorded at stations, weighted according to egg abundance.

[*3]: Estimated using equation from RYLAND *et al.* (1975).

[*4]: Stage duration divided by 2.

[*5]: Number of stage I eggs within survey grid divided by estimated average age.

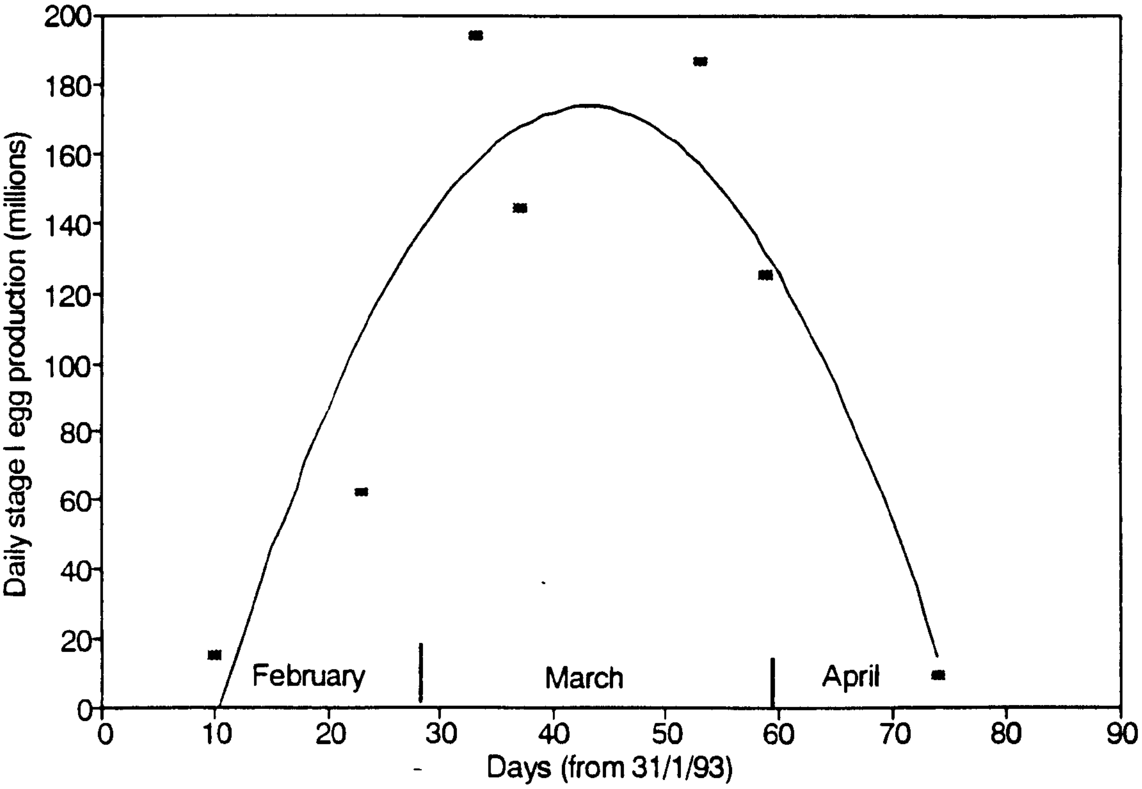


Figure 2.7: Estimates of production of stage I plaice eggs within survey grid on west coast of the Isle of Man in 1993. See text for equation of fitted curve.

Local Significance of west coast spawning ground

Although egg production from the spawning ground is low in comparison to total egg production in the Irish Sea, it may be of importance in supplying local nurseries. This can be assessed by predicting whether sufficient larvae would survive to supply local nurseries.

From published estimates of mortality in the Irish Sea, the number of stage 4 larvae potentially produced by this spawning ground can be estimated at 55 x 10^6 (see Table 2.4). From mortality rates and stage durations given in a life table for North Sea plaice (BEVERTON & ILES, 1992a), total instantaneous mortality between stage I eggs and post settlers on July 10 can be estimated at 7.97 (0.30/2 + 2.66 + 3.98 + 0.49 + 0.69). Applying this mortality to the estimate of stage I egg production predicts the number of 0-group plaice on July 10 at 2.6 x 10^6. RILEY & CORLETT (1966) estimated the population size of 0-group plaice in Port Erin Bay in July 1963 (a strong year-class, see Figure 1.2) at 5 x 10^4.

COLMAN (1966) dismissed the presence of a spawning ground local to Port Erin and assumed that larvae would be derived from one of the main spawning grounds in the Irish Sea. This study has shown the presence of a spawning ground local to Port Erin with enough eggs spawned to theoretically supply local nurseries.

Whether the larvae produced do supply the local nurseries depends upon the actual mortality rates and transport in the pelagic phase. The time-averaged residual current in the Irish Sea is northwards and the main flow may pass to the west of the IoM (DICKSON *et al.*, 1988) which would carry the eggs and larvae away from Manx waters. However the restricted coastal distribution may reduce the impact of such a flow.

Time of spawning and significance for larval feeding

No plaice eggs were found in mid January 1992. Low densities of eggs were recorded at the beginning of February in 1992 and 1993. Spawning therefore starts in early February. This is in accord with the results of SCOTT (1913) and BAL (1940)

Table 2.4: Pelagic stage "life table" for eggs spawned on west coast spawning ground. Estimates of mortality rate taken from HARDING & TALBOT (1973). Stage duration of eggs taken as weighted average from Table 2.3.

Stage	Number (x 10^6)	Stage duration (days)	Mortality
Fertilized ova	8894		
		1.7	M = 0.095
Stage I ova	7568		
			99.27%
Stage 4 larvae	55		

(see Table 2.5). March is the main period of egg production (Figure 2.7). Very few eggs were present at the beginning of April 1992 and mid April 1993. Spawning therefore finishes around mid April. SCOTT (1915) did find very large numbers of eggs off Bradda head on 4 April 1914, which presumably had recently been spawned (COLMAN, 1966). Sampling of this location at the same time of year in 1992 produced very few plaice eggs. Spawning may therefore be delayed or extended in some years, as noted by POXTON (1986).

In the Southern Bight of the North Sea peak spawning occurs in January or February (HARDING *et al.*, 1978). SIMPSON (1959b) stated that spawning in the Irish Sea is some four to six weeks later than in the Southern Bight of the North Sea, which agrees with the present results. The time of spawning is thought to be synchronised to the time of the spring plankton bloom (CUSHING, 1990b). It is interesting to note that the spring phytoplankton bloom in the Irish Sea occurs about one month later than in the North Sea and English Channel (COLEBROOK, 1979; see SAVIDGE & KAIN, 1990 for review).

In the Irish Sea stage 1 plaice larvae feed mainly on copepod nauplii, with *Oikopleura*, copepodites and copepods becoming more important as they grow (COLMAN, 1966). The copepod bloom starts late in the Irish Sea (GRAZIANO, 1988), in April with numbers reaching a peak between May and August (HERDMAN *et al.*, 1913; COLEBROOK, 1979; SCROPE-HOWE & JONES, 1985; GRAZIANO, 1988). At 7°C, the development time from spawning to first feeding (stage 1b: RYLAND *et al.*, 1975) larvae is approximately three weeks (using equations from RYLAND *et al.*, 1975). Larval feeding will therefore start as copepod numbers are increasing, but before the peak in numbers.

There is considerable inter-annual variation in the timing of the spring phytoplankton bloom in the Irish Sea (SLINN & EASTHAM, 1984; see SAVIDGE & KAIN, 1990 for review). Assuming that spawning is synchronised with the average annual production cycle (CUSHING, 1990b), food mismatch conditions could be set

Table 2.5: Summary of SCOTT's and BAL's data on occurrence of plaice eggs in regular plankton hauls around the south of the Isle of Man.

Year	First Recorded	Generally Distributed	Last Recorded	Reference
1907	22 February			SCOTT (1913)
1908		13/3 - 23/4	23 April	SCOTT (1913)
1909	18 February	April	8 May	SCOTT (1913)
1910	28 February		22 April	SCOTT (1913)
1911	9 February	April		SCOTT (1913)
1912	4 March		15 April	SCOTT (1913)
1913	Data only available for cruises in east Irish Sea			SCOTT (1914)
1914	26 February	Bulk early to mid April	20 April	SCOTT (1915)
1918	19 February		April	SCOTT (1919)
1939	10 February		5 May	BAL (1940)

up if the time of plaice spawning is as consistent as it is in the North Sea. Plaice have an protracted period of high egg production compared to other species (see Figure 5 in CUSHING, 1990b). Individual plaice release 'batches' of eggs, and fish of different ages spawn at different times (HORWOOD, 1990). If the timing of the spring plankton bloom is variable, a protracted spawning season may reduce the chances of complete mismatch in the production of plaice larvae and their food (CUSHING, 1990b).

CHAPTER 3:

A FIELD STUDY OF CLUPEID PREDATION ON PLAICE EGGS

INTRODUCTION

The stochastic variability in year-class strength of plaice is thought to be generated in the pelagic stage (BERGMAN *et al.*, 1988), probably largely in the egg stage, and is related to temperature (ZIJLSTRA & WITTE, 1985). The total mortality of plaice eggs is reduced at low temperatures (BANNISTER *et al.*, 1974). The apparent temperature-dependent mortality of plaice eggs therefore generates variation in year-class strength.

The daily instantaneous mortality rate of plaice eggs is 0.019-0.116, equivalent to a total mortality in the egg stage of 49-81% (BANNISTER *et al.*, 1974). Despite this high mortality rate (TUNGATE, 1975), and the importance of egg mortality in determining the year-class strength of plaice, the causes of mortality remain a matter of belief. The potential causes of mortality of plaice eggs were presented in Chapter 1. COOMBS *et al.* (1990) recently suggested that weather conditions (e.g. wave action) may have a direct effect on the mortality of plaice eggs. However, predation is usually assumed to be the main cause of mortality (POMMERANZ, 1981; HUNTER, 1984; BAILEY & HOUDE, 1989; RIJNSDORP & JAWORSKI, 1990), even though the predators responsible for the high mortality remain unidentified.

Pelagic fish eggs are non-motile and are therefore relatively safe from those invertebrate predators that detect prey by mechano-reception, such as chaetognaths (TUNGATE, 1975; BAILEY & HOUDE, 1989). TUNGATE (1975) found no evidence that chaetognaths ate plaice eggs in the southern North Sea, although chaetognaths have been recorded containing fish eggs in the Irish Sea (ALVAREZ-CADENA, 1988). Pelagic fish eggs are vulnerable to contact entangling invertebrate predators (see BAILEY & HOUDE, 1989). LEBOUR (1923) recorded *Pleurobranchia pileus* as a predator of plaice eggs, but TUNGATE (1975) found that *P. pileus* were scarce at the time when plaice eggs develop.

Pelagic fish eggs are highly vulnerable to planktivorous fishes, which could be significant predators (HUNTER, 1984; BAILEY & HOUDE, 1989). Recent studies have shown the importance of clupeids as predators of pelagic fish eggs in upwelling systems (HUNTER & KIMBRELL, 1980; ALHEIT, 1987; VALDÉS SZEINFELD, 1991). POMMERANZ (1981) suggested that predation by clupeids (herring *Clupea harengus* and sprat *Sprattus sprattus*) may, at least locally, be an important cause of mortality of plaice eggs. However, the only publication (DAAN *et al.*, 1985) in which a source of mortality of plaice eggs has been quantified, that is predation by herring in the North Sea, was shown to be of little significance.

Although herring are not thought to be a major predator of plaice eggs in the North Sea, their importance in the Irish Sea has not been examined. Nor has the significance of sprat been assessed. Having gained information on the timing and areas of plaice spawning around the Isle of Man (Chapter 2), herring and sprat were sampled in areas of known high plaice egg density. Evidence of predation on, and selection for, plaice eggs was found. The importance of clupeid predation to the egg mortality rate, and hence its possible role in the establishment of plaice year-class strength is discussed. It is proposed in this chapter that density-dependent mortality is likely to occur in the early egg stages of plaice.

MATERIALS AND METHODS

Samples of herring and sprat were obtained by trawling from *R.V. Roagan* off the west and east coasts of the Isle of Man (IoM) in March 1993 (Table 3.1; Figure 3.1). Trawl 2, and trawls 4 and 5 were made in the vicinity of the plaice spawning grounds off the west and east coasts of the IoM respectively (see Chapter 2). The demersal trawl used was a Borris Goshawk rockhopper trawl (45 mm mesh in cod-end liner) towed at approximately 2 knots. The pelagic trawl was a 32 m IC mid-water trawl (45 mm mesh in cod-end liner), towed at 4 knots. The demersal trawl was used during the day and the pelagic trawl was used at night because clupeids were expected to be near the bottom during the day, and rise into the water column after dusk (BLAXTER & HUNTER, 1982).

Table 3.1: Details of trawls made in clupeid sampling programme.

Trawl	Date	Location	Sea surface temp.	Trawl type	Start Time	Duration	Number sampled	
							Herring	Sprat
1	8/3/93	W IoM		Demersal	11:00	1:25 h	16	0
2	8/3/93	W coast IoM		Demersal	13:15	1:20 h	1	0
3	11/3/93	E coast IoM	6.6°C	Pelagic	20:00	2:00 h	49	106
4	15/3/93	E IoM		Demersal	12:00	2:30 h	108*	0
5	24/3/93	E IoM	6.8°C	Pelagic	20:00	2:00 h	264*	86

* indicates sub-sample

The clupeids were sorted from the catch and killed with an overdose of the anaesthetic benzocaine. The fish were preserved whole in 4% buffered formaldehyde after the body wall in the region of the stomach had been slit open to facilitate preservation of stomach contents. Samples of other fish species taken in the pelagic trawls were preserved in a similar manner.

In the laboratory total length (TL: to nearest mm) and weight (to nearest 0.1 g) of each fish were recorded and the "stomach" was removed. The "stomach" was taken to include the oesophagus, caecum and pylorus (HANSEN, 1955). Each stomach was dissected open in filtered sea water under a dissecting microscope. To compare feeding activity, "stomach fullness" was judged on an arbitrary scale of 0-10 (0: empty, 10: full). Stomach contents were identified to broad categories and assigned points (totalling 10) on the basis of their relative volumes. A coarse assessment of the importance of different prey items was made by multiplying fullness by relative volume for each fish, and summing the values for all individuals of a species within a sample (see HYNES, 1950).

Fish eggs found in the stomachs were retained and counted. They were present in a wide range of digestion states from intact eggs with the embryo clearly visible to empty chorions. Despite digestion, plaice eggs were easily distinguished from other fish eggs by their large size (see Figure 3.2).

To allow comparison of fish eggs found in stomachs with those in the plankton, plankton samples were taken at station 25 (Figure 3.1; see Chapter 2) on 11/3/93 and 25/3/93. Sampling, preservation, sorting, diameter measurement, and the identification of plaice eggs were as described in Chapter 2.

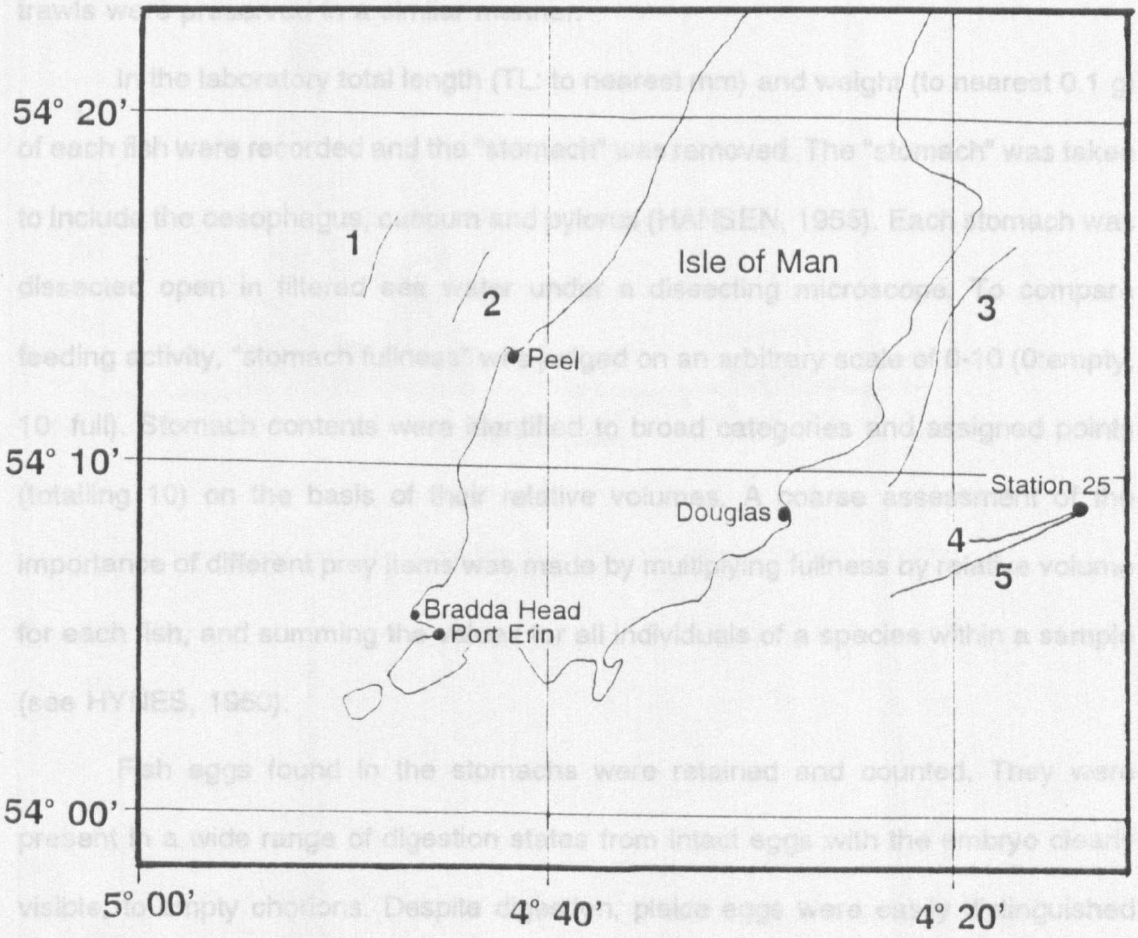


Figure 3.1: Approximate tracks of trawls taken in clupeid sampling programme. Trawls were taken in areas of high plaice egg density around the Isle of Man. Trawls 1, 2 and 4 were demersal trawls, and trawls 3 and 5 were pelagic trawls. See Table 3.1 for further details.

The clupeids were sorted from the catch and killed with an overdose of the anaesthetic benzocaine. The fish were preserved whole in 4% buffered formaldehyde after the body wall in the region of the stomach had been slit open to facilitate preservation of stomach contents. Samples of other fish species taken in the pelagic trawls were preserved in a similar manner.

In the laboratory total length (TL: to nearest mm) and weight (to nearest 0.1 g) of each fish were recorded and the "stomach" was removed. The "stomach" was taken to include the oesophagus, caecum and pylorus (HANSEN, 1955). Each stomach was dissected open in filtered sea water under a dissecting microscope. To compare feeding activity, "stomach fullness" was judged on an arbitrary scale of 0-10 (0:empty, 10: full). Stomach contents were identified to broad categories and assigned points (totalling 10) on the basis of their relative volumes. A coarse assessment of the importance of different prey items was made by multiplying fullness by relative volume for each fish, and summing the values for all individuals of a species within a sample (see HYNES, 1950).

Fish eggs found in the stomachs were retained and counted. They were present in a wide range of digestion states from intact eggs with the embryo clearly visible, to empty chorions. Despite digestion, plaice eggs were easily distinguished from other fish eggs by their large size (see Figure 3.2).

To allow comparison of fish eggs found in stomachs with those in the plankton, plankton samples were taken at station 25 (Figure 3.1, see Chapter 2) on 11/3/93 and 25/3/93. Sampling, preservation, sorting, diameter measurement, and the identification of plaice eggs were as described in Chapter 2.

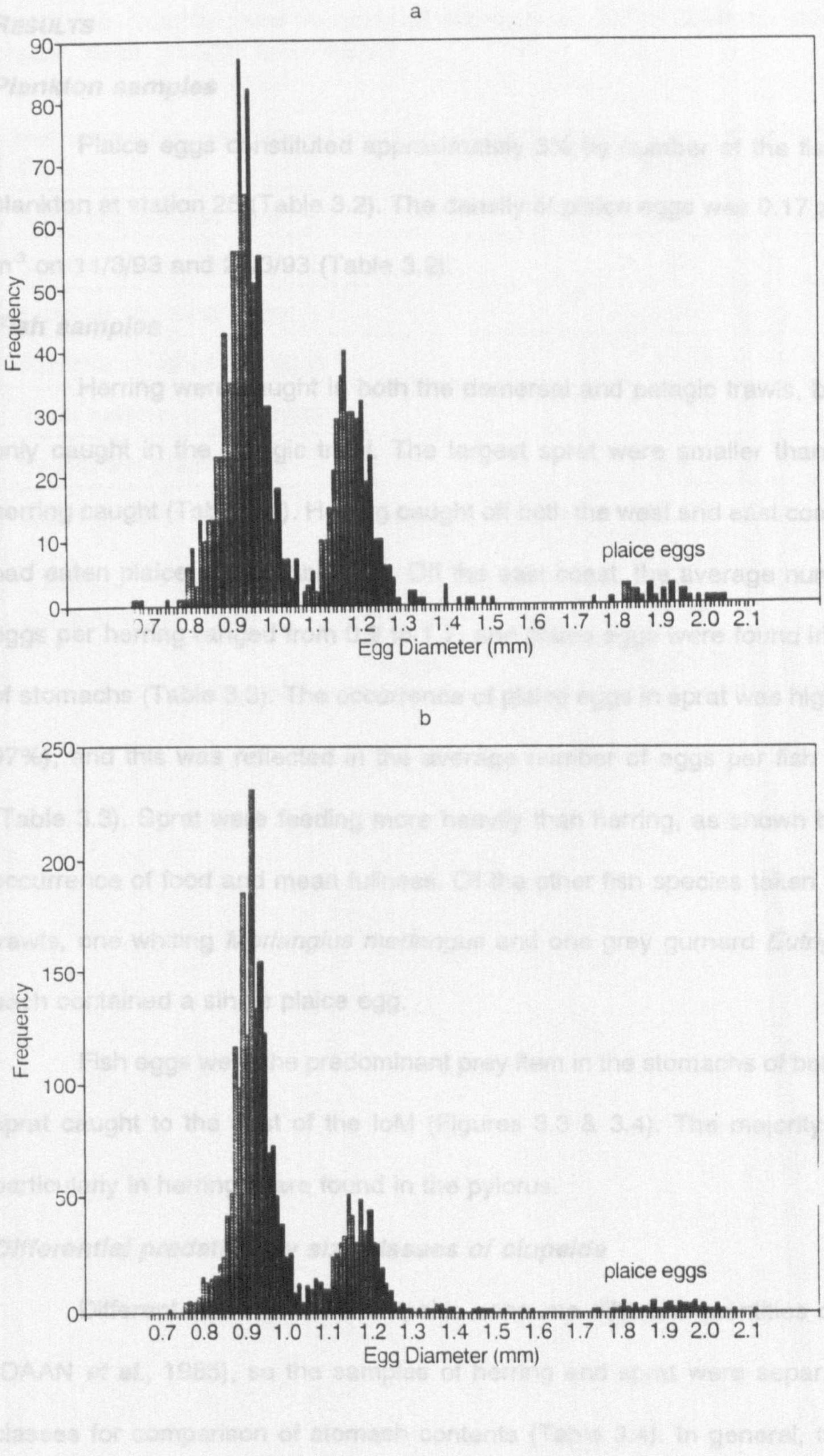


Figure 3.2: Size-frequency distributions of all fish eggs taken in plankton samples off the east coast of the Isle of Man (station 25). a: 11/3/93; b: 24/3/93.
Note large size and relative scarcity of plaice eggs.

RESULTS

Plankton samples

Plaice eggs constituted approximately 3% by number of the fish eggs in the plankton at station 25 (Table 3.2). The density of plaice eggs was 0.17 and 0.43 eggs m^{-3} on 11/3/93 and 24/3/93 (Table 3.2).

Fish samples

Herring were caught in both the demersal and pelagic trawls, but sprat were only caught in the pelagic trawl. The largest sprat were smaller than the smallest herring caught (Table 3.3). Herring caught off both the west and east coasts of the IoM had eaten plaice eggs (Table 3.3). Off the east coast, the average number of plaice eggs per herring ranged from 0.9 to 1.7, and plaice eggs were found in 25% to 48% of stomachs (Table 3.3). The occurrence of plaice eggs in sprat was higher (57% and 97%), and this was reflected in the average number of eggs per fish (2.7 and 8.7) (Table 3.3). Sprat were feeding more heavily than herring, as shown by the greater occurrence of food and mean fullness. Of the other fish species taken in the pelagic trawls, one whiting *Merlangius merlangus* and one grey gurnard *Eutrigla gurnardus* each contained a single plaice egg.

Fish eggs were the predominant prey item in the stomachs of both herring and sprat caught to the east of the IoM (Figures 3.3 & 3.4). The majority of fish eggs, particularly in herring, were found in the pylorus.

Differential predation by size classes of clupeids

Different size-classes of clupeids consume different quantities of plaice eggs (DAAN *et al.*, 1985), so the samples of herring and sprat were separated into size classes for comparison of stomach contents (Table 3.4). In general, the number of plaice eggs per fish increased with increasing sprat size, but decreased with increasing herring size (Table 3.4).

Trends in fullness, number of all fish eggs, number of plaice eggs, and the proportion that plaice eggs formed of all fish eggs, with size were analyzed by

Table 3.2: Numbers and densities of fish eggs in Gulf III plankton samples taken at station 25 on 11/3/93 and 24/3/93.

Date		11/3/93	24/3/93
Total volume sampled (m^3)		189.8	158.0
Bottom depth (m)		27	27
Number of plaice eggs		33	68
Number of other fish eggs		1154	2252
Total number of fish eggs		1187	2320
Proportion plaice eggs		2.8%	2.9%
Density plaice eggs	eggs m^{-3}	0.17	0.43
	eggs l^{-1}	0.00017	0.00043
Density all fish eggs	eggs m^{-3}	6.25	14.68
	eggs l^{-1}	0.00625	0.01468

Table 3.3: Fish and plaice egg occurrence and number per individual in herring, sprat, whiting, grey gurnard, mackerel *Scomber scombrus*, poor-cod *Trisopterus minutus*, dragonet *Callionymus lyra* and hook-nose *Agonus cataphractus* sampled in trawls 1-5.

Trawl	Date	Species	TL Range (mm)	Mean TL (mm)	Mean Weight (g)	n	% with food	Mean Fullness (0-10)	% Occurrence		Eggs/fish	
									Fish Eggs	Plaice Eggs	All	Plaice
1	8/3	Herring	176-298	263	117.1	16	87.5	2.3	0	-	-	-
2	8/3	Herring	-	252	120.4	1	100	2.0	100	100	3.00	1.00
3	11/3	Herring	153-296	251	110.7	52	46.2	0.5	42.9	38.8	1.47	0.90
		Sprat	65-147	117	12.6	106	84.0	1.6	75.5	56.6	17.04	2.71
		Mackerel	-	226	83.1	0	-	-	-	-	-	-
		Whiting	132-331	241	135.7	47	68.1	1.5	2.1	2.1	0.02	0.02
		Poor-cod	81-98	87	5.5	6	83.3	6.5	0	-	-	-
		Dragonet	-	235	93.2	1	100	1.0	0	-	-	-
		Hook-nose	-	131	24.4	1	0	-	-	-	-	-
		Grey Gurnard	140-145	143	21.2	2	100	1.5	0	-	-	-
4	15/3	Herring	200-305	258	116.7	108	75.0	0.8	63.0	48.1	3.83	1.70
5	24/3	Herring	175-291	228	84.0	264	37.1	0.4	36.0	25.4	4.11	0.91
		Sprat	94-146	123	12.5	86	96.5	2.7	96.5	96.5	38.22	8.73
		Mackerel	-	210	72.4	1	0	-	-	-	-	-
		Whiting	189-315	230	99.8	26	38.5	1.5	0	-	-	-
		Grey Gurnard	136-205	161	32.4	25	56.0	1.2	4.0	4.0	0.04	0.04
		Poor-cod	86-121	101	9.3	5	100	5.6	0	-	-	-

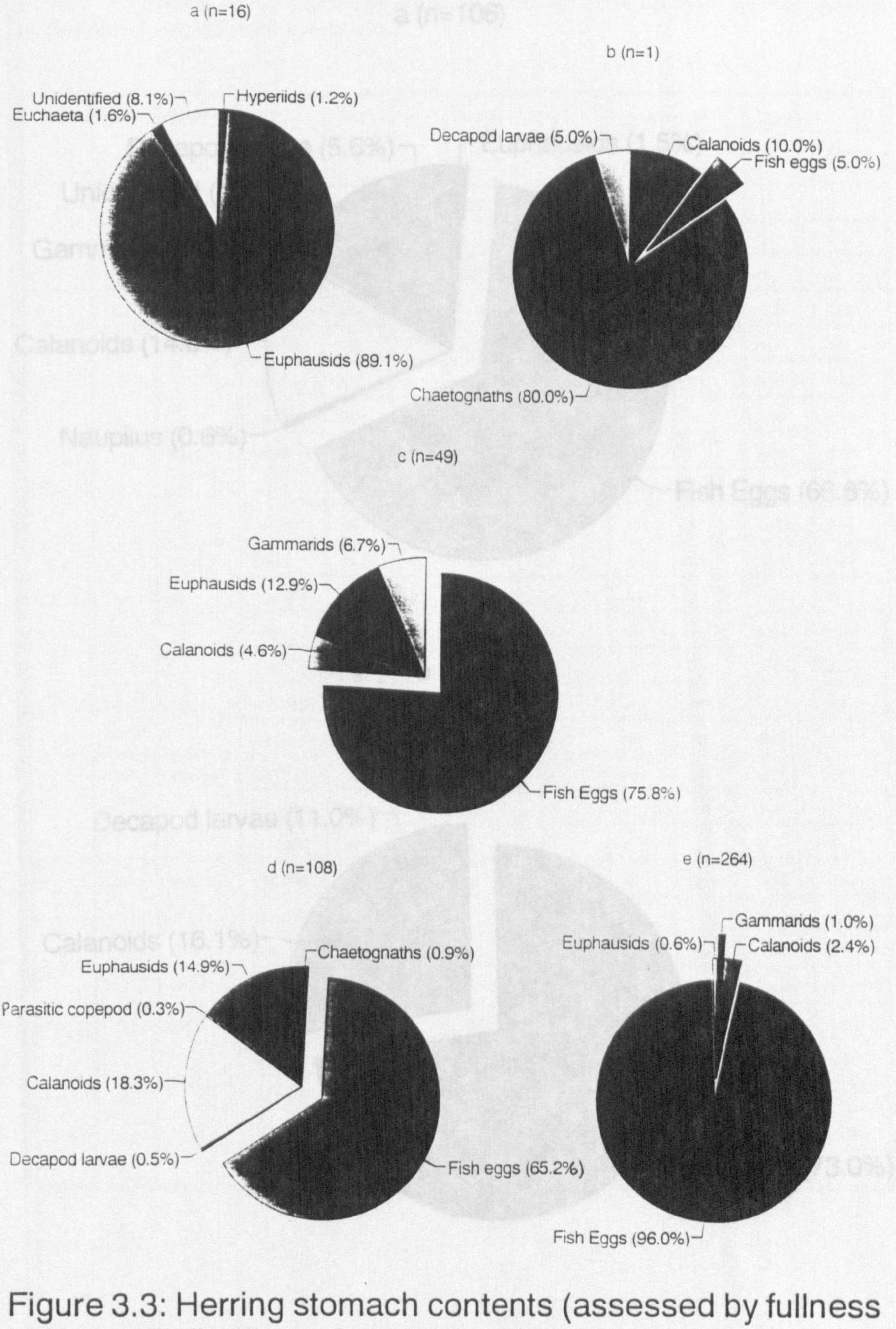


Figure 3.3: Herring stomach contents (assessed by fullness index multiplied by point composition).
a: Trawl 1, west IoM, 8/3/93; b: Trawl 2, west IoM, 8/3/93; c: Trawl 3, east IoM, 11/3/93; d: Trawl 4, east IoM, 15/3/93; e: Trawl 5, east IoM, 24/3/93.

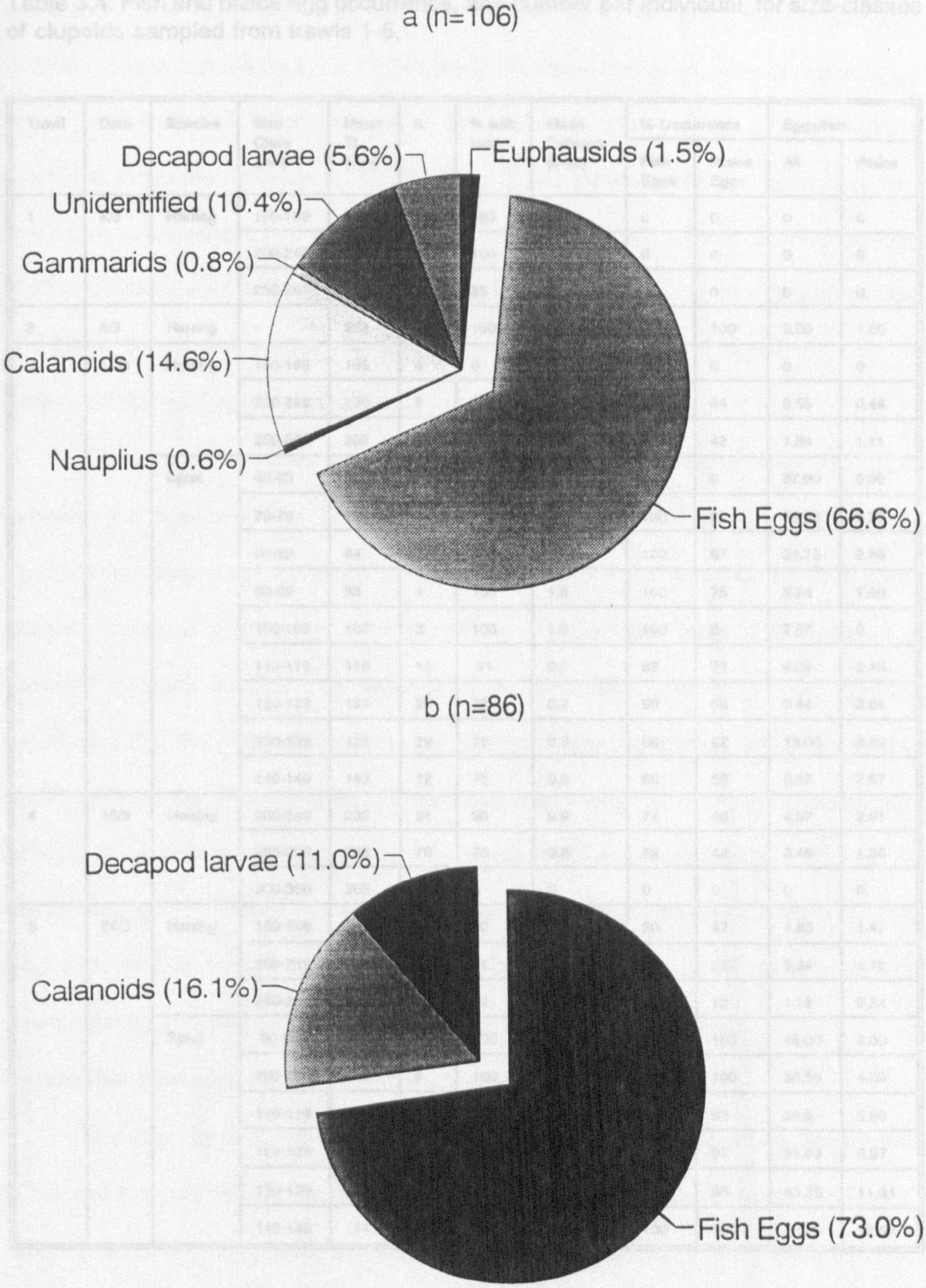


Figure 3.4: Sprat stomach contents (assessed by fullness index multiplied by point composition).
a: Trawl 3, east IoM, 11/3/93; b: Trawl 5, east IoM, 24/3/93.

Table 3.4: Fish and plaice egg occurrence, and number per individual, for size-classes of clupeids sampled from trawls 1-5.

Trawl	Date	Species	Size Class (mm)	Mean TL (mm)	n	% with food	Mean Fullness (0-10)	% Occurrence		Eggs/fish	
								Fish Eggs	Plaice Eggs	All	Plaice
1	8/3	Herring	150-199	176	1	100	2.0	0	0	0	0
			200-249	241	2	100	2.0	0	0	0	0
			250-299	273	13	85	2.4	0	0	0	0
2	8/3	Herring	-	252	1	100	2.0	100	100	3.00	1.00
3	11/3	Herring	150-199	165	4	0	0	0	0	0	0
			200-249	238	9	44	0.4	44	44	0.55	0.44
			250-299	268	36	55	0.6	47	42	1.86	1.11
		Sprat	60-69	65	1	100	5	100	0	87.00	0.00
			70-79	75	9	100	4.7	100	22	58.00	0.22
			80-89	84	12	100	4.6	100	67	34.75	2.08
			90-99	93	4	100	1.8	100	75	8.25	1.50
			100-109	107	3	100	1.0	100	0	2.67	0
			110-119	116	11	91	0.9	82	73	6.09	2.45
			120-129	124	25	72	0.7	60	56	9.44	3.64
			130-139	134	29	79	0.8	66	62	13.00	3.58
			140-149	143	12	75	0.8	66	58	5.67	2.67
4	15/3	Herring	200-249	232	31	90	0.9	74	65	4.87	2.61
			250-299	268	76	70	0.8	59	42	3.46	1.36
			300-350	305	1	0	0	0	0	0	0
5	24/3	Herring	150-199	194	30	50	0.5	50	47	4.93	1.47
			200-249	218	160	41	0.4	39	287	5.34	1.12
			250-299	263	74	22	0.2	23	12	1.12	0.24
		Sprat	90-99	96	3	100	8.7	100	100	45.00	6.00
			100-109	106	9	100	3.2	100	100	36.56	4.89
			110-119	114	15	93	1.7	93	93	29.6	5.86
			120-129	123	30	97	2.5	97	97	35.93	8.97
			130-139	134	26	96	2.7	96	96	43.35	11.31
			140-149	144	3	100	3.3	100	100	58.00	12.67

correlation (see Table 3.5). Fullness and the number of all fish eggs in stomachs decreased with increasing sprat TL (11/3/93). However the proportion of plaice eggs eaten increased with increasing sprat TL (11/3/93). The number of plaice eggs therefore increased with sprat TL (24/3/93). Such trends were not evident in the herring samples except for the sample taken on 24/3/93. Both fullness and the number of all eggs decreased with increasing herring TL. However, the number of plaice eggs and proportion of plaice eggs also decreased with increasing herring TL.

Selection for and against plaice eggs in the plankton

There was no significant difference in the ratio of plaice to other fish eggs between the duplicate Gulf III samples on 11/3/93 and 24/3/93 (Table 3.6). The replicate samples were therefore combined for comparison with herring and sprat stomach contents (Table 3.6). The numbers of plaice and other fish eggs were summed for each suitable size class of herring and sprat (Table 3.6). On the null hypothesis that the proportions in the plankton and stomachs were not different, the numbers of the two classes of eggs were compared with χ^2 tests (2 by 2 contingency tables). The proportion of plaice eggs was greater than expected in all size classes of herring and sprat >80 mm, but less than expected in sprat <80 mm (Table 3.6). The proportion of plaice eggs eaten increased with increasing sprat TL up to a size of approximately 100 mm, and then remained constant (Figure 3.5a+b).

Differential selection for developmental stages of plaice eggs

The majority of plaice eggs found in clupeid stomachs could not be staged due to the rapid digestion of embryos. In the sample of herring taken around midday on 15/3/93, sufficient eggs were staged to allow a comparison of the frequencies of stages in stomachs and in plankton samples (11/3/93), when egg stages I and II, and III-V were pooled (Table 3.7). The herring ate more plaice eggs in the later stages of development (III-V) than expected.

Table 3.5: Analysis of change in stomach content of clupeids stomachs with fish size. Results of Spearman rank correlations of fullness, total number of fish eggs, number of plaice eggs and proportion of plaice eggs with clupeid total length.

Date	Species		Spearman rank correlations with TL for individuals			
			Fullness	Total eggs	Plaice eggs	Proportion plaice eggs
11/3	Sprat	r_s	-0.567	-0.363	0.155	0.455
		n	106	106	106	80
		p	p<0.001	p<0.001	n.s.	p<0.001
24/3	Sprat	r_s	-0.015	0.171	0.214	0.105
		n	86	86	86	83
		p	n.s.	n.s.	p<0.05	n.s.
11/3	Herring	r_s	0.294	0.188	0.152	-0.114
		n	52	52	52	21
		p	p<0.05	n.s.	n.s.	n.s.
15/3	Herring	r_s	-0.202	-0.104	-0.108	-0.068
		n	108	108	108	68
		p	p<0.05	n.s.	n.s.	n.s.
24/3	Herring	r_s	-0.165	-0.204	-0.240	-0.216
		n	264	264	264	94
		p	p<0.01	p<0.001	p<0.001	p<0.05

n.s.: not significant at 5% probability level.

Table 3.6: Details of numbers of plaice and other fish eggs found in plankton samples and stomachs of clupeids of different size-classes (trawls 3-5). Selection for or against plaice eggs by clupeids was assessed by χ^2 tests, comparing the numbers of plaice and other fish eggs in stomachs with those in plankton samples. The stomach contents of herring caught on 15/3/93 were compared with plankton samples taken on 11/3/93.

Date	Sample	Gulf III sample/ Clupeid Size-Class	n	Total eggs	Plaice Eggs	Other Eggs	χ^2: plaice and other eggs (d.f.=1)	p	Ratio Plaice: Other eggs	Selection for/ against plaice eggs
11/3	Gulf III	Sample 1		526	13	513	0.333	$p>0.5$	0.025	
		Sample 2		661	20	641			0.031	
		Combined		1187	33	1154			0.029	
	Sprat	60-79	10	600	2	598	12.2	$p<0.001$	0.003	Against
		80-89	12	417	25	392	9.2	$p<0.005$	0.064	For
		90-119	18	108	33	75	157.9	$p<0.001$	0.440	For
		120-129	25	236	91	145	316.8	$p<0.001$	0.628	For
		130-149	41	445	136	309	269.1	$p<0.001$	0.440	For
	Herring	150-300	52	72	44	28	402.3*	$p<0.001$	1.571	For
15/3	Herring	200-249	31	151	81	70	444.6	$p<0.001$	1.157	For
		250-325	77	263	103	160	335.3	$p<0.001$	0.644	For
24/3	Gulf III	Sample 1		904	24	880	0.397	$p>0.5$	0.027	
		Sample 2		1416	44	1372			0.032	
		Combined		2320	68	2252			0.030	
	Sprat	90-109	12	464	62	402	94.5	$p<0.001$	0.154	For
		110-119	15	444	88	356	199.6	$p<0.001$	0.247	For
		120-129	30	1078	269	809	399.6	$p<0.001$	0.333	For
		130-139	26	1127	294	833	432.7	$p<0.001$	0.353	For
		140-149	3	174	38	136	142.2	$p<0.001$	0.279	For
	Herring	175-199	30	148	44	104	230.6	$p<0.001$	0.423	For
		200-224	119	723	162	561	299.3	$p<0.001$	0.289	For
		225-300	115	214	35	179	90.5	$p<0.001$	0.196	For

* 1 cell with expected frequency < 5.0

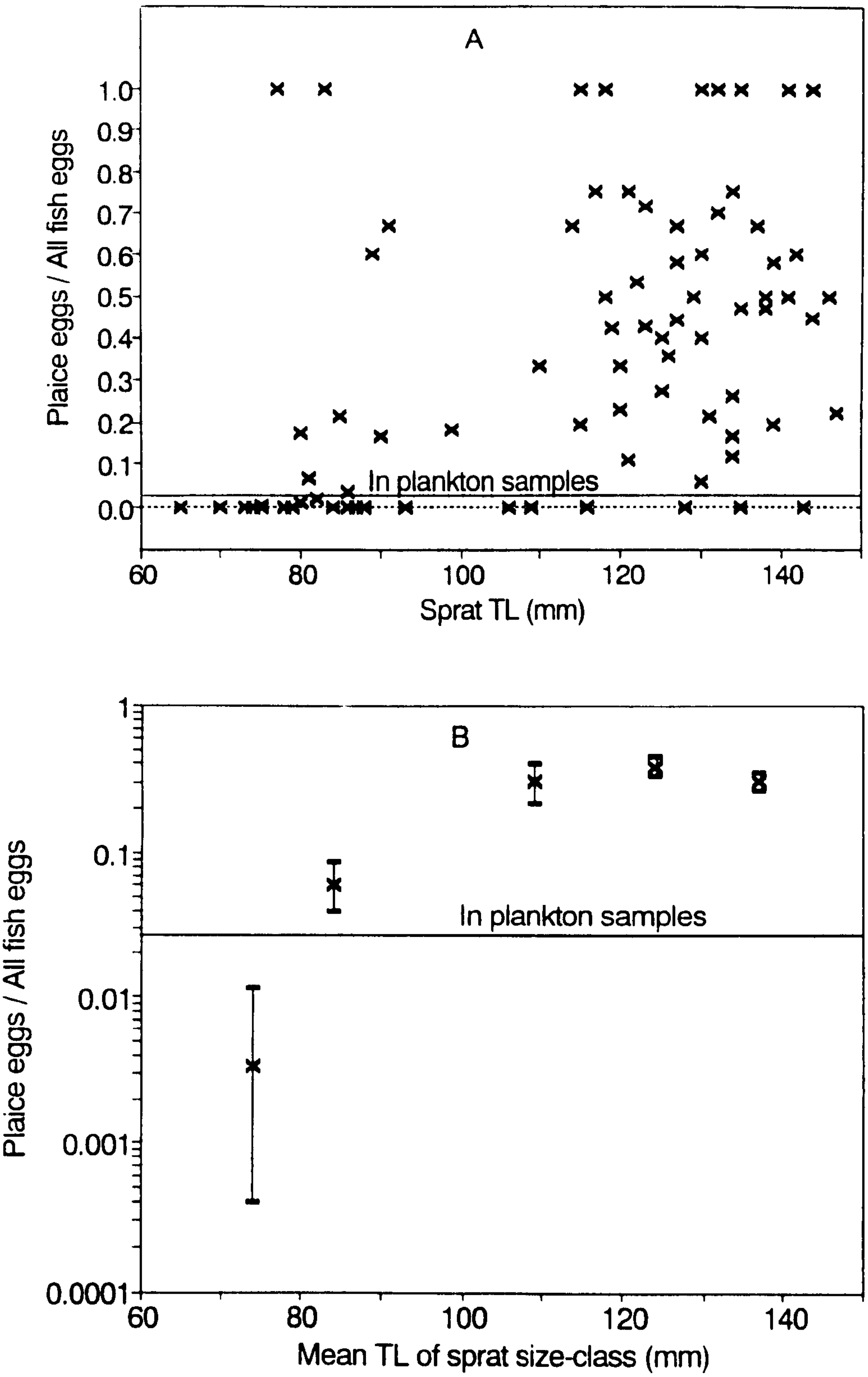


Figure 3.5: Selection for plaice eggs by different sizes of sprat (trawl 3, east IoM, 11/3/93). Selection estimated by proportion of number of fish eggs in stomach constituted by plaice eggs. A: data for individual sprat. B: data grouped into size-classes. For derivation of confidence intervals from proportions see ZAR (1984).

Table 3.7: Comparison of frequency of different stages of plaice eggs found in stomachs of herring caught on 15/3/93 with frequency in plankton samples at station 25 on 11/3/93.

	Plaice egg stages I & II	Plaice egg stages III, IV & V
Identifiable in stomachs of herring caught on 15/3/93	22	34
In plankton samples taken at station 25 on 11/3/93	25	8
χ^2	11.083 (df= 1; p=0.001)	

DISCUSSION

Non-clupeid predators

Whiting and gurnard ate plaice eggs. Whiting and gurnard have previously been recorded as predators of plaice eggs (HARDING *et al.*, 1978; GARROD & HARDING, 1981). However, the low incidence and low number of eggs per individual suggest that they will not eat a significant number of plaice eggs. GARROD & HARDING (1981) recorded other fish species as predators of plaice eggs (Table 3.8), but only the pelagic feeding fish (sprat, sandeel (Ammodytidae), anchovy *Engraulis encrasicolus*, herring and young whiting) were considered significant predators.

Clupeid predation on plaice eggs

The herring caught offshore off the west coast of the IoM did not contain plaice eggs, whereas the single individual taken inshore did contain a plaice egg. This reflects the near-shore distribution of stage I plaice eggs off the west coast (see Chapter 2).

LAST (1989) found that fish eggs were not an important constituent of the diet of herring. However, fish eggs comprised a large proportion of the diet of herring and sprat caught off the east coast of the IoM in March (Figures 3.3 & 3.4). The occurrence of plaice eggs and number of eggs per herring caught off the east coast are comparable to previous studies (see Table 3.8). However the occurrence and number of plaice eggs per sprat recorded in this study was high compared to previous studies (see Table 3.8), and higher than the herring because the sprat were feeding more actively.

The increase in number of plaice eggs per sprat between 11/3/93 and 24/3/93 was expected because the density of plaice eggs at station 25 increased from 0.17 to 0.44 plaice eggs m^{-3}. An increase in predation rate due to an increase in prey density is termed a functional response. Functional responses are discussed further in Chapter 7.

Table 3.8: Fish predation on plaice eggs. Percent occurrence or number per individual of fish and plaice eggs recorded in previous studies in the North Sea.

	Month	Species	Area		Size Range (mm)	n	% with food	% Occurrence Eggs		Eggs/fish	
								Fish	Plaice	All	Plaice
a	April	Herring	S. North Sea		-	156	95	2.9	0		
		Sprat			-	400	99	13.6	0		
		Whiting			-	519	79		2.0		
		Gurnard			-	123	78		1.7		
b	Feb	Herring	North Sea		All	1653	29		5.7		0.67
					All	764	50		9.6	0.96	0.77
					All	2619	47		10.8	0.24	0.24
c	Jan	Herring	S. North Sea	Inshore	All	205				14.0	
				Offshore	All	270				0.1	
		Sprat		Inshore	All	60				0.3	
				Offshore	All	231				0.7	
d	Jan	Herring	Bloden Ground		All	143				0.5	
	Feb				All	49				7.8	3.9
	Mar				All	105				5.8	5.22
e	Feb	Herring	S E North Sea		100-150	516	81				2.49
					150-200	380	88				6.01
					200-250	125	65				0.17
					250-300	52	79				0.27
f	Feb/ March	Herring	Southern Bight		100-150	25				1.84	1.08
					150-200	144				51.73	2.09
					200-300	142				18.54	5.64
		Sprat			70-100	110				4.11	0.78
					100-150	139				31.68	2.01
					150-200	5				19.00	3.00
		Stickleback	German Bight		50-70	15				1.47	1.20
g	Feb-April	Anchovy	West Central North Sea		80-140	319	90			6.83	6.40
		Sprat			30-150	1018	83			3.21	1.24
		Herring			30-230	42	71			0.12	0.12
		Whiting			70-290	183	83			0.262	0.22
		Sandeels			60-240	239	62			1.32	0.134
		Gurnards			70-340	167	52			0.01	0.01
		Lumpsucker			210-500	2	100			46.00	30.00
		Dab			6-350	274	77			0.07	0.02
		Wolf-fish			20-40	6	100			1.00	1.00

References:
a: HARDING *et al.* (1978); b: LAST (1989); c: POMMERANZ (1981); d: HANSEN (1955); e: DAAN *et al.* (1985); f: DAAN (1976); g: GARROD & HARDING (1981)

Scientific names not included in the text:
3-spined stickleback: *Gasterosteus aculeatus*; Lumpsucker: *Cyclopterus lumpus*; Dab: *Limanda limanda*; Wolf-fish: *Anarhichas lupus*

Feeding behaviour of clupeids: particulate- or filter-feeding on fish eggs?

Herring have two modes of prey capture, particulate- and filter-feeding (GIBSON & EZZI, 1985), and presumably so do sprat. The sprat and herring sampled in this study were thought to have been particulate-feeding.

Development of the embryo in plaice eggs increased the vulnerability to predation by herring. The older embryos which have developed pigment and eyes are assumed to be more easily seen by visual predators (GARROD & HARDING, 1981). Such selection implies particulate-feeding, as particulate-feeding is dependent on the visual detection of prey (LAZZARO, 1987).

The density of holoplankton in the Irish Sea is low in March, as the peak of the spring plankton bloom occurs later (see Chapter 2). Herring only filter-feed at relatively high prey densities, >4 prey l^{-1} (BATTY *et al.*, 1990). Fish eggs formed the majority of the stomach contents of herring and sprat caught in trawls off the east coast of IoM (Figures 3.3 & 3.4) and the average density of fish eggs was only 0.006 and 0.015 eggs l^{-1} (11/3/93 and 24/3/93 respectively).

Size-selection of larger prey has been observed by both particulate-feeding (BATTY *et al.*, 1990), and filter-feeding herring (GIBSON & EZZI, 1985). Filter-feeding can also result in differential selection by different size classes of fish (GIBSON & EZZI, 1985), as the structure of the gill rakers determines the minimum size of prey (HUNTER & DORR, 1982). Size-selection of fish eggs by filter-feeding can be dismissed because the diameter of the smallest fish eggs (Figure 3.2) was greater than the largest gap between gill rakers of a large (300 mm) herring (see GIBSON, 1988).

The selection of plaice eggs by particulate feeding clupeids

LAST (1989) suggested that a size of 1.89 mm would be near the lower limit of non-mobile organisms acceptable as prey to herring, as he recorded low numbers of smaller pelagic fish eggs. However, many fish eggs other than those of plaice were recorded in herring stomachs in this study. Intact eggs of 0.85-0.90 mm diameter were regularly recorded, and eggs of 0.74-0.79 mm were found in herring >200 mm.

Herring and sprat (>80 mm) selected plaice eggs from the other fish eggs. Selection for plaice eggs had been suggested before (DAAN, 1976; LAST, 1989), but statistical evidence was lacking. It is assumed that plaice eggs are selected due to their large size (LAST, 1989).

Evidence for size-selective predation on larger eggs from stomach contents assumes that the gastric residence time is similar for eggs of all sizes. However, digestion time will probably increase with egg size. The great difference between stomach contents and plankton samples in the ratios of plaice to other fish eggs (Table 3.6) is very unlikely to be due solely to differential digestion times. The analysis demonstrating selection also assumes that all fish eggs were homogenously distributed in the water column (as represented by plankton samples) which is admittedly atypical. Feeding may have concentrated on localised small patches of plaice eggs (GARROD & HARDING, 1981). However, the clupeids would then be showing selection for plaice eggs by foraging in areas of high plaice egg density. Apparent selection for plaice eggs could also be caused by selection against other fish eggs. The conspicuous eggs of dragonet *Callionymus lyra* (see RUSSELL, 1976) were common in plankton samples, but were not noted from the stomachs of herring or sprat.

The smaller sprat probably selected against plaice eggs because of gape limitation (see LAZZARO, 1987) or the "risk" associated with prolonged ingestion of prey large in proportion to mouth size (see KISLALIOGLU & GIBSON, 1976). The larger herring and sprat selected for plaice eggs. Particulate-feeding planktivorous fish generally exhibit size-selection for larger prey items (GARDNER, 1981) and there are two theories accounting for such selection. The "apparent size hypothesis" (O'BRIEN *et al.*, 1976) predicts that selection is determined solely by the encounter rate. Encounter rate is a function of prey density and reactive distance, and reactive distance is influenced by prey size (GARDNER, 1981). The "basic prey model" (STEPHENS & KREBS, 1986) implies a behavioural decision by the predator, and selection is determined by both the encounter rates with, and energy contents of, different prey. Both theories could account for selection of plaice eggs, as the reactive distance and energy content will be greater than that of smaller eggs.

A predator selecting for a particular prey type will gain more experience of that prey than other prey types, and experience may improve foraging efficiency (CROY & HUGHES, 1991). Experience can lead to prey "switching" and concentration of feeding on that prey (HUGHES *et al.*, 1992). In this study individual sprat (Figure 3.5a) and herring (Figure 3.6) concentrated feeding on plaice eggs. GARROD & HARDING (1981) also noted that individual herring, sprat, anchovy and sandeels fed almost exclusively on plaice eggs.

Differential predation by different size-classes of clupeids

DAAN *et al.* (1985) and LAST (1989) noted that the smaller size classes of herring contained more plaice eggs per individual. In this study such a trend was only significant in one sample of herring, which could be due to the restricted length range (153-305 mm), and low numbers of individuals <200 mm (Table 3.3). LAST (1989) noted that plaice eggs are mainly eaten by herring <200 mm.

Large differences were evident in the number of plaice eggs consumed by different size-classes of sprat, probably due to an adequate size range (65-147 mm), but the number of plaice eggs per sprat increased with fish size. The feeding activity of sprat decreased with sprat size but larger sprat showed a greater selection for plaice eggs. The number of plaice eggs consumed is a product of feeding intensity and selection for plaice eggs. Thus the number of plaice eggs per fish increased over the size range of sprat.

As herring and sprat are morphologically similar, it is probable that similar relationships exist between feeding intensity, selection for plaice eggs and fish size. The number of plaice eggs per herring increases with size up to the 150-200 mm size class and then falls (see DAAN *et al.*, 1985: LAST, 1989; Table 3.8). Sprat and herring of 100-200 mm will therefore eat the most plaice eggs per individual.

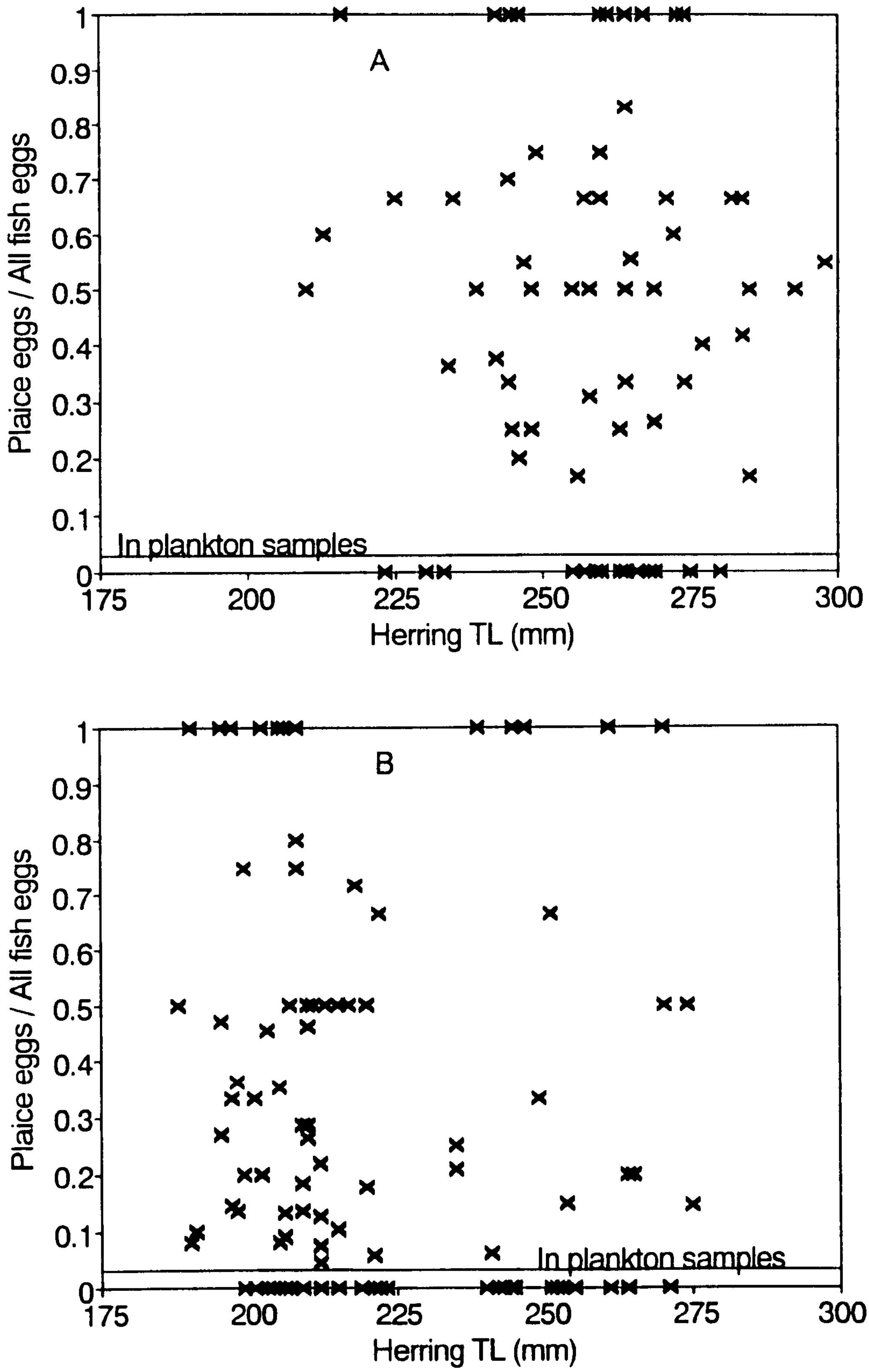


Figure 3.6: Selection of plaice eggs by individual herring sampled in trawl 4, 15/3/93 (A), and trawl 5, 24/3/93 (B). Selection estimated by proportion of number of fish eggs in stomach constituted by plaice eggs.

DE SILVA (1973) found that both 0-group sprat and herring feed over the winter, while larger fish show a more seasonal feeding pattern. In this study, small sprat ate more than larger sprat, which in turn ate more than the larger herring. Feeding activity may be inversely related to energy reserves. The fat content over winter is higher in large sprat than small sprat (WALLACE & HULME, 1977).

Quantification of plaice egg mortality due to clupeid predation

To quantify the mortality of plaice eggs due to herring and sprat predation, the predation rate and abundance of predators and prey have to be estimated. To estimate predation rate from stomach content data, information is required on feeding periodicity and gastric residence time.

The clupeids were particulate-feeding. Herring are unable to particulate-feed in the dark (BATTY *et al.*, 1990), so feeding was restricted to the day. Feeding by day has been demonstrated in the field for both herring (DE SILVA, 1973; DAAN *et al.*, 1985) and sprat (DE SILVA, 1973; SHVETSOV *et al.*, 1983).

No work has been done on the gastric residence time of fish eggs in herring or sprat, so estimates must be made using different food types as models. The gastric residence time of mesozooplankton has been estimated at 21 h for herring at 6 °C (SZYPULA & ZALACHOWSKI, 1984), 22 h for sprat at 3-4 °C (SHVETSOV *et al.*, 1983), 11 h for sprat at 10.5 °C (SZYPULA & ZALACHOWSKI, 1984) and 12 h for sprat at 14°C (SHVETSOV *et al.*, 1983). The sea temperature in March was 6-7 °C (Table 3.1), so a gastric residence time of 12-24 h seems reasonable. In the study of DAAN *et al.* (1985), they simply assumed that the gastric residence time of plaice eggs in herring would be approximately 12 h.

Estimates of the mortality rate of plaice eggs due to clupeids could be made from samples taken on 24/3/93 because samples of plankton and herring and sprat were taken in the same area. The day-length in March is approximately 12 h. If gastric residence time is between 12 and 24 h, and feeding is restricted to the day, then when sampled soon after dusk, the number of eggs in the stomach will approximate to the daily predation rate. Estimates of sprat and herring density were taken from ARMSTRONG *et al.* (1993) and plaice egg density was estimated from plankton samples.

The daily instantaneous mortality rates of plaice eggs due to herring and sprat predation were estimated at 0.001 and 0.023 respectively (see Table 3.9). The total daily instantaneous mortality rate of plaice eggs in the Irish Sea has only been estimated once at 0.095 for the Great Orme spawning ground in 1965 (HARDING & TALBOT, 1973). Herring and sprat may therefore cause approximately 1% and 25% respectively of the mortality of plaice eggs in the Irish Sea.

These estimates of mortality rate due to predation must be viewed as a first approximation because of assumptions made in the calculations, i.e.

1. The number of eggs recorded from stomachs of fish sampled after dusk represented the daily predation rate.
2. The weight loss of herring and sprat during preservation in formaldehyde solution was insignificant.
3. The size distributions, spatial distributions and densities during sampling in March 1993 were the same as in July 1992 when ARMSTRONG *et al.* (1993) estimated biomass.
4. The acoustic estimates of biomass were absolute, although they should only be regarded as an index (ARMSTRONG *et al.*, 1993).
5. The samples of the plaice eggs and clupeid populations were representative.

Despite these problems in estimating the mortality rate due to predation, it can be assumed that sprat are an important predator of plaice eggs, whereas herring are probably not. Sprat contained more eggs per individual than herring. Sprat are one of the most abundant fish species in the Irish Sea (COOMBS *et al.*, 1992) and as the biomass of the sprat population is greater than that of herring (ARMSTRONG, 1992; ARMSTRONG *et al.*, 1993), and sprat are smaller, there are far more sprat in the Irish Sea than herring. Sprat congregate to spawn in spring, and the locations of sprat

Table 3.9: Estimation of predation rate by herring and sprat on plaice eggs. Data from trawl and plankton samples taken on 24/3/93, east IoM. Estimate of daily instantaneous mortality rate due to clupeid predation (i) calculated following VAN DER VEER & BERGMAN (1986).

		Herring	Sprat	Source
a	Biomass (tonnes)	1149	513	ARMSTRONG *et al.* (1993), data for east of IoM, July 1992.
b	Area (km^2)	1290		
c	Biomass (gm^{-2})	0.891	0.398	a/b
d	Weight of clupeids sampled (g)	22183	1076	Trawl 5 (this study)
e	Total number of plaice eggs in stomachs	241	751	
f	Predation rate (eggs g^{-1}d^{-1})	0.011	0.698	e/d
g	Predation rate (eggs m^{-2}d^{-1})	0.010	0.278	f.c
h	Plaice egg density (eggs m^{-2})	12.44		Plankton sampling: station 25 (this study)
i	Daily instantaneous mortality rate due to clupeid predation	0.001	0.023	-ln((h-g)/h)
j	Total daily instantaneous mortality rate	0.095		HARDING & TALBOT (1973)

spawning grounds in the Irish Sea are similar to those of plaice, and other fish species (see COOMBS *et al.*, 1992; NICHOLS *et al.*, 1993; Chapter 2). Sprat may therefore be aggregated over the spawning grounds when plaice are spawning.

RIJNSDORP & JAWORSKI (1990) suggested that plaice and cod *Gadus morhua* eggs were subject to a similar mortality process. Cod eggs are large (RUSSELL, 1976) and selected by herring and sprat (DAAN, 1976). Sprat may, therefore, also be important predators of cod eggs in the Irish Sea.

The mortality rate of pelagic fish eggs is size-dependent, smaller eggs suffering higher mortality rates (RIJNSDORP & JAWORSKI, 1990). Selection of smaller eggs by predators will result in such size-selective mortality and sprat <80 mm selected against plaice eggs. However, sprat and herring >80 mm selected for plaice eggs. Mortality rates are thought to decrease with size due to a reduction in the number of potential predators (CUSHING, 1974; RIJNSDORP & JAWORSKI, 1990). This suggests that larger predators, such as clupeids >80 mm, are the main predators of larger fish eggs.

Smaller fish eggs, although eaten by herring and sprat >80 mm, are selected against. Eggs smaller than those of plaice and cod may therefore have different major predators. Small clupeids (<80 mm) are numerous and feed more actively than larger clupeids. They may be important predators of smaller fish eggs. 0-group sprat and herring feed over winter and feed heavily in early spring following the first winter (DE SILVA, 1973).

Significance for inter-annual variations in plaice year-class strength

BANNISTER *et al.* (1974) suggested that in cold winters, when the mortality of plaice eggs is reduced, the numbers, distribution and/or feeding activity of the egg predators may be changed. If clupeids are a major cause of mortality, then their feeding activity may have a profound effect on year class strength.

The feeding activity of herring is favoured by higher temperatures (Blaxter & Holliday, 1958: cited in POMMERANZ, 1981), and DAAN *et al.* (1985) noted that the feeding activity of herring is limited in February, possibly due to low temperatures. The temperature-dependent feeding activity of clupeids could possibly result in the negative relationship between total mortality and temperature. However feeding activity would have to be reduced to such a degree that cumulative mortality was also reduced despite the extended embryonic development time (BANNISTER *et al.*, 1974).

The "stage duration hypothesis" of Houde suggests that mortality should increase with an extended development time (see PIHL, 1990). It could be that the apparent effect of temperature on plaice egg mortality is indirect, due to an association of temperature with other abiotic factors, e.g. turbulence. In spring, low temperatures are associated with prolonged anti-cyclonic conditions, which result in calm seas (LOCKWOOD, 1990). Turbulence affects the relative velocity of planktonic organisms and hence the encounter rate with predators and mortality rate (ROTHSCHILD & OSBORN, 1988).

Significance for reduction in inter-annual variation in year-class strength

BAILEY & HOUDE (1989, p. 61) stated that

> "in the sea predation losses of eggs and larvae are likely to be density-independent because most predators probably consume them only incidental to other, more common plankton organisms. Exceptions to this generalisation will occur when predators aggregate on patches of prey, and perhaps when predators are selective and demonstrate density-dependent prey-switching behaviour."

Plaice spawn before the spring plankton bloom in the Irish Sea (see Chapter 2) and North Sea (see Figure 5 in CUSHING, 1990b). The density of the common plankton organisms which usually form the bulk of the diet of herring and sprat (see DE SILVA, 1973 ; LAST, 1989) is therefore low. Due to the lack of alternative food, fish eggs, particularly plaice eggs, formed a large part of the diet of clupeids caught to the east of the IoM at this time of year.

Plaice eggs are large in comparison to other fish eggs and holoplankton. Plaice eggs do not show an escape response to predators and the round smooth chorion and lack of appendages would facilitate capture and ingestion, and result in a low handling time. Plaice eggs may therefore be a "profitable" food item, i.e. provide a high return for little effort. As newly spawned plaice eggs are concentrated over well defined areas (see SIMPSON, 1959a+b), they may form large patches of high density food for planktivores, at a time when the standing stock of other plankton is low.

Herring and sprat caught off the east coast of the IoM selected strongly for plaice eggs. As stated earlier, the selection for plaice eggs due to their size, will increase experience, and may lead to "prey-switching". Individual fish fed exclusively on plaice eggs at times as noted by GARROD & HARDING (1981). DAAN (1976) suggested that plaice eggs would have to be over a minimum density to promote predation by herring and sprat. Although DAAN (1976) did not seem to realise the significance of his observation, the statement implies switching behaviour in relation to prey density. Such switching behaviour will produce density-dependent mortality (see review by MURDOCH & OATEN, 1975). It is proposed here that density-dependent mortality is likely to occur in the early egg stages of plaice.

If sprat are a major predator of plaice eggs, then large inter-annual variations in egg mortality would be expected because of variability in the body size, and migratory and feeding patterns of sprat (GARROD & HARDING, 1981). However, the inter-annual variability in mortality during the pelagic stages of plaice is low compared to other fish species (BERGMAN *et al.*, 1988). This suggests that density-dependent mortality does occur in the egg stage of plaice. Density-dependent mortality in the egg stage of plaice, and the behavioural mechanisms of predation producing such mortality, are discussed further in Chapter 8.

Possible importance of life history traits to mortality in the egg stage

A large egg size may reduce vulnerability to smaller predators (BAILEY & HOUDE, 1989). The large size of plaice eggs did provide a refuge from predation by the smaller sprat (<80 mm). BAILEY & HOUDE (1989) also suggested that the transparency of pelagic eggs would reduce mortality due to visual predators. The transparency of newly spawned eggs does seem to provide a refuge from predation, as plaice eggs were more vulnerable to predation in the later stages of development when the contrast between the embryo and the water would be greater.

The duration of feeding, and therefore food intake, of visual-feeding clupeids is restricted by day length (see BLAXTER & HUNTER, 1982). Plaice spawn early in the year compared to other fish species (see RUSSELL, 1976). If clupeids are an important predator of plaice eggs, spawning early in the year may be a reproductive strategy to reduce predation mortality of the eggs due to restricted day-length. However, the timing of spawning seems to make plaice eggs vulnerable to predation because of the lack of alternative food for predators. The reduced mortality of plaice eggs at low temperatures may also account for the time of spawning.

THE DEMERSAL PHASE

CHAPTER 4:

A MARK AND RECAPTURE EXPERIMENT TO ESTIMATE POPULATION SIZE AND MORTALITY RATES OF THE 1991 YEAR-CLASS OF 0-GROUP PLAICE IN PORT ERIN BAY, ISLE OF MAN.

INTRODUCTION

After the cessation of larval recruitment to nursery grounds, the population size of 0-group plaice decreases due to mortality and emigration (e.g. RILEY & CORLETT, 1966; MACER, 1967; EDWARDS & STEELE, 1968; GIBSON, 1973; VAN DER VEER, 1986). For at least the first few months on the nursery, this decrease is attributed primarily to mortality (ILES & BEVERTON, 1991). The estimation of mortality rates, and comparison between different years and nurseries have enabled factors affecting mortality rate, and hence year-class strength, to be examined (STEELE & EDWARDS, 1970; LOCKWOOD, 1980; VAN DER VEER, 1986; BERGMAN *et al.*, 1988; VAN DER VEER *et al.*, 1990; BEVERTON & ILES, 1992b).

Mortality is usually measured as the rate of decrease of density and estimated from beam trawl catches (e.g. RILEY & CORLETT, 1966; MACER, 1967; EDWARDS & STEELE, 1968; LOCKWOOD, 1980, VAN DER VEER, 1986; ILES & BEVERTON, 1991). Mortality rates can be estimated over short periods of time from successive pairs of density estimates (e.g. VAN DER VEER, 1986). However mortality rates are usually estimated by regressing the logarithm of density against time to give a seasonal average mortality rate (ILES & BEVERTON, 1991). Regression over time removes the dependency of the estimate on single points, and gives a more "precise" estimate of mortality (ILES & BEVERTON, 1991). Regression, however, will average mortality over time. Mortality rates will fluctuate with changes in size (see Chapter 6), density (VAN DER VEER, 1986), predator density (VAN DER VEER & BERGMAN, 1987) and temperature (VAN DER VEER *et al.*, 1990).

To estimate density from trawl catches, they must be corrected for gear efficiency (ILES & BEVERTON, 1991). The efficiency of sampling gear is the proportion of fish in the area sampled that are retained in the cod end. Escape may be due to mesh selection, escape underneath the gear or gear avoidance. Gear efficiency is usually assumed either to be a constant for all size classes over long periods of time (RILEY & CORLETT, 1966; EDWARDS & STEELE, 1968) or to vary only with length (KUIPERS, 1975). However gear efficiency will change, not only with fish size, but also with time of day, tidal state, and various environmental factors (e.g. temperature, substrate topography, turbidity, light intensity).

KUIPERS (1975) did not consider escape underneath the net to be a problem for his gear in the Wadden Sea. However, ROGERS & LOCKWOOD (1989) recorded a twofold increase in catches when they changed to heavier tickler chains. Escape underneath the net is due either to active fish escaping under the ground-rope due to uneven ground (EDWARDS & STEELE, 1968; KUIPERS *et al.*, 1992) which will vary with topography and substratum (ILES & BEVERTON, 1991), or buried fish remaining undisturbed. The number of buried fish will depend upon activity levels, and therefore upon time of day and tidal state (NASH *et al.*, 1994; BURROWS *et al.*, 1994).

Gear avoidance is due to fish swimming out of the path of the net. To avoid the gear the fish must first be aware of its presence and direction, which will depend upon the disturbance caused by the boat and gear (KUIPERS, 1975), the speed of the tow, turbidity (ILES & BEVERTON, 1991; KUIPERS *et al.*, 1992) and light intensity. KUIPERS (1975) found escape due to disturbance was size related, probably due to a greater reactive distance of larger fish. Once aware of the gear, the fish can then escape by swimming upwards, in front, or to the side of the net (KUIPERS, 1975). KUIPERS (1975) dismissed upward and forward escape, suggesting only lateral escape to be important. However, diver observations reported by EDWARDS & STEELE (1968) suggested both forward and lateral escape. The ability of the fish to escape the gear will depend upon the speed of the tow and fish escape speed. Escape speed will change with fish size and water temperature (ILES & BEVERTON, 1991; KUIPERS *et al.*, 1992).

There are therefore problems in estimating mortality rates from beam trawl catches, in both the analysis (as mortality rate is assumed constant over a long time period), and in the original data (as density is estimated from catches corrected for gear efficiency).

An alternative to the use of simple catch data may be mark and recapture methods, which can be used to estimate survival over short periods of time. Survival is estimated from the proportions of marked fish rather than actual catches, so problems of gear efficiency can theoretically be minimized. The primary use of mark and recapture methods is to estimate population size. Population size estimates are difficult to derive from catch data because the limits of distribution and density of the population have to be known.

A mark and recapture experiment was carried out on the 1991 year-class of 0-group plaice on the Port Erin Bay nursery ground, Isle of Man (see JONES & KAIN, 1964; RILEY & HOLFORD, 1965; RILEY & CORLETT, 1966; NASH *et al.*, 1992, 1994 for details of this nursery ground). The primary aim was to estimate survival at various times in the season, and relate trends in mortality to size, density and time of year. Due to the possibility that the survival estimates were unreliable, the results are only discussed as estimates of population size, and compared to previous estimates (RILEY & CORLETT, 1966). The data were also of use in examining the effect of an anthropogenic action (release of hatchery-reared turbot *Scophthalmus maximus*) on 0-group plaice population size. Population size estimates of I- and II-group plaice in Port Erin Bay are included.

MATERIALS AND METHODS

0-group mortality rates and population size

The 1991 year-class of plaice was sampled in Port Erin Bay between 11 July 1991 and 20 July 1992. The gear used consisted of a 1.5 m beam trawl (3 mm mesh throughout) towed by hand and from a 5.5 m Dory, a 2 m beam trawl towed by *R.V. Sula* (see NASH *et al.*, 1992), a push-net (RILEY, 1971) and a beach-seine (see NASH *et al.*, 1994). The hand towed beam trawl, push-net and seine samples were taken at low water, and the boat towed trawl samples were taken at high water.

The total lengths (TL, mm) and weights (to nearest 0.1 g) of 0-group plaice were recorded and any recaptures noted. Only fish ≥40 mm were retained for marking to try to eliminate tagging and handling mortality. RILEY (1973) marked fish as small as 25 mm, although EDWARDS & STEELE (1968) noted that tagging mortality could be quite high in fish <30 mm.

Once sufficient fish were accumulated for a release, they were batch marked with coloured latex on the ventral un-pigmented side (RILEY, 1966a). Six colours of latex (red, green, blue, yellow, purple and orange), and three different marking positions on the fish (anterior right, B; posterior left, C; posterior right, D) were used, allowing for 18 batch releases. The fish were held for at least 2 h after marking, and any fish in poor condition were not released. Fish showing no adverse effects of marking after the first hour are not thought to suffer marking mortality in the subsequent 12 months (RILEY, 1973).

Fish were released in batches, at periodic intervals varying from 1 to 6 weeks. All fish within a batch were similarly marked and released at the same time. However, fish for each batch release varied in time of capture. They were maintained in the laboratory until a sufficient number had been caught. The period held in captivity varied between 1 day and two weeks, depending on the batch and when the fish within each batch were caught. If fish were held for longer than a few days they were fed with live or frozen mysids.

Between July 1991 and March 1992, 13 batches of fish were released. Fish were released between mid and low tide and distributed along the beach at a depth of *c.* 0.75 m. Release was usually within an hour of dusk to reduce vulnerability to visual predators due to pigmentation changes during captivity. EDWARDS & STEELE (1968) released marked fish at night. However, the logic behind release at night may be flawed as predation pressure is now thought to be greatest at night (ANSELL & GIBSON, 1993).

The 12th batch of fish released was marked with wire microtags (see WICKINS *et al.*, 1986) in addition to latex. The tags were located in the head region, in muscle posterior to the left eye. No mortality or tag loss were recorded in a six week laboratory trial (February-March 1992; n=34; TL: 41-96 mm), and growth, although variable, did occur. No tag loss was recorded from fish recaptured from the field (n=16, tagged fish recognised by latex mark), although magnetic identification was restricted to within three weeks of release.

Population size is affected by mortality, emigration, birth and immigration, and mark and recapture models cannot distinguish between mortality and emigration as marked fish are lost from the population (KREBS, 1989). Birth can be ignored in 0-group plaice populations. Recruitment, i.e. true immigration, of 0-group plaice to Port Erin Bay occurs between April and July (COLMAN, 1966; RILEY & CORLETT, 1966; R.D.M. NASH, *pers. comm.*) and in 1991 had finished before the start of the experiment (*pers. obs.*). However the population under study consisted of fish ≥40 mm. Fish <40 mm grew and "immigrated" into this population during the study. Immigration must therefore be considered while part of the population was <40 mm.

From the numbers of fish released, captured and recaptured, population sizes, survival rates and immigration were estimated using the Jolly-Seber method with immigration (from KREBS, 1989). The Jolly-Seber model uses the time of last capture, so only the most recent mark was considered for fish with two or more marks.

To estimate total population size, population estimates (≥40 mm) were corrected for the proportion of fish in the catches <40 mm. When all fish in the population were ≥40 mm no "immigration" occurred and the Jolly-Seber special case method for enclosed populations (from SEBER, 1982) was used to estimate population sizes and mortality rates.

It is vital for all mark and recapture studies to include a test of equal catchability (KREBS, 1989). Appropriate tests differ with the mark and recapture model used, according to the number of samples taken, whether natural mortality and immigration occur, and the magnitude of the mortality rate (see KREBS (1989) for selection of test).

Leslie, Chitty and Chitty's test of equal catchability (SEBER, 1982) was used for the first analysis (immigration present). This test considers only marked fish and tests for equal catchability within the marked population (KREBS, 1989). Fish with only one mark are termed "unmarked" and fish with two or more marks are termed "marked".

Chapman's test (KREBS, 1989) was used to test for unequal catchability between marked and unmarked fish for the second analysis, i.e. no immigration. The data for Chapman's test differs from that for the Jolly-Seber model as it uses the time of first capture.

I- and II-group population size

I- and II-group plaice were caught with a beach seine over two fortnight periods in May/June and September 1991 (see NASH *et al.*, 1994). All plaice ≥90 mm were tagged with Floy anchor tags (see NASH *et al.*, 1992) and released. As sampling was restricted to periods of a fortnight, the population was considered closed, i.e. no births, deaths, immigration or emigration. From recaptures of fish tagged during the course of the experiment, population size was estimated using the Shumacher and Eschmeyer method (RICKER, 1975) which assumes a closed population.

Turbot predation on 0-group plaice

A turbot-farming company experiencing financial difficulties released cultured turbot into Port Erin Bay in mid-June 1991. Turbot are a predator of 0-group plaice in Port Erin Bay (RILEY & CORLETT, 1966), so turbot, both cultured and indigenous, caught during sampling were retained for stomach content analysis. Cultured turbot were distinguished by abnormal pigmentation.

RESULTS

0-group mortality and population size

A total of 4,300 fish were marked and released, and 890 fish (21%) were recaptured (Table 4.1). The recapture data from of all gear types is presented and was

Table 4.1: Numbers of 0-group plaice released, captured and recaptured in mark and recapture experiment in Port Erin Bay, July 1991-July 1992. The horizontal demarcation denotes the limit of data used for the Jolly-Seber method. The other demarcation denotes the smaller data set used for Jolly-Seber special case method with no immigration. The numbers in brackets refer to recaptured fish with two or more marks, and these figures were used in the Leslie, Chitty and Chitty test of equal catchability.

Date	R_i	n_i all	n_i ≥40 mm	Recaptures from batch releases (m_{hi})													d_i
				1	2	3	4	5	6	7	8	9	10	11	12	13	
12/07	Red B 38																
24/07	Green B 178	581	317	2 (0)													1
17/08	Blue B 618	1593	944	3 (0)	13 (0)												6
24/08	Yellow B 377	467	435	0 (0)	6 (0)	24 (0)											2
31/08	Purple B 353	404	358	0 (0)	5 (0)	17 (0)	15 (2)										0
14/09	Orange B 797	900	864	0 (0)	4 (0)	27 (0)	25 (3)	39 (5)									8
29/09	Red C 917	1084	1069	1 (0)	13 (0)	41 (2)	34 (3)	30 (0)	78 (5)								38
23/10	Green C 388	804	799	2 (0)	5 (0)	15 (0)	16 (0)	25 (3)	50 (8)	72 (17)							89
20/11	Blue C 102	201	201	0 (0)	2 (0)	7 (0)	3 (0)	1 (1)	9 (3)	16 (4)	17 (3)						29
6/12	Yellow C 127	196	196	1 (0)	1 (0)	9 (1)	1 (1)	3 (1)	5 (0)	14 (2)	6 (4)	4 (2)					16
18/01	Purple C 145	214	214	0 (0)	3 (0)	7 (0)	5 (0)	5 (0)	5 (2)	13 (2)	5 (2)	3 (1)	8 (1)				18
26/02	Orange C 128	273	273	1 (0)	0 (0)	3 (0)	0 (0)	2 (0)	15 (4)	19 (2)	11 (3)	8 (3)	10 (2)	13 (5)			50
21/03	Red D 132	167	167	0 (0)	1 (0)	2 (0)	0 (0)	4 (0)	4 (0)	5 (2)	10 (6)	2 (0)	0 (0)	10 (2)	16 (4)		10
to 20/7		219	219	0	0	1	1	0	1	3	2	6	2	3	7	13	

Key:

R_i (SEBER, 1982): number of marked fish released after i^{th} sample = S_t (KREBS, 1989)

n_i (SEBER, 1982): number of fish caught in i^{th} sample = n_t (KREBS, 1989)

m_{hi} (SEBER, 1982): number of fish caught in i^{th} sample last caught in h^{th} sample = m_{it} (KREBS, 1989)

d_i (SEBER, 1982): number of marked fish caught in i^{th} sample not returned to population = d_t (KREBS, 1989) used in the analyses.

Examination of fish for marks was not undertaken by me after March 1992. Recapture information was not used after 21 March 1992, because the proportion of marked fish was significantly lower (38 marked, 181 unmarked) than in the proceeding period (54 marked, 113 unmarked) ($\chi^2=11.718$; $p<0.001$), despite the addition of 138 marked fish (Red D) to the population. Although recaptures were still recorded up to a year after release (R.D.M. NASH, *pers. comm.*), the recapture information was judged untrustworthy. A spring immigration (LOCKWOOD, 1974; GIBSON *et al.*, 1978) of unmarked fish could reduce the proportion of marked fish. However any immigrants would have formerly belonged to the marked population, and RILEY (1973) suggested that there was no immigration between January and March.

Population size, survival and immigration were estimated (Table 4.2) between July 1991 and March 1992 using the Jolly-Seber method with immigration (KREBS, 1989) and population size estimates were corrected for the proportion of the catches <40 mm. Population size estimates ranged from 19,000 individuals in August 1991 to 1,200 in February 1992.

Leslie, Chitty and Chitty's test (SEBER, 1982) (data in Table 4.1) relies upon comparisons of M_t with $N_{.i}$, ϕ_t with $\phi_{.i}$, and actual values of v_i with estimates of v_i (see SEBER, 1982). The estimates of these parameters (Table 4.3) suggest that there was unequal catchability within the marked population.

Using the Jolly-Seber special case method for enclosed populations, i.e. no immigration (SEBER, 1982), population size and survival were estimated (Table 4.4) from data for 20 November 1991 to 21 March 1992 (when all fish >40 mm, see Table 4.1). Population size was estimated at 7,500 in November 1991 and fell to 1,400 in March 1992. The data for Chapman's test (Table 4.5) showed no evidence of unequal catchability (6 sampling periods, 5 negative differences; $p=0.661$, from Table 2.4 in KREBS, 1989).

Table 4.2: Estimates of population size and survival, with upper and lower confidence limits, and immigration from Jolly-Seber method (after KREBS, 1989).

Date	Population size (N_t			Corrected* N_t			Survival ϕ_t			Number of immigrants B_t
	Lower C.L.	Estimate	Upper C.L.	Lower C.L.	Estimate	Upper C.L.	Lower C.L.	Estimate	Upper C.L.	
12/7							0.42	0.75	1.37	3023
24/7	894	3023	9882	1644	5558	18170	0.74	0.97	1.30	8217
17/8	5306	11010	15169	8945	18559	25571	0.67	0.83	1.04	470
24/8	4889	9300	10732	5249	9984	11521	0.62	0.77	0.98	217
31/8	3987	7312	7994	4499	8251	9021	0.94	1.15	1.43	2897
14/9	6761	11319	11027	7043	11790	11487	0.67	0.81	1.01	-543
29/9	5364	8577	8129	5444	8705	8251	0.49	0.64	0.87	959
23/10	3747	6350	6601	3771	6390	6643	0.36	0.58	0.96	69
20/11	1733	3501	4481	1733	3501	4481	0.53	0.93	1.72	973
6/12	1994	4115	5390	1994	4115	5390	0.37	0.63	1.12	-30
18/1	1300	2518	3105	1300	2518	3105	0.30	0.50	0.89	-11
26/2	669	1223	1600	669	1223	1600				
21/3										

* Corrected for proportion of fish in catch <40 mm TL (see Table 4.1).

N_t (KREBS, 1989): Estimate of total number in population just before time t= N_i (SEBER, 1982)

ϕ_t (KREBS, 1989): Probability of marked fish surviving from time t to t+1 = ϕ_i (SEBER, 1982)

B_t (KREBS, 1989): Number of new fish joining population from time t to t+1 = B_i (SEBER, 1982)

Table 4.3: Comparison of M_t and Φ_t from Jolly-Seber method with $N._i$, $\Phi._i$ and v_i from Leslie, Chitty and Chitty test of equal catchability (SEBER, 1982) for period 12 July 1991 to 21 March 1992.

Date	From Jolly-Seber model			From Leslie, Chitty and Chitty test of equal catchability			
	M_t	Φ_t	v_i	$N._i$	$\Phi._i$	Est v_i	σ[Est vi]
12/7	0	0.75	38				
24/7	29	0.97	315				
17/8	198	0.83	928		0.93		
24/8	661	0.77	405		1.05		
31/8	774	1.15	321	722	0.75	157	564
14/9	1256	0.81	769	659	1.05	1998	821
29/9	1587	0.64	872	2789	0.56	-831	982
23/10	1476	0.58	614	1066	0.65	170	347
20/11	971	0.92	146	748	1.60	-61	263
6/12	940	0.63	152	1052	0.43	854	766
18/1	644	0.50	160	818	0.67	-156	303
26/2	370		191	427			
21/3	54		113				

From Jolly-Seber model (KREBS, 1989):
M_t: Estimated size of marked population just before sample time t = M_i (SEBER, 1982)
ϕ_t: Probability of survival from time t to t+1 = ϕ_i (SEBER, 1982)

From Leslie, Chitty and Chitty test (SEBER, 1982):
$N._i$: Estimate of size of population of marked fish
$\phi._i$: Estimate of survival of marked fish from time i to i+1
v_i: Number of unmarked individuals in population of = u_i (KREBS, 1989)
Est v_i: Estimate of v_i
σ[Est v_i]: Standard deviation of estimate of v_i

Table 4.4: Estimates from special case Jolly-Seber model with no immigration (SEBER, 1982).

Date	N_i	$\sigma(N_i)$	$\phi_i \pm\sigma(\phi_i)$	t (days)	M: Instantaneous daily mortality rate (day^{-1})
20/11/92	7608	990	0.61 (±0.15)	16	0.031 (0.017 - 0.049)
6/12/92	4641	995	0.91 (±0.28)	43	0.002 (0 - 0.011)
18/01/92	4151	878	0.65 (±0.18	39	0.011 (0.005 - 0.019)
26/02/92	2653	482	0.55(±0.15)	24	0.025 (0.015 - 0.038)
21/03/92	1419	285			

N_i: Estimate of population size on sampling occasion i
ϕ_i: Estimate of probability of survival of marked fish from time i to i+1
t : time (days) between release i and i+1
M : Instantaneous daily mortality rate = $-\ln(\phi_i)/t$

Table 4.5: Data used for Chapman's test of equal catchability (KREBS, 1989)

Date	ni	ui	Recaptures from batch release				
			9	10	11	12	13
23/10/92	388	388					
20/11/92	201	184	17				
6/12/92	196	186	6	4			
18/01/92	214	198	6	3	7		
26/02/92	273	231	12	8	11	11	
21/03/92	167	129	11	3	0	10	14

N.B. This is a method C table (i.e. time of first capture), and is different from the method B table (Table 4.1: time of last capture) (see KREBS, 1989).

n_i : total number of fish in catch
u_i : number of unmarked fish in catch

I- and II-group population size

From the capture and recapture data (Table 4.6), the number of I- and II-group plaice in Port Erin Bay was estimated at 665 (518-929) in May 1991 and 187 (125-371) in September 1991.

Turbot predation on 0-group plaice

More cultured turbot (n=70) were captured during routine sampling than indigenous turbot (n=42). Both indigenous and cultured turbot ate plaice, and individuals often contained more than one flatfish (Table 4.7).

DISCUSSION

Latex marking of 0-group plaice has been used to examine gear efficiency, migrations, and size related differences in mortality, as well as to estimate population size (RILEY & CORLETT, 1966; EDWARDS & STEELE, 1968; RILEY, 1973; LOCKWOOD, 1980). Latex marking has not previously been used to estimate mortality rates. BEVERTON & ILES (1992a) suggested its use in estimating mortality of newly-settled fish. However the technique will not be of use for such small fish because of marking mortality (see EDWARDS & STEELE, 1968).

The present study would appear to be the most intensive marking study undertaken on 0-group plaice to date with multiple releases, and the use of the sophisticated Jolly-Seber methods to estimate population size and mortality for discreet time periods. The other studies (RILEY & CORLETT, 1966; EDWARDS & STEELE, 1968; LOCKWOOD, 1980) examining population size were, or at least assumed to be, single release experiments and the Petersen method was used to estimate population size for single points in time.

The survival estimates from the first analysis are unreliable, even exceeding 1 (Table 4.2). The poor reliability of the estimates was substantiated by the Leslie, Chitty and Chitty test. In biological populations, unequal catchability seems to be the rule rather than the exception (Caughley, cited in KREBS, 1989).

Table 4.6: I- and II-group plaice catch data from beach-seine experiments in May/June and September 1991 for estimation of population size using Schumacher and Eschmeyer method (RICKER, 1975).

Date	t	C_t	C_t ≥90 mm	R_t	m_t
20/5/91	1	8	7	0	6
20/5/91	2	14	9	0	4
22/5/91	3	18	16	1	15
23/5/91	4	16	15	0	15
25/5/91	5	25	23	0	23
26/5/91	6	7	6	1	5
26/5/91	7	17	13	3	10
27/5/91	8	4	4	1	3
28/5/91	9	8	7	0	7
29/5/91	10	18	15	1	14
30/5/91	11	20	18	4	14
31/5/91	12	19	17	4	13
1/6/91	13	12	11	2	9
2/6/91	14	10	10	2	8
16/9/91	1	2	2	0	2
16/9/91	2	1	1	0	1
18/9/91	3	14	14	0	14
18/9/91	4	0	0	0	0
20/9/91	5	15	15	1	14
20/9/91	6	3	3	0	3
23/9/91	7	8	8	0	8
25/9/91	8	10	10	3	7
26/9/91	9	12	12	3	9

After RICKER (1975)
t: sampling occasion
C_t: number in sample at time t
R_t: number of recaptures in sample C_t
m_t: number of newly marked fish released from sample Ct

Table 4.7: Occurrence of flatfishes in stomachs of indigenous and cultured turbot caught in Port Erin Bay, 20 May to 10 October 1991. The cultured turbot were released into Port Erin Bay in mid-June 1991. Identification of flatfish remains was from external features only, hence many were not identified. However plaice are more common in Port Erin than dab *Limanda limanda* (*pers. obs.*; see NASH *et al.*, 1994), so most of the unidentified flatfish (unident) were probably plaice.

Date	INDIGENOUS TURBOT					CULTURED TURBOT				
	n	TL (mm)	Containing flatfish			n	TL (mm)	Containing flatfish		
			n	TL	Species & size			n	TL	Species & size
20/5	4	58-78	1	64	Plaice					
20/6						2	147-197	0		
26/6						2	133-186	0		
3/7						1	142	1	142	Unident SL=26
10/7						1	184	1	184	Unident SL=35
11/7	1	120	1	120	Plaice TL=42 Plaice TL=32	12	131-195	2	152 170	Plaice SL=28 Plaice TL=47
24/7						8	148-194	1	163	Unident SL=22
26/7	1	128	0			1	170	0		
8/8	1	137	0							
9/8	2	147-153	2	153 147	Unident SL=24 Unident SL=31 Unident SL=28 Unident SL=33	8	159-203	3	197 159 160	Unident SL=41 Unident SL=42 Unident SL=30 Unident SL=51 Plaice SL=41
21/8	4	132-237	1	139	Unident SL=31	5	182-206	3	202 206 198	Unident Plaice TL=51 Plaice TL=43 Plaice TL=49 Dab TL=50 Dab TL=44 Plaice TL=55 Plaice TL=49 Plaice TL=49 Plaice TL=49
29/8	6	128-166	0			7	151-217	1	201	Unident
6/9	5	142-165	1	144	Unident TL=43	4	196-222	2	203 196	Dab TL=42 Unident Plaice TL=55 Plaice TL=42 Plaice TL=56
13/9	4	152-182	0			5	176-212	1	208	Plaice TL=67
16/9	3	123-161	0							
26/9	3	145-177				8	150-223	3	223 219 211	Unident Plaice TL=59 Plaice SL=35 Plaice TL=47 Unident SL=39
9/10	5	158-201	3	201 163 195	Plaice TL=39 Unident Unident Plaice	4	167-192	0		
10/10	3	161-178	0			2	142-205	0		

The data for the second analysis passed Chapman's test of equal catchability. The mortality rates, corrected for time period (Table 4.4), are within the range previously recorded (see ILES & BEVERTON, 1991). However no trend is apparent and, if they are to be believed, then mortality fluctuates greatly over short periods of time. Fish are thought to be the main predators of 0-group plaice after the summer (VAN DER VEER *et al.*, 1990). The mortality rate may then fluctuate due to fluctuations in the abundance of migrant fish predators (see BERGMAN *et al.*, 1988). However, the large standard deviations show no significant differences in mortality rate between periods. Larger sample sizes and numbers of released fish may have produced more reliable estimates, but were not achieved because of effort constraints.

There are various assumptions implicit in the Jolly-Seber model (BEGON, 1979; SEBER, 1982; KREBS, 1989).

1. The marks are permanent for the duration of the experiment.
2. All recaptures are noted.
3. Capture, handling and marking do not affect the probability of survival.
4. Capture and marking do not affect the probability of subsequent capture.
5. All individuals in a population have an equal probability of capture.
6. Sampling is ideally instantaneous, or rather short in comparison to the experimental time period.

It is believed that the assumptions 1-4 were not violated. The marks were permanent for the duration of the experiment (RILEY, 1966a), although they may have become less visible over time. Data was excluded from the analysis when recording efficiency was doubtful. Only fish in good condition were released. Chapman's test (using data from the 8th to the 12th release) showed no statistical difference in the probability of capture between marked and unmarked fish.

Assumption 5 was violated. The Leslie, Chitty and Chitty test showed unequal catchability between different segments of the marked population. This could be due to differential mortality, different depth distributions or different catchabilities.

Assumption 6 was transgressed because sampling typically spanned the time between releases due to the size of the population sampled, the need to obtain large sample sizes for recapture information and marking, and concurrent projects. This is not thought to pose a problem for estimates of population size, as estimates are based upon the proportions of marked fish and, provided that there is no extra mortality among marked fish, the proportion will hold constant between releases.

The major problem with the data collection was the use of different gears which sampled different size fractions of the population. The small meshed gears (push-net and 1.5 m beam trawl) probably under-sampled larger individuals because of gear avoidance, while the 2 m beam trawl (large mesh) probably under-sampled smaller fish due to mesh selection. Whether the beach seine is size-selective is unknown. However it is interesting to compare the mark and recapture estimates of population size in September 1991 of 0-group fish (data from all gears) with I- and II-group fish (data from beach seine catches), i.e. 8705:187= 47:1, with the ratio in the beach seine catches (853:65 = 13:1). This suggests that the larger I- and II-group plaice are more vulnerable to capture by the beach seine, or it could reflect differences in the depth distribution.

The use of a mark and recapture experiment therefore did not avoid the problem of gear efficiency. The data for the different gear types (small mesh and large mesh) were analyzed separately but the results are not presented here. Estimates from the large mesh gears consistently gave population size estimates lower than those from the small mesh gears. The data for the different gears were pooled for the analyses because intermediate estimates resulted and the increase in sample sizes, resulted in an increase in precision of estimates.

That a reduction in population size did occur is shown by the great difference in the first and last estimates of population size from both analyses, and the steady decrease in population size over time. Although the estimates of mortality from the first analysis are dubious, the population size estimates over the summer are comparable to previous studies (Figure 4.1). The population size of the 1963 year class of 0-group plaice in Port Erin Bay was estimated from quadrat counts (JONES & KAIN, 1964), and from recaptures in trawl samples (RILEY & CORLETT, 1966; RILEY, 1973). Population sizes for the 1964 and 1965 year-classes were estimated by comparing catches with those in 1963 at dates when population size was estimated (see Figure 3 in RILEY & CORLETT, 1966). The estimates of population size in the summer of 1991 were comparable to previous studies, if a bit low. It must be remembered that the 1963 year-class of plaice in the Irish Sea was exceptionally strong (see Figure 1.2). The estimates for January 1992 are very similar to previous estimates.

The second analysis estimated the number of 0-group plaice in February at 2650 (Table 4.4). This compares to estimates of I- (and II-) group plaice population size in Port Erin Bay of 665 in May 1991, and 190 in September 1991. The size of the I- and II-group plaice population remaining after the winter will be important for the mortality of the following year-class of plaice. I- and II-group plaice are cited as important predators of 0-group plaice in Port Erin Bay (RILEY & CORLETT, 1966) and Red Wharf Bay, Wales (MACER, 1967).

The cultured turbot released into Port Erin Bay significantly increased the number of turbot within the bay and they were a source of mortality of 0-group plaice. It had been hypothesised that the mortality rate in 1991 would therefore have been higher than in previous years. This was tested by comparing estimates of population size and mortality rate.

The population size estimates for January 1992 were within the range previously recorded for Port Erin (Figure 4.1). The average mortality rate of 0-group plaice in 1991-2 was estimated from the decrease in the corrected estimates of population size (17 August to 26 February; n=10) from the first analysis. The average daily instantaneous mortality rate was estimated by linear regression ($p<0.001$, $R^2=0.92$) of $\log_e$ population size against time in days. The mortality rate (0.0119) is similar to previous estimates for Port Erin Bay over a similar time period (0.0161,

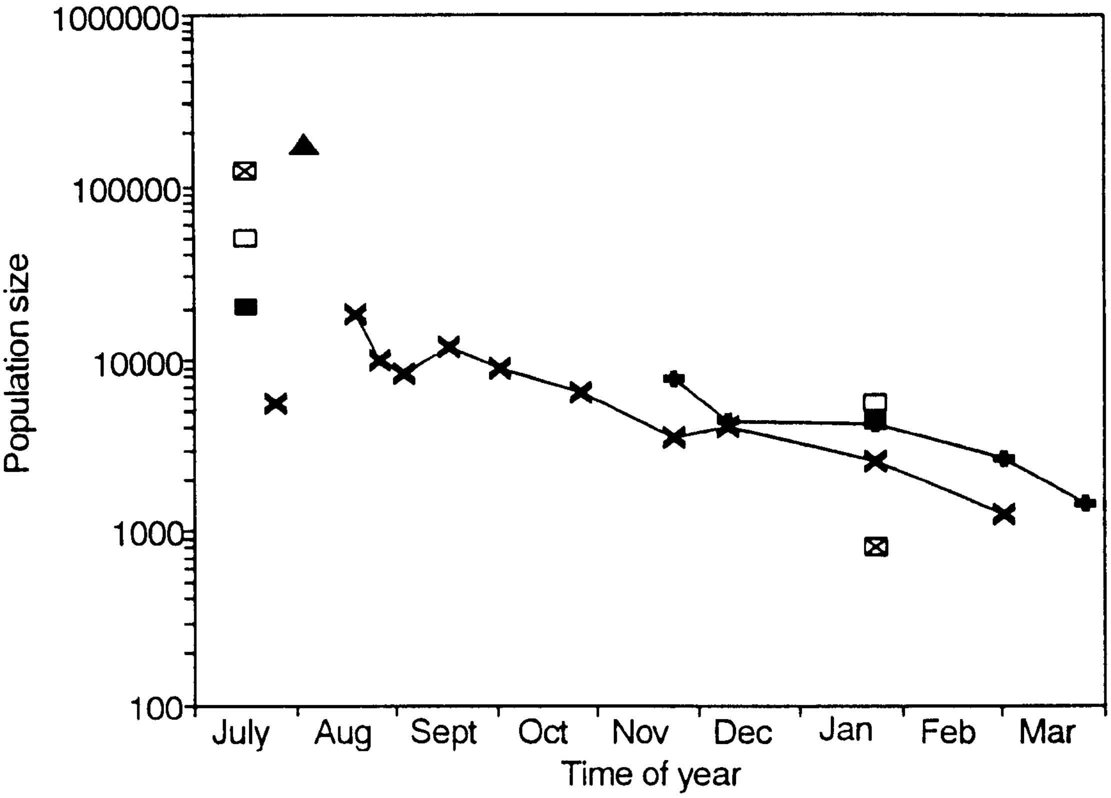


Figure 4.1: Estimates of population size of 0-group plaice in Port Erin Bay between July and March, for various years.

▲ : 1963 from JONES & KAIN (1964)
□ : 1963 from RILEY & CORLETT (1966)
■ : 1964 from RILEY & CORLETT (1966)
⊠ : 1965 from RILEY & CORLETT (1966)
—✕— : 1991 from present study, Jolly-Seber with immigration
—✚— : 1991 from present study, special case Jolly-Seber method with no immigration

0.0132, 0.0235: ILES & BEVERTON, 1991).

However, the mortality rate of 0-group plaice populations is positively correlated with population density (see BEVERTON & ILES, 1992b). Therefore the average mortality rate was compared to previous estimates (1963-1965, from ILES & BEVERTON, 1991), in relation to population size. Population size had been estimated in mid-July 1963-1965 (see above). The population size in mid-July 1991 was not directly estimated in this study, but was gauged at 20,150 by extrapolation from the regression line used for the calculation of mortality rate. The mortality rate estimated for 1991 was comparable to that for 1964, when the population size estimates were very similar (Figure 4.2).

Estimates of population sizes in January (Figure 4.1), mortality rates, and mortality rates in relation to population density in July (Figure 4.2), show that the release of the cultured turbot into Port Erin Bay did not have a severe effect on the population dynamics of the 0-group plaice population.

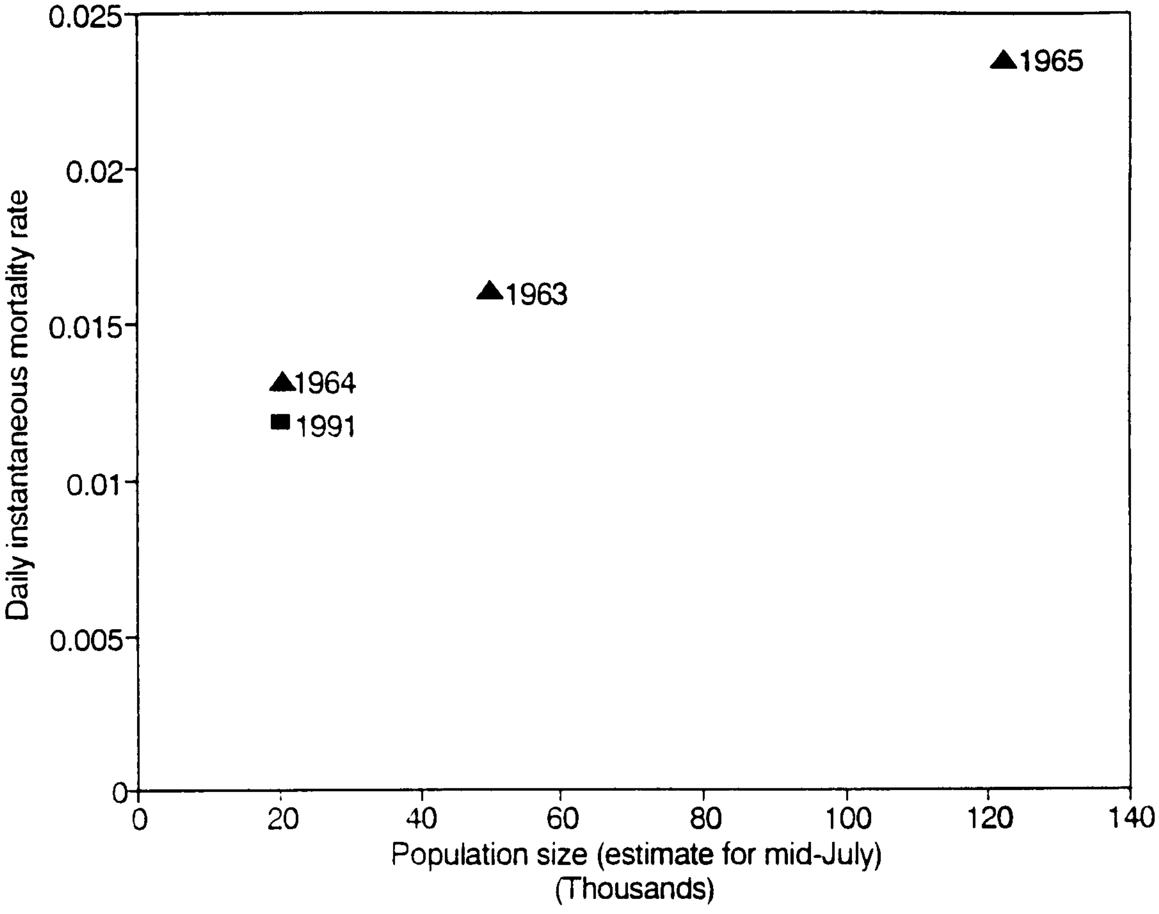


Figure 4.2: Estimates of average daily instantaneous mortality rate of 0-group plaice populations in Port Erin Bay, plotted against population size estimates for mid-July. Mortality rates for 1963, 1964, 1965 taken from ILES & BEVERTON (1991). Population estimates for 1963, 1964, 1965 taken from RILEY & CORLETT (1966). Population size and mortality rates for 1991 were estimated in this study.

CHAPTER 5:

A FIELD STUDY OF FISH PREDATION ON 0-GROUP FLATFISHES ON A SCOTTISH NURSERY GROUND.

INTRODUCTION

0-group flatfish populations on nursery grounds suffer mortality (ILES & BEVERTON, 1991) and the role of this mortality in determining the year-class strength of plaice has attracted much interest (LOCKWOOD, 1980; VAN DER VEER, 1986; BERGMAN *et al.*, 1988; VAN DER VEER *et al.*, 1990; BEVERTON & ILES, 1992b). Despite the paucity of quantitative evidence, predation is assumed to be the major cause of mortality in all nurseries (MACER, 1967; STEELE & EDWARDS, 1970; VAN DER VEER *et al.*, 1990; BEVERTON & ILES, 1992a).

0-group plaice are eaten by crustaceans, fish and birds (RILEY & CORLETT, 1966; MACER, 1967; EDWARDS & STEELE, 1968; LOCKWOOD, 1972; PIHL, 1982; VAN DER VEER & BERGMAN, 1987; BERGMAN *et al.*, 1988; VAN DER VEER *et al.*, 1990; BAILEY, 1994). Predation by shrimp *Crangon crangon* on newly settled plaice has been quantified in the Wadden Sea and is approximately equal to the total observed mortality (VAN DER VEER & BERGMAN, 1987). Predation by shrimp is therefore thought to be the primary cause of mortality of 0-group plaice in the Wadden Sea.

The mortality rate of 0-group plaice on open beaches is higher than in the Wadden Sea, and the difference is attributed to predation by fishes (BERGMAN *et al.*, 1988). However, the information on fish predators of 0-group plaice is fragmentary (RILEY & CORLETT, 1966; MACER, 1967; EDWARDS & STEELE, 1968; LOCKWOOD, 1972; PIHL, 1982); their effect has not been quantified, and the interpretation of their role in mortality and determination of year-class strength is highly conjectural (see LOCKWOOD, 1980; VAN DER VEER & BERGMAN, 1987; BERGMAN *et al.*, 1988; VAN DER VEER *et al.*, 1990).

I- and II-group flatfishes have been cited as the major predators of 0-group flatfishes in Irish Sea nurseries (RILEY & CORLETT, 1966; MACER, 1967). However, the importance of the different fish predators differs between nurseries (EDWARDS & STEELE, 1968). Gadoids are commonly cited as predators of 0-group plaice (RILEY

& CORLETT, 1966; EDWARDS & STEELE, 1968; LOCKWOOD, 1980; PIHL, 1982). In particular, 0-group cod *Gadus morhua* have been recorded as the most important predator in a Scottish fjordic nursery (EDWARDS & STEELE, 1968).

This field study was undertaken to examine the nature and extent of predation by fishes on 0-group flatfishes (plaice, dab *Limanda limanda* and flounder *Pleuronectes flesus*) in the first few months after settlement on a Scottish fjordic nursery ground. In 1992 sampling was directed towards gadoids, primarily cod. In spite of the abundance of plaice, none was found in gadoid stomachs. Therefore, in 1993 sampling was extended to all potential fish predators to examine which fish species, if any, ate 0-group plaice, and whether such predation was a significant source of mortality.

MATERIALS AND METHODS

Site

All samples were taken on Tralee Beach (56°31'N 5°29'W). Tralee Beach is a south-west facing open sandy beach situated at the north end of Ardmucknish Bay on the west coast of Scotland (see GIBSON *et al.*, 1993).

Surveys

In 1992 sampling was directed towards gadoids. The abundance of 0-group gadoids at Tralee was monitored by daytime trawling conducted in connection with a different project (see Chapter 7). There were low numbers of 0-group gadoids in May and early June (Figure 5.1A). Sampling was started in mid June and continued until September. Six surveys of the gadoid and flatfish populations were made, at fortnightly intervals in June and July and at monthly intervals in August and September. All sampling of the gadoid and flatfish populations was conducted at night. Juvenile cod are nocturnal in shallow inshore areas (HAWKINS *et al.*, 1974; PIHL, 1982) and underwater television observations at Tralee have shown that juvenile gadoids move into shallow water at night (BURROWS *et al.*, 1994), presumably to feed. All surveys were conducted around the time of low water (midnight) on spring tides.

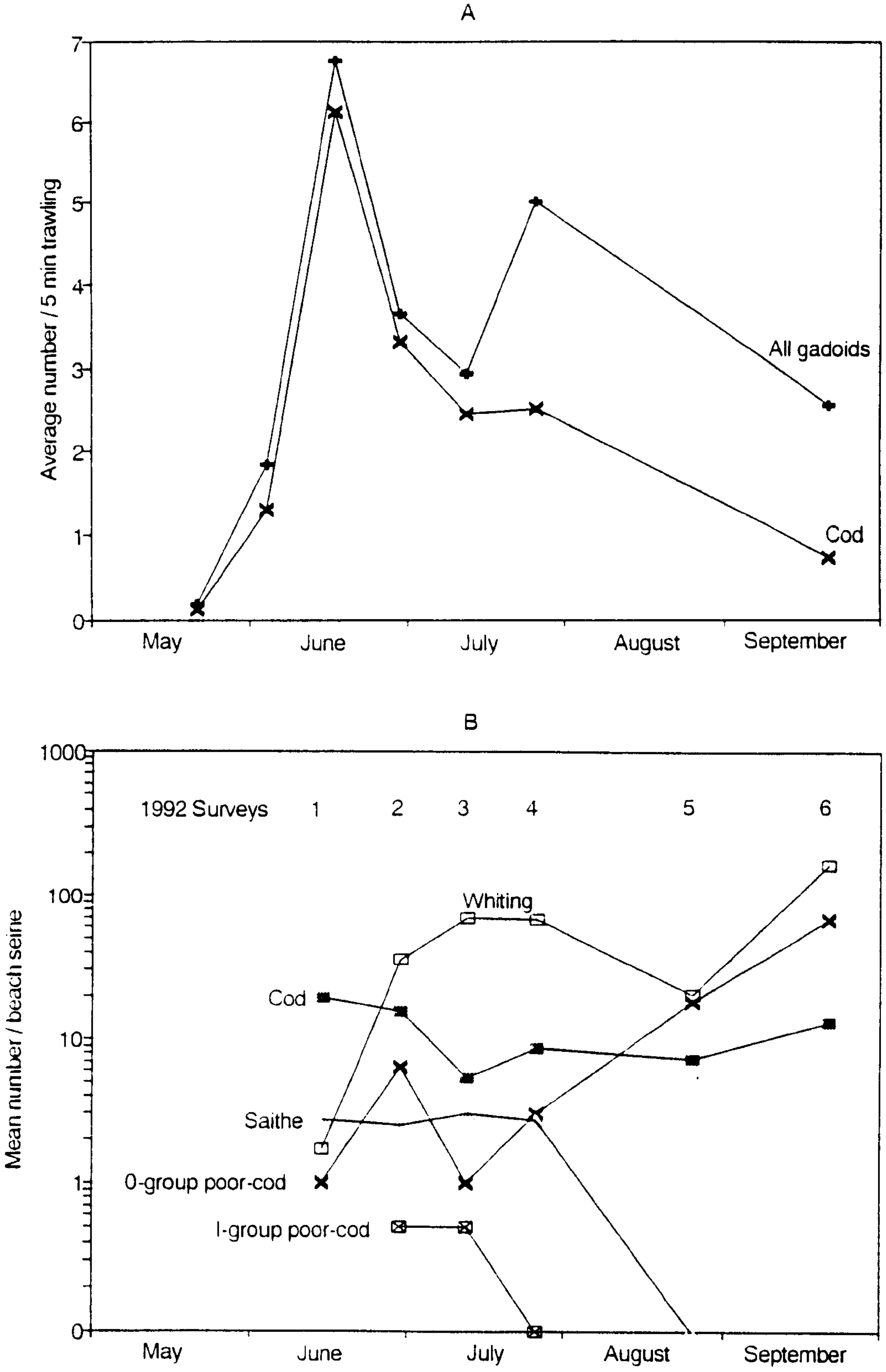


Figure 5.1: Indices of abundance of gadoids at Tralee in 1992.
A: Number of gadoids caught per 5 min trawling from *R.V. Seol Mara* during the day (May to September).
B: Number of gadoids caught per beach seine sample at night in the six surveys of 1992 (mid-June to September).

In 1993 sampling was restricted to the period of recruitment of the flatfishes, so they would be at relatively high densities. Five surveys were made of the flatfish and predatory fish populations at fortnightly intervals between early May and early July. Samples were again taken at night, around low water on spring tides.

Predator Sampling

In both 1992 and 1993 potential predators of 0-group flatfishes were sampled close to shore (0-1.5 m depth) with a 38 x 1.8 m beach seine (8 mm stretched mesh in the central portion). The beach seine was set from a 4 m dory with an outboard motor. The first hauling rope was set as the dory went out perpendicular to the shore. The net was set parallel to the shore and the second hauling rope was set as the boat returned to the shore. The net was then hauled in by hand. Two or three beach seine samples were taken on each survey.

In 1992, in addition to the inshore samples, gadoids were obtained at a depth of 4-5 m with a 3 m beam trawl (8 mm stretched mesh in cod end) towed at 2 knots from *R.V. Seol Mara* for approximately 5 min. It was not possible to obtain samples from 4-5 m in August 1992 due to adverse weather conditions.

Flatfish Sampling

The 0-group flatfish populations were sampled with a standard Lowestoft 2 m beam trawl with a 3 mm liner in the cod end (RILEY *et al.*, 1986). A cyclometer was fitted to the trawl so the distance towed could be calculated (see GIBSON *et al.*, 1993).

In 1992 the flatfish populations were sampled by trawling parallel to the beach in 0.5 m at low tide. A hauling rope was tied to each shoe and the trawl was pulled by two people wading *c.* 4 m apart. In 1993 orthogonal hauls were used to estimate the density of the flatfish populations (see ILES & BEVERTON, 1991). The trawl was set on the beach, attached to the dory by a 45 m rope, and towed out to a depth of approximately 5 m. The average distance covered by the trawl was 150 m. Three samples were usually taken.

Preservation and sorting

Fishes were sorted from the catch and preserved. If a large amount of filamentous alga was present, the entire catch was preserved and sorted later. Fishes were killed with an overdose of the anaesthetic benzocaine to prevent regurgitation of stomach contents (EDWARDS & STEELE, 1968), and preserved in approximately 4% formaldehyde in sea-water.

Analysis of samples

In the laboratory the total length (TL) of the 0-group flatfishes was measured to the nearest mm. Gadoids were identified using WATSON (1982), and other fish species according to WHEELER (1969). Each potential predator was measured to the nearest mm (TL) and weighed (to 1 mg). The stomach and oesophagus were removed intact. The stomach was dissected open in tap-water under a dissecting microscope and fish remains recognisable as flatfishes were retained.

Identification of flatfish remains

Varying degrees of digestion meant that it was rarely possible to use external features (e.g. lateral line, fin rays, body shape) to identify to species those flatfishes found in stomachs. Skeletal features were therefore used. The flatfish remains were partially dissolved with 2% potassium hydroxide, stained with Alizarin Red S, and then cleared with increasing concentrations of glycerol (see MAHONEY, 1968). The calcified tissue was clearly visible and stained red.

The species of the flatfish were identified mainly using the number of abdominal vertebrae. According to NORMAN (1934), the numbers of abdominal vertebrae of plaice, dab and flounder are 13, 10-11 and 11-12, while RUSSELL (1976) gives 12-14, 9-11 and 10-12 vertebrae respectively. In samples of fish taken on Tralee beach, 100% of plaice had 13 (n=54), 98% and 2% of dab had 10 and 11 respectively (n=120), and 4% and 96% of flounder had 10 and 11 abdominal vertebrae (n=23) respectively. Additional aids to species identification was the shape of the terminal vertebra (see Figure 122 in RUSSELL, 1976), size (all plaice and dab in beam trawl samples ≥14 mm, flounder only 10-13 mm) and the number of caudal vertebrae. Flounder have fewer caudal vertebrae (24-25: NORMAN, 1934; 22-26: RUSSELL, 1976) than plaice and dab (29-30: NORMAN, 1934; 28-32: RUSSELL, 1976).

Estimation of mortality rate due to fish predation

Because of the common assumption that predation is the primary cause of mortality of 0-group flatfishes, despite the absence of quantitative studies, first estimates of mortality rates due to fish predation were made. Daily instantaneous mortality rates were calculated from the equation given by VAN DER VEER & BERGMAN (1987) and used in Chapter 3. The method requires estimates of flatfish population density, and predation rate per unit area per day.

To estimate fish densities from catches, the area sampled must be known as well as gear efficiency. The area covered by the beam trawl was estimated from the calibrated cyclometer and the width of the net (1.9 m). The efficiency of the beam trawl was assumed to be 0.35 (ROGERS & LOCKWOOD, 1989) across all size classes.

The efficiency of the beach seine will depend not only upon how it is used, but also upon the topography and coarseness of the substratum, presence of vegetation and snags, time of day, fish size, and whether species are pelagic or demersal (LYONS, 1986; ROSS *et al.*, 1987; PARSLEY *et al.*, 1989; PIERCE *et al.*, 1990; Chapter 4). The substratum at Tralee below the low water mark consists of fine sand (GIBSON *et al.*, 1993) and is relatively clear of obstructions, and sampling was done at night. The efficiencies of beach seines used without ropes have been estimated at 0.13-0.96 and 0.12-0.91 for pelagic and demersal species respectively (PARSLEY *et al.*, 1989; PIERCE *et al.*, 1990). As there is no published estimate for beach seine efficiency for the conditions and species sampled, and the estimation of such a parameter was outside the scope of this project, an intermediate efficiency (0.5) was arbitrarily chosen for all species. The number of flatfishes found in stomachs was therefore multiplied by 2 as an estimate of the number eaten in the area of the beach seine. GIBSON *et al.* (1993) estimated the area fished by the beach seine at 1160 m^2.

To convert the number of flatfishes eaten per unit area, to a number eaten per unit area per day, information is required on the gastric residence time of flatfishes and the feeding periodicity of the different predators. The time for which prey can be recognised from predator stomachs is dependent on temperature, predator size, prey size, prey surface area, meal size and feeding history (FOLKVORD, 1993). Lacking information of gastric residence times and feeding periodicities, it was assumed that the numbers recognisable as flatfish in stomachs represented those consumed within the previous 24 h.

RESULTS

As there is little published data on seasonal abundance of gadoids on sandy beaches, the 1992 sampling will be discussed first in some detail. The results of the 1993 sampling follow.

1992

Relative abundance of gadoids

The gadoid species regularly taken in samples were cod, whiting *Merlangius merlangus*, poor cod *Trisopterus minutus* and saithe *Pollachius virens*, although saithe were only caught with a beach seine. From length distributions, all cod and whiting were assumed to be 0-group, whereas poor-cod could be differentiated into 0- and I-groups. In addition two 0-group bib *Trisopterus luscus* and two haddock *Melanogrammus aeglefinis* were caught.

Gadoids were present in low numbers before the beginning of the study (Figure 5.1A). During the period of the surveys, the beach seine catches (Figure 5.1B) are a better representation of the gadoid populations than trawl catches (Figure 5.1A) which are considered to be more size-dependent.

Cod started to recruit to Tralee beach in May and numbers increased to mid-June. Cod dominated the gadoid community in June after which numbers decreased slightly. Whiting and poor-cod numbers increased through the study. Whiting were the dominant gadoid species between July and September. Saithe and I-group poor-cod were only taken in small numbers in June and July.

Piscivory of gadoids

Cod were found to have eaten fish when caught both in shallow water (0-2 m) and at 4-5 m, with the occurrence varying from 0-22% (Table 5.1). The occurrence of dabs ranged from 0-11%. In mid June all cod eating fish (n=13) ate flatfish, mainly dab but one individual ate only flounders. There was a trend for the occurrence of dabs to decrease over the season, with no dabs recorded from cod stomachs in August or September. More than one dab was often found in each cod stomach (Figure 5.2). The other fish eaten included both demersal and pelagic species, with a tendency towards demersal species (Table 5.2).

Whiting were highly piscivorous in shallow water, the occurrence of fish ranging up to 58% (Table 5.1). The fish eaten were, however, mainly pelagic species (Table 5.2). The occurrence of dabs was low, although they were eaten between July and September. Only a single dab was found in each of these stomachs.

Of the seven I-group poor-cod caught in both shallow water and in 4-5 m, three contained fish and two of these contained dabs. Only a single dab was found in each of these stomachs.

There was a very low incidence of predation on fish by 0-group poor-cod and only one individual had eaten a sandeel (Tables 5.1 & 5.2). There was no evidence of 0-group poor-cod having eaten dabs.

Saithe were highly piscivorous in July (Table 5.1), but there was no evidence of predation on dabs. Saithe fed mainly on pelagic species (Table 5.2).

Relative importance of the gadoids as predators of dabs in 1992

The relative importance of the different gadoids as predators of dabs was estimated over the six surveys by calculating the average number of dabs found in gadoid stomachs per beach seine sample and per 5 min trawl in 4-5 m (Figure 5.3 A & B). This index takes into account the occurrence of dabs in each gadoid species, the

Table 5.1: Occurrence of fish and flatfish remains in stomachs of gadoids sampled in the 6 surveys in 1992.

Species	Depth (m)	Survey	1	2	3	4	5	6
		Date	15/6 & 18/6	1/7	14/7	28/7	28/8	24/9
Cod	0-2	n	69	36	11	26	22	26
		Mean TL (mm)	46.7	60.0	64.4	72.9	91.3	98.4
		% Occ Fish	1.5	16.7	0	19.3	0	7.7
		% Occ Flatfish	1.5 Flounder	8.3 Dab	0	3.9 Dab	0	0
	4-5	n	102	16	9	25		2
		Mean TL (mm)	43.0	51.6	68.0	69.3		105.5
		% Occ Fish	9.8	18.8	22.2	0		0
		% Occ Dab	9.8	6.3	11.1	0		0
Whiting	0-2	n	5	72	139	206	67	71
		Mean TL (mm)	65.4	67.9	99.4	111.6	98.7	99.3
		% Occ Fish	20.0	4.2	57.6	52.4	4.5	19.7
		% Occ Dab	0	1.4	1.4	0.5	0	1.4
	4-5	n	6	5	13	8		1
		Mean TL (mm)	54.2	67.0	75.7	90.5		99
		% Occ Fish	0	0	15.4	25.0		0
		% Occ Dab	0	0	0	0		0
I-group Poor-cod	0-2	n	1	1	1	0	0	0
		Mean TL (mm)	117	128	141			
		% Occ Fish	0	100	100			
		% Occ Dab	0	100	0			
	4-5	n	3	1	0			
		Mean TL (mm)	101.3	118				
		% Occ Fish	33.3	0				
		% Occ Dab	33.3	0				
0-group Poor-cod	0-2	n	3	15	3	6	57	38
		Mean TL (mm)	39.7	46.6	49.3	60.8	73.0	77.5
		% Occ Fish	0	0	0	0	0	2.6
		% Occ Dab	0	0	0	0	0	0
	4-5	n	7	4	16	53		24
		Mean TL (mm)	34.1	53.0	59.3	59.6		77.3
		% Occ Fish	0	0	0	0		0
		% Occ Dab	0	0	0	0		0
Saithe	0-2	n	8	5	6	8	0	0
		Mean TL (mm)	77.9	88.0	114	124		
		% Occ Fish	0	0	50	87.5		
		% Occ Dab	0	0	0	0		

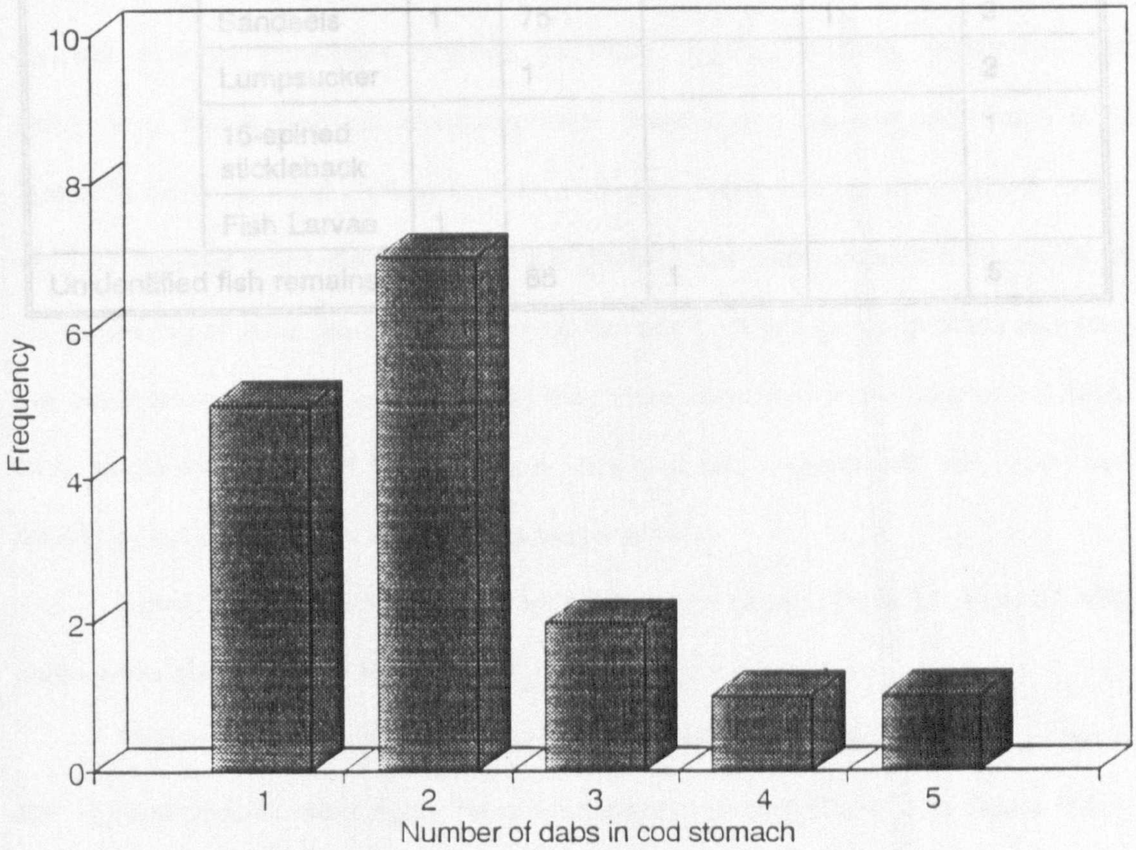


Figure 5.2: Number of dabs found in individual 0-group cod stomachs (n=16), caught in the first four surveys of 1992. The figure shows that cod were often found containing more than one dab.

Table 5.2: Classification of fish remains found in gadoid stomachs in the 6 surveys in 1992. Figures refer to number of individuals containing prey item.

Gadoid species		Cod	Whiting	I-group poor-cod	O-group poor-cod	Saithe
Demersal	Flounder	1				
	Dab	17	5	2		
	Turbot	1				
	Goby	2	2			
	Unidentified roundfish	1	2			
Pelagic	Clupeids	1	65			3
	Sandeels	1	75		1	3
	Lumpsucker		1			2
	15-spined stickleback					1
	Fish Larvae	1				
Unidentified fish remains		6	85	1		5

number of dabs eaten by each individual and the abundance of each gadoid species.

The numbers of dabs eaten by gadoids per unit area decreased over the season. Cod were the predominant gadoid predator of dabs at the start of the summer. Predation by I-group poor-cod was lower due to very low abundance. Through July the importance of cod decreased and there was no recorded predation on dab after July. 0-group whiting became the predominant predator in July and were recorded feeding on dabs in September.

1993

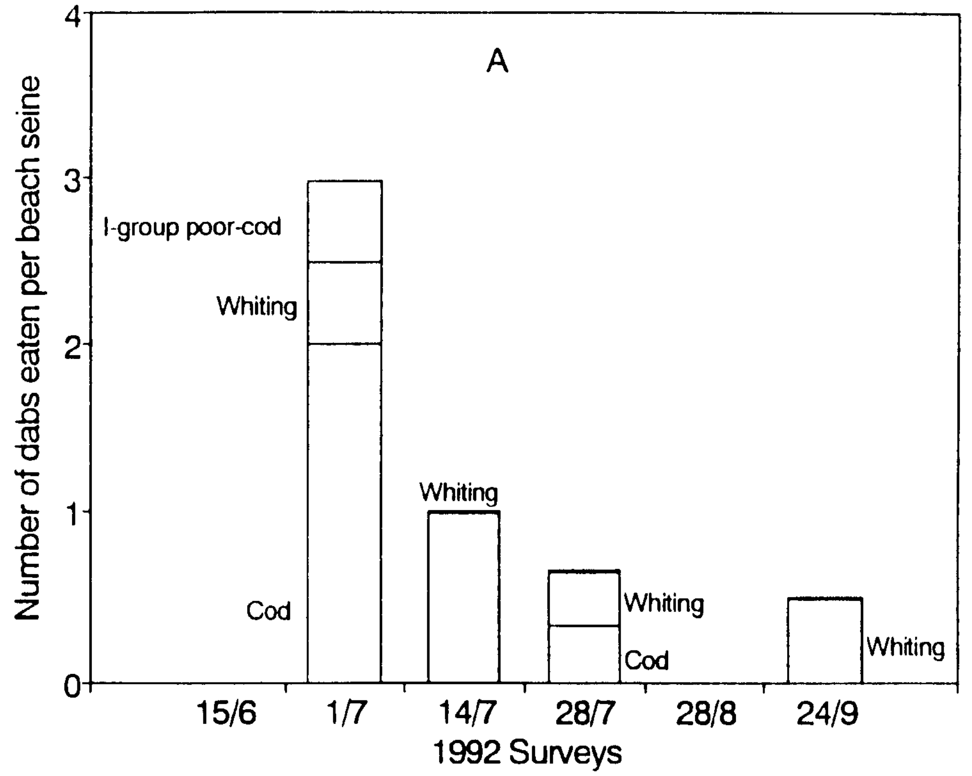
In the 1993 surveys plaice were recorded from the stomachs of I-group grey gurnard *Eutrigla gurnardus*, I-group poor-cod, I-group whiting, lesser weever *Echiichthys vipera*, bull-rout *Myoxocephalus scorpius* and 0-group cod (Table 5.3). Gurnards were the most important predator (Figure 5.4A), having fed on plaice in the first four surveys (May-June). The I-group gadoids were also important predators at the beginning of June (survey 3). Although the numbers of I-group gadoids was low, the occurrence of plaice was high and they often contained more than one flatfish. Only single individuals of lesser weaver, bull-rout and 0-group cod were recorded having eaten plaice, each containing a single plaice.

Gurnards were the most important fish predator of dab (Table 5.3, Figure 5.4B). Dabs were also eaten by I-group poor-cod and 0-group cod.

Flounders were eaten by a greater variety of fish species, although gurnards and I-group gadoids were again the predominant predators (Table 5.3; Figure 5.4C). Flounder were also eaten by hook-nose *Agonus cataphractus*, I-group plaice, sand goby *Pomatoschistus minutus* and 0-group cod. Flounder larvae were recorded from the stomachs of two herring *Clupea harengus* in mid May.

Mortality rate due to fish predation

The daily instantaneous mortality rates of 0-group plaice, dab and flounder due to fish predation were estimated at 0.001-0.026, 0.002-0.014 and 0.061-0.315 respectively (Table 5.4). The results must, however, only be considered as first



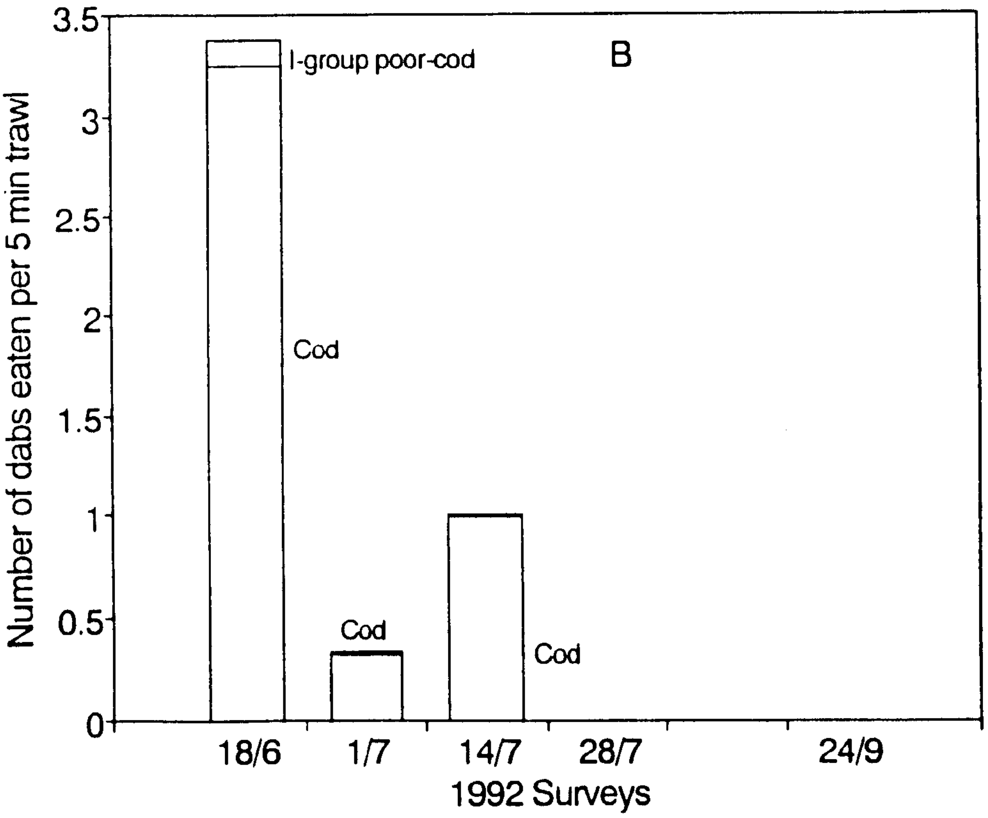


Figure 5.3: Importance of different gadoids as predators of dab in the 6 surveys of 1992. Indices are numbers of dab found in gadoid stomachs per beach seine (A) and per 5 min trawl in 4-5 m at night from *R.V. Seol Mara* (B). Note no sample taken in 4-5 m on 28/8/92.

Table 5.3: Occurrence of flatfishes in samples of fish predators caught in first 3 surveys in 1993. The herring could be differentiated into two "cohorts" on the basis of size. The larger fish were caught in surveys 1-3, and the smaller herring were caught in surveys 2-5. The fifteen-spined stickleback *Spinachia spinachia* is not mentioned in the text.

Survey (& number of seines)	Date	Species	Age	No. caught	No. analyzed	Mean TL (mm)	% Occurrence				
							Food	Fish	Plaice	Dab	Flounder
1 (3)	6/5/93	Grey gurnard	I *	32	32	92.3	100	9.4	3.1	-	3.1
		Lesser weever	≥I	5	5	78.2	80	0	-	-	-
		Hook-nose	≥I	8	8	60.3	100	12.5	-	-	12.5
		Goby	≥I	8	8	65.6	75	0	-	-	-
		Whiting	I	2	2	127.5	100	0	-	-	-
		Plaice	I	135	135	93.3	100	0	-	-	-
		Dab	I	6	6	76.7	100	0	-	-	-
		Flounder	≥I	1	1	93	100	0	-	-	-
		Turbot	I	1	1	88	100	100	-	-	-
		15-spined stickleback		4	4	106.0	100	0	-	-	-
		Herring (large)		350	0	-	-	-	-	-	-
2 (3)	19/5/93	Grey gurnard	I	32	32	100.8	100	40.6	18.8	6.3	9.4
		Lesser weever	≥I	11	11	67.9	90.9	18.2	9.1	-	-
		Goby	≥I	13	13	52.5	84.6	0	-	-	-
		Plaice	I	102	102	98.3	100	0	-	-	-
		Dab	I	4	4	86.5	100	0	-	-	-
		Flounder	≥I	9	9	110.6	88.9	0	-	-	-
		15-spined stickleback		1	1	102	100	0	-	-	-
		Herring (large)		7	7	113.6	100	42.9	-	-	28.6
		Herring (small)		15	15	56.8	100	0	-	-	-
3 (3)	2/6/93	Grey gurnard	I	3	3	100.7	100	33.3	33.3	33.3	33.3
		Lesser weever	≥I	3	3	70.3	100	0	-	-	-
		Bull-rout	≥I	1	1	143	100	100	100	-	-
		Goby	≥I	8	8	59.9	87.5	12.5	-	-	12.5
		Poor-cod	I	3	3	101.3	100	100	66.7	-	66.7
		Whiting	I	1	1	130	100	100	100	-	100
		Cod	0	5	5	39.0	100	0	-	-	-
		Plaice	I	29	29	108.2	100	10.3	-	-	6.9
		Flounder	≥I	7	7	143.3	57.1	0	-	-	-
		Herring (large)		1	1	135	100	0	-	-	-
		Herring (small)		23	23	64.8	100	0	-	-	-

Table 5.3 (cont.): Occurrence of flatfish in fish predators caught in the latter two surveys of 1993.

Survey (& number of seines)	Date	Species	Age	No. caught	No. analyzed	Mean TL (mm)	% Occurrence				
							Food	Fish	Plaice	Dab	Flounder
4 (3)	16/6/93	Grey gurnard	I	11	11	108.6	100	36.4	18.2	9.1	9.1
		Lesser weever	≥I	6	6	87.2	100	16.7	-	-	-
		Goby	≥I	17	17	57.2	64.7	0	-	-	-
		Poor-cod	I	7	7	111.9	100	28.6	-	-	14.3
		Whiting	I	1	1	154	100	0	-	-	-
		Cod	0	26	26	54.3	100	30.8	3.8	3.8	15.4
		Saithe	0	1	1	55	100	0	-	-	-
		Plaice	I	24	24	110.1	100	0	-	-	-
		Flounder	≥I	1	1	142	100	0	-	-	-
		Herring (small)		1	1	69	100	0	-	-	-
5 (2)	1/7/93	Grey gurnard	I	40	40	114.8	90	17.5	-	7.5	-
		Grey gurnard	0	9	9	51.9	100	0	-	-	-
		Lesser weever	≥I	4	4	78.8	100	50.0	-	-	-
		Bull-rout	0	1	1	28	100	0	-	-	-
		Hook-nose	≥I	2	2	70	100	0	-	-	-
		Goby	≥I	41	41	60.5	73.2	2.4	-	-	-
		Poor-cod	I	6	6	103.3	100	33.3	-	16.7	-
		Poor-cod	0	6	6	40.5	83.3	0	-	-	-
		Cod	0	144	144	58.3	98.6	6.3	-	-	-
		Whiting	0	52	52	71.2	92.3	3.8	-	-	-
		Saithe	0	1	1	108	100	100	-	-	-
		Plaice	I	50	50	129.7	100	16.0	-	-	-
		Flounder	≥I	7	7	171.9	71.4	42.9	-	-	-
		Herring (small)		854	87	90.5	95.4	0	-	-	-
		15-spined stickleback		2	2	106	50	0	-	-	-
		Sea trout		1	1	210	100	100	-	-	-

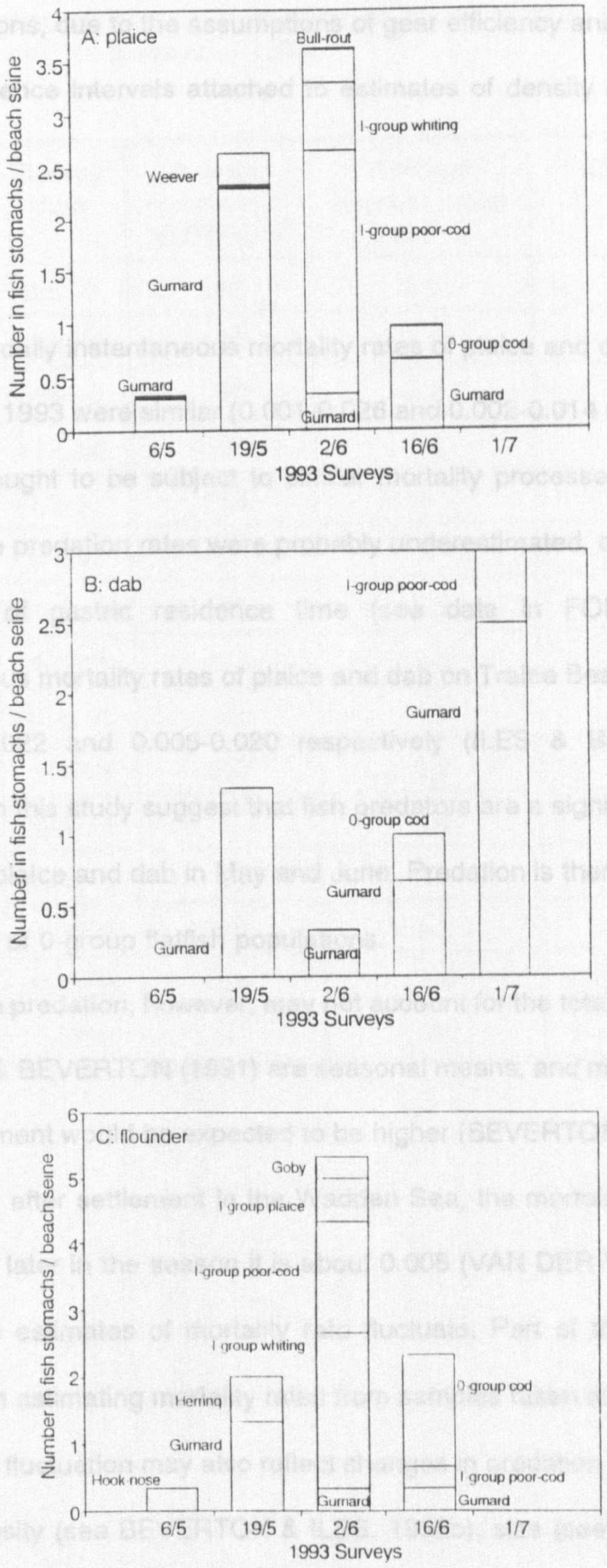


Figure 5.4: Index of importance of different fish species as predators of flatfishes in the five surveys of 1993. The index is the number of flatfishes found in fish stomachs per beach seine. A: Predators of plaice; B: Predators of dab; C: Predators of flounder.

approximations, due to the assumptions of gear efficiency and predation rate, and the large confidence intervals attached to estimates of density and predation rate (see Table 5.5).

DISCUSSION

The daily instantaneous mortality rates of plaice and dab due to fish predators in May-July 1993 were similar (0.001-0.026 and 0.002-0.014 respectively). Plaice and dab are thought to be subject to similar mortality processes (BEVERTON & ILES, 1992a). The predation rates were probably underestimated, due to the probable over-estimation of gastric residence time (see data in FOLKVORD, 1993). Daily instantaneous mortality rates of plaice and dab on Tralee Beach have been estimated at 0.007-0.022 and 0.005-0.020 respectively (ILES & BEVERTON, 1991). The estimates in this study suggest that fish predators are a significant source of mortality of juvenile plaice and dab in May and June. Predation is therefore a significant cause of mortality of 0-group flatfish populations.

Fish predation, however, may not account for the total mortality. The estimates from ILES & BEVERTON (1991) are seasonal means, and mortality rates at and soon after settlement would be expected to be higher (BEVERTON & ILES, 1992a). During and shortly after settlement in the Wadden Sea, the mortality rate of plaice is about 0.04, while later in the season it is about 0.005 (VAN DER VEER, 1986).

The estimates of mortality rate fluctuate. Part of this fluctuation will reflect problems in estimating mortality rates from samples taken at single times from limited areas. The fluctuation may also reflect changes in predation pressure with changes in flatfish density (see BEVERTON & ILES, 1992b), size (see Chapter 6), temperature (VAN DER VEER *et al.*, 1990) and predator abundance (e.g. VAN DER VEER & BERGMAN, 1987).

VAN DER VEER *et al.* (1991) estimated the total daily instantaneous mortality rate of flounder at 0.08. The mortality rates of flounder due to fish predation estimated

Table 5.4: Estimates of daily instantaneous mortality rates of flatfishes due to fish predators for the five surveys of 1993.

Species	Survey date	Average density No/1000 m^2	Average number eaten /1000 m^2	Daily instantaneous mortality rate
Plaice	6/5/93	283	0.6	0.002
	19/5/93	179	4.6	0.026
	2/6/93	656	6.3	0.010
	16/6/93	1296	1.7	0.001
	1/7/93	756	0	0
Dab	6/5/93	0	0	-
	19/5/93	0	2.3	-
	2/6/93	283	0.6	0.002
	16/6/93	209	1.7	0.008
	1/7/93	387	5.2	0.014
Flounder	6/5/93	0	0.6	-
	19/5/93	13	3.4	0.315
	2/6/93	156	9.2	0.061
	16/6/93	37	4.0	0.115
	1/7/93	0	0	-

Table 5.5: Estimates of mean size, density and number eaten per beach seine, of flatfishes in the five surveys of 1993.

Species	Survey date	Mean TL (mm) ±95% C.I.	Mean density* (m^{-2}) ±95% C.I.	Mean predation rate (no. in fish stomachs/ beach seine) ±95% C.I.
Plaice	6/5/93	19.3±5.1	0.099±0.179	0.33±1.17
	19/5/93	20.1	0.063	2.67±3.10
	2/6/93	25.9±3.8	0.229±0.186	3.67±3.10
	16/6/93	28.9±6.1	0.454±0.206	1.00±0.00
	1/7/93	41.8±1.6	0.265±0.176	0
Dab	6/5/93	-	-	0
	19/5/93	-	-	1.33±3.10
	2/6/93	17.4±1.3	0.099±0.152	0.33±1.17
	16/6/93	19.7±2.1	0.073±0.034	1.00±2.03
	1/7/93	26.4±2.4	0.135±0.106	3.00±17.97
Flounder	6/5/93	-	-	0.33±1.17
	19/5/93	11.0	0.004	2.00±7.03
	2/6/93	11.0±1.0	0.082±0.295	5.33±6.20
	16/6/93	11.8±2.5	0.013±0.018	2.33±6.52
	1/7/93	-	-	0

* Uncorrected for gear efficiency

in this study (0.06-0.32) were higher, and higher than those estimated for plaice and dab. This may be due to the density of the small flounder being underestimated in beam trawl samples due to mesh selection, or poor sorting efficiency. It is probable that the mortality rate of flounder is higher because of the small size (10-13 mm), as opposed to that of plaice and dab (≥14 mm). This is discussed further in Chapter 6. The very high mortality rate due to predation by fishes will probably combine with a high mortality rate from crustacean predators, and may explain why no flounder >13 mm were recorded in beam trawl samples. The use of low salinity areas as nurseries by 0-group flounder (KERSTAN, 1991) may provide a refuge from many "marine" predators.

I-group grey gurnard were the predominant fish predator of 0-group plaice and dab on Tralee beach in 1993. Similarly the I-group gadoids (whiting and poor-cod) were important predators in 1992 and 1993. These three species have not previously been quoted as predators of 0-group flatfishes on nursery grounds. Grey gurnards have recently been identified as important consumers of pre-recruits of commercial fish species in the North Sea (DE GEE & KIKKERT, 1993). I-group cod have been recorded as predators of plaice in fjordic nurseries (PIHL, 1982), but have not been recorded from Tralee.

The fishes usually quoted as predators of plaice, i.e. 0- and I-group cod, I- and II-group plaice, flounder, turbot *Scophthalmus maximus*, dab and sole *Solea solea*, lesser weever, hook-nose, goby, dragonettes *Callionymus spp.* and angler *Lophius piscatorius* (RILEY & CORLETT, 1966; MACER, 1967; EDWARDS & STEELE, 1968; LOCKWOOD, 1972; PIHL, 1982), were either not present, less important, or fed more on flounder. The major fish predators of plaice therefore differ between nurseries, as suggested by EDWARDS & STEELE (1968).

In mid May (survey 2) 1993, the stomachs of two herring contained flounder still undergoing metamorphosis. Large numbers of herring were caught in early May 1993 (Table 5.3), but unfortunately were not retained for examination. Juvenile clupeids are often found inshore in shallow water (BLAXTER & HUNTER, 1982). Then may then predate upon flatfish larvae recruiting to nurseries, in a similar way to coelenterates that feed on larval plaice and flounder recruiting to the Wadden Sea nursery (VAN DER VEER, 1985).

I-group gurnards and gadoids were the major predators of plaice on Tralee. Predation is, to a large extent, controlled by the relative sizes of both predator and prey (see Chapter 6). 0-group grey gurnard, whiting and poor-cod appear to be too small to predate plaice (Table 5.3). However, if there is a sufficient overlap in sizes, 0-group fish may eat 0-group flatfishes as shown by the finding that 0-group cod ate plaice, dab and flounder and 0-group whiting ate dab in 1992.

Gadoids, particularly 0-group cod, had been suspected as major predators of 0-group plaice in a fjordic environment. This study showed that in 1992 and 1993 0-group gadoids were not significant predators of plaice at Tralee. GIBSON (1973) suggested that the tidal migration of plaice at night might provide a spatial separation of plaice and cod. However, such a spatial refuge seems unlikely. Cod were caught close to shore with the beach seine and beam trawl. A turbot was recorded from a cod stomach (Table 5.2) indicating feeding in very shallow water because of the depth distribution of turbot (see GIBSON, 1973). In addition underwater television observations have shown that gadoids move inshore at night at Tralee (BURROWS *et al.*, 1994).

The importance of the 0-group gadoids as predators of dab changed through the season in 1992. Cod recruited to Tralee in May and June and ate many dab. However numbers decreased as did the occurrence of flatfish. Whiting recruited later and although the occurrence of dabs in their stomachs was low, the large numbers of whiting meant they were probably a significant predator. Saithe have been recorded as a predator of flatfishes (RILEY & CORLETT, 1966), and although they ate fish, there was no evidence of predation on flatfish. 0-group poor-cod can be dismissed as a predator of flatfishes, as in both 1992 and 1993 0-group poor-cod seemed to recruit too late and were too small to eat dab or flounder.

Predation on 0-group plaice by fishes had apparently ceased by early July 1993 (Table 5.3; Figure 5.4). The plaice had seemingly out-grown the fish predators assumed to be responsible for mortality after 1 July (VAN DER VEER *et al.,* 1990), and potential crustacean predators (see VAN DER VEER & BERGMAN, 1987). It is therefore unclear as to whether mortality from predation does occur during and after July. The mark and recapture experiment in Port Erin Bay (Chapter 4) suggested that the decrease in population size after 1 July is real, and not just an artefact of decreasing gear-efficiency as the plaice grow. The only remaining potential predators are larger fish e.g. thornback ray *Raja clavata* (EDWARDS & STEELE, 1968), bass *Dicentrarchus labrax* (VAN DER VEER *et al.*, 1990) and salmonids, sea-birds (LOCKWOOD, 1972; BERGHAHN *et al.*, 1993; BAILEY, 1994) and mammals (e.g. seals and sea otters). BAILEY (1994) suggested that sea-birds are important predators and would be a valuable subject for study.

Density-dependent mortality

VAN DER VEER & BERGMAN (1987) proposed that in open nurseries such as Tralee, density-dependent mortality, in contrast to the Wadden Sea, was not restricted to newly settled plaice, and was therefore caused by fish predators. BERGMAN *et al.* (1988) assumed that because of seasonal migratory habits of predatory fishes, there would be large differences in predator abundance between years which would lead to variability in predation and hence increase, rather than decrease, variability in year-class strength. VAN DER VEER *et al.* (1990) suggested that despite causing mortality, predatory fishes would not affect the variation in year class strength. I-group gurnards and gadoids would appear to be resident in the nursery, lingering from recruitment in the previous year, and cannot be considered migratory. The number of plaice eaten will depend primarily upon the strength of the previous year-class of these species, so mortality will be density-independent.

LOCKWOOD (1980) suggested that certain fish predators would cause density-dependent mortality of 0-group plaice by migrating to nurseries in years of high plaice density. R. GIBSON (*pers. comm.*) provided data on the abundance of 0-group cod at Tralee (1986-1989, see Table 5.6), and indices of abundance of 0-group plaice and dab at Tralee were taken from ILES & BEVERTON (1991). There appears to be a positive relationship between cod and plaice numbers (r_s=0.8, n=4, 0.25>p>0.1). A positive correlation is not, however, evidence for a migration response, but probably the result of similar processes affecting the survival in the pelagic phase of both species, and/or advection to the nursery ground. GIBSON *et al.* (1993) found that 0-group plaice, cod, hook-nose and bull-rout showed similar patterns in inter-annual abundance at Tralee. If cod were to show a migration response to flatfish density, then a closer correlation would be expected for dab as they are a more reliable and prevalent food item. However, the correlation is less significant (r_s=0.4, n=4, p>0.25).

For fish predators to migrate to areas of high plaice density, plaice would have to form a significant part of the diet. The abundant fishes had a low occurrence of plaice in their stomachs in this study. VAN DER VEER & BERGMAN (1987) suggested that the apparent density-dependent mortality of newly-settled 0-group plaice was, in part, due to a migration of predatory shrimp to areas of high plaice density. However, the occurrence of plaice in shrimp was low (6%). It is difficult to envisage how shrimps would show a migration response to the abundance of a food item of such seemingly limited importance. The apparent immigration could have been due to other environmental variables.

Only in the studies of MACER (1967) and EDWARDS & STEELE (1968) has there been a high occurrence (20% and 50%) of 0-group plaice in predators (I-group plaice and 0-group cod) stomachs. Evidence for density-dependent predation on nursery grounds should therefore be sought from the nurseries used in these studies (see BAILEY, 1994).

Table 5.6: Indices of abundance of 0-group cod, plaice and flounder on Tralee beach for years 1986-1989. Index for cod is total number caught on Tralee beach in trawl samples (R. GIBSON, *pers. comm.*). Indices for plaice and dab are maximum density (D_{MAX}) recorded (from ILES & BEVERTON, 1991).

Year	Total number of cod caught	D_{MAX} plaice (No./ 1000 m^2)	D_{MAX} dab (No./ 1000 m^2)
1986	20	3547	87
1987	0	33	111
1988	1	211	275
1989	58	1586	286

Chapter 6:

The importance of prey size and predator size to predation on 0-group flatfishes, with particular reference to 0-group cod.

INTRODUCTION

Body size greatly affects vulnerability to predation and hence mortality (see GULLAND, 1987). Crustaceans and fishes are thought to be the main predators of 0-group flatfishes on nursery grounds (see VAN DER VEER *et al.*, 1990). VAN DER VEER & BERGMAN (1987) showed that predation by shrimp *Crangon crangon* on 0-group plaice was highly dependent upon the sizes of both prey and predator. Such size relationships between 0-group flatfishes and their fish predators have not been examined. Chapter 5 described a study of fish predation on 0-group flatfishes, and fishes were shown to be a significant cause of mortality. The material provided an opportunity to analyze the effect of flatfish size on vulnerability to predation.

EDWARDS & STEELE (1968) found that 0-group cod were the major predator of 0-group plaice on a Scottish fjordic nursery. However, cod were not an important predator of plaice at Tralee in either 1992 or 1993 (Chapter 5). It is well documented that the size of cod influences the size of food, in the larval (ECONOMOU, 1991a), juvenile pelagic (ROBB & HISLOP, 1980), juvenile demersal (HAWKINS *et al.*, 1985) and adult (DAAN, 1973; DEKKER, 1983; DAAN *et al.*, 1990; KIKKERT, 1993) stages. It was hypothesised that predator-prey size relationships would affect predation by 0-group cod on 0-group flatfishes, and such relationships were examined from field samples.

MATERIALS AND METHODS

0-group flatfish remains, identified as plaice, dab or flounder, were recovered from the stomachs of predatory fishes caught from Tralee nursery ground (see Chapter 5). It was rarely possible to obtain a direct measurement of TL of the flatfish remains due to digestion. Calcified tissue had been stained (see Chapter 5), so parts of the skeleton were measured using the eyepiece graticule of a dissecting microscope.

Relationships for predicting TL from the lengths of parts of the skeleton were derived from intact fish caught from Tralee which had been preserved in 4%

formaldehyde in sea water. The total lengths of 54 plaice (14-40 mm), 45 dab (15-41 mm) and 23 flounder (10-13 mm) were measured in the same way as the preserved samples of the flatfish populations (see Chapter 5). The fish were then stained and cleared and parts of the skeleton measured in the same way as the flatfishes recovered from fish stomachs (see Chapter 3).

The relationships of TL with the lengths of various parts of the skeleton and standard length (SL) were derived by predictive regression for plaice and dab. Due to the restricted size range of flounder available, mean ratios were used rather than regression relationships, but prediction was only required within this size range. Skull length (*SkL*) was measured ventrally, from the tip of the upper jaw to the end of the skull above the vertebral column. $VL_{i\text{-}j}$ refers to the length of the vertebral column from vertebra *i* to *j*, and *T* refers to the terminal vertebra. Abdominal vertebrae were measured from the second vertebra as the first vertebra was often concealed behind the operculum.

When estimating TL of the flatfish remains, the relationship with the smallest multiplying value was used. This was to minimise any amplification of inaccuracies in measurements. Measurement of TL before treatment with potassium hydroxide eliminated the problem of any changes in length during the staining and clearing process. The relationships are therefore not valid for fish which have not been processed in such a manner.

The lengths of flatfishes eaten were compared using Mann-Whitney U-tests with the lengths of flatfishes available to the predators, as recorded in beam trawl samples.

RESULTS

The relationships used for predicting TL of flatfishes recovered from fish stomachs, are given below.

Plaice

$$TL=4.112 \times SkL^{1.078} \quad (n=54,\ R^2=0.991)$$

$$TL=5.952 \times VL_{2\text{-}13}^{0.991} \quad (n=54,\ R^2=0.988)$$

$$TL=6.597 \times VL_{14\text{-}23}^{1.029} \quad (n=54,\ R^2=0.991)$$

$$TL=1.680 \times VL_{2\text{-}T}^{0.987} \quad (n=54,\ R^2=0.995)$$

$$TL=1.125 \times SL^{1.008} \quad (n=54,\ R^2=0.997)$$

Dab

$$TL = 3.92 \times SkL^{1.13} \quad (n=45,\ R^2=0.983)$$

$$TL = 10.71 \times VL_{2\text{-}7}^{1.04} \quad (n=45,\ R^2=0.989)$$

$$TL = 6.93 \times VL_{2\text{-}10}^{1.03} \quad (n=45,\ R^2=0.991)$$

$$TL = 7.87 \times VL_{11\text{-}18}^{1.03} \quad (n=45,\ R^2=0.982)$$

$$TL = 6.25 \times VL_{11\text{-}20}^{1.03} \quad (n=45,\ R^2=0.980)$$

$$TL = 1.57 \times VL_{2\text{-}T}^{1.02} \quad (n=45,\ R^2=0.990)$$

$$TL = 1.02 \times SL^{1.05} \quad (n=45,\ R^2=0.996)$$

Flounder

$$TL=4.219 \times SkL \quad (n=23)$$

$$TL=5.988 \times VL_{2\text{-}11} \quad (n=23)$$

$$TL=5.618 \times VL_{12\text{-}21} \quad (n=23)$$

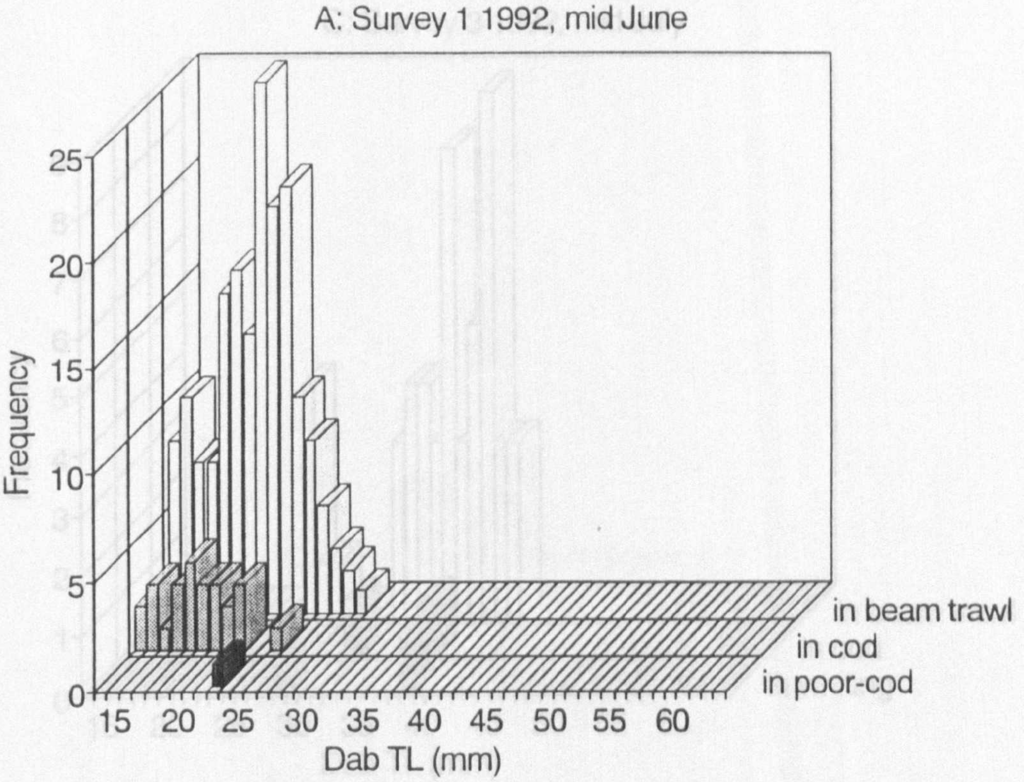
$$TL=1.650 \times VL_{2\text{-}T} \quad (n=23)$$

$$TL=1.142 \times SL \quad (n=23)$$

Size of flatfishes eaten

The fish predators apparently concentrated feeding upon the smaller size-classes of dab in 1992 (Figure 6.1) and plaice and dab in 1993 (Figures 6.2, 6.3). There was little evidence for predation on the smaller size classes of flounder, over the restricted size range (Figure 6.4).

The length frequency distributions of plaice in beam trawl catches and in stomachs were significantly different for samples taken on 19/5/93 ($p=0.0017$) and 2/6/93 ($p=0.0027$), the plaice in stomachs being smaller. Similarly, the length frequency



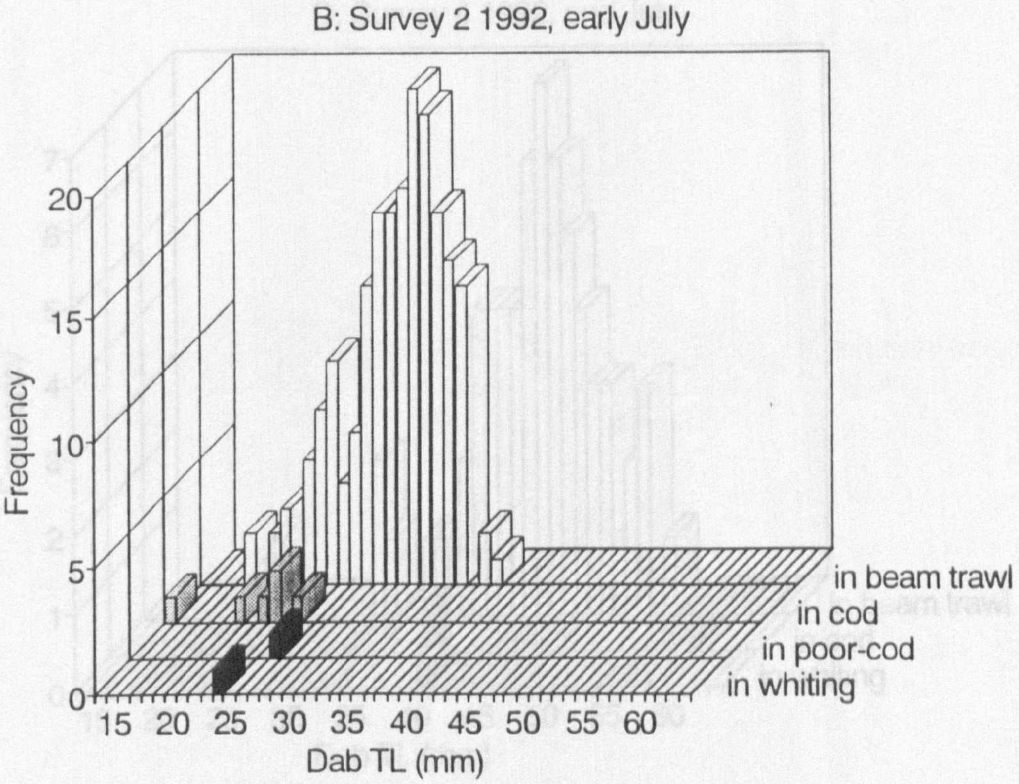
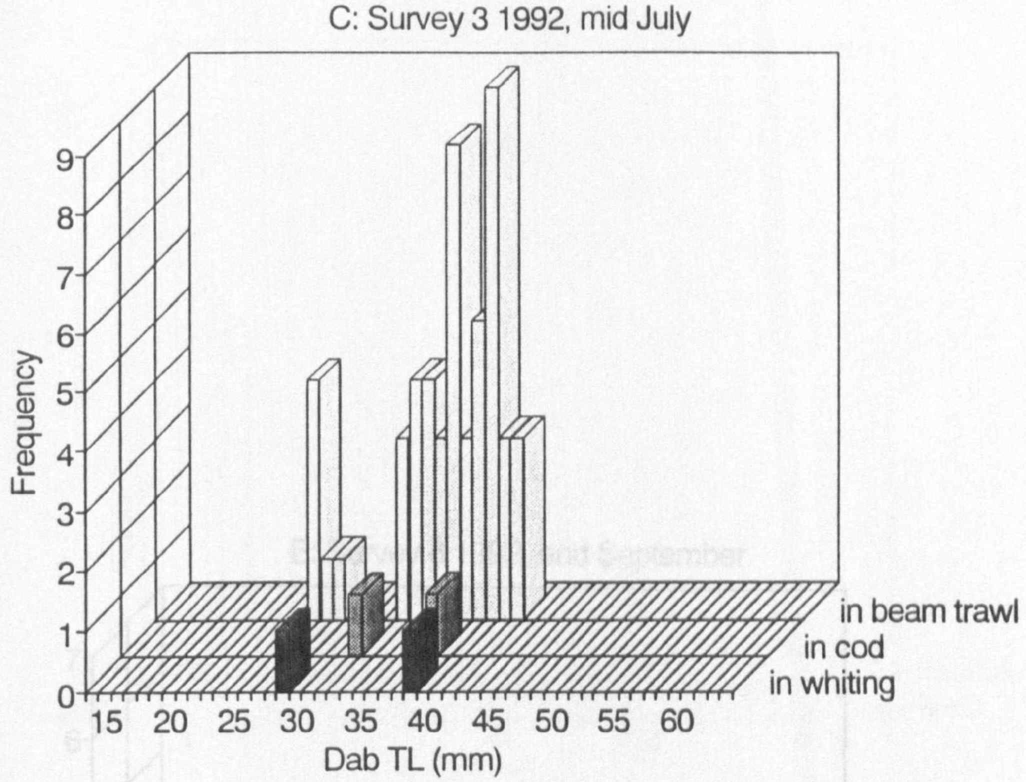


Figure 6.1: Length frequency distributions of dabs recovered from gadoid stomachs, and dab population on Tralee beach in 1992. A: 18/6/92; B: 1/7/92. Length distributions of dab population from beam trawl samples.


C: Survey 3 1992, mid July

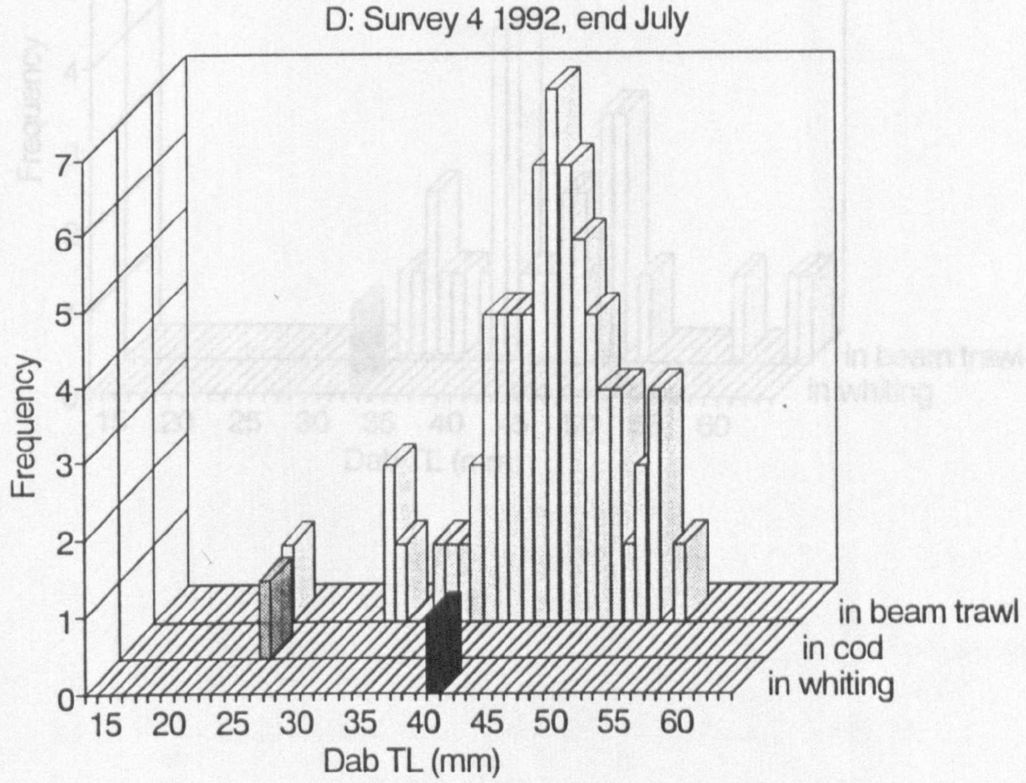

D: Survey 4 1992, end July

Figure 6.1 (continued): Length frequency distributions of dabs recovered from gadoid stomachs, and dab population on Tralee beach in 1992. C: 14/7/92; D: 2/7/92. Length distributions of dab population from beam trawl samples.

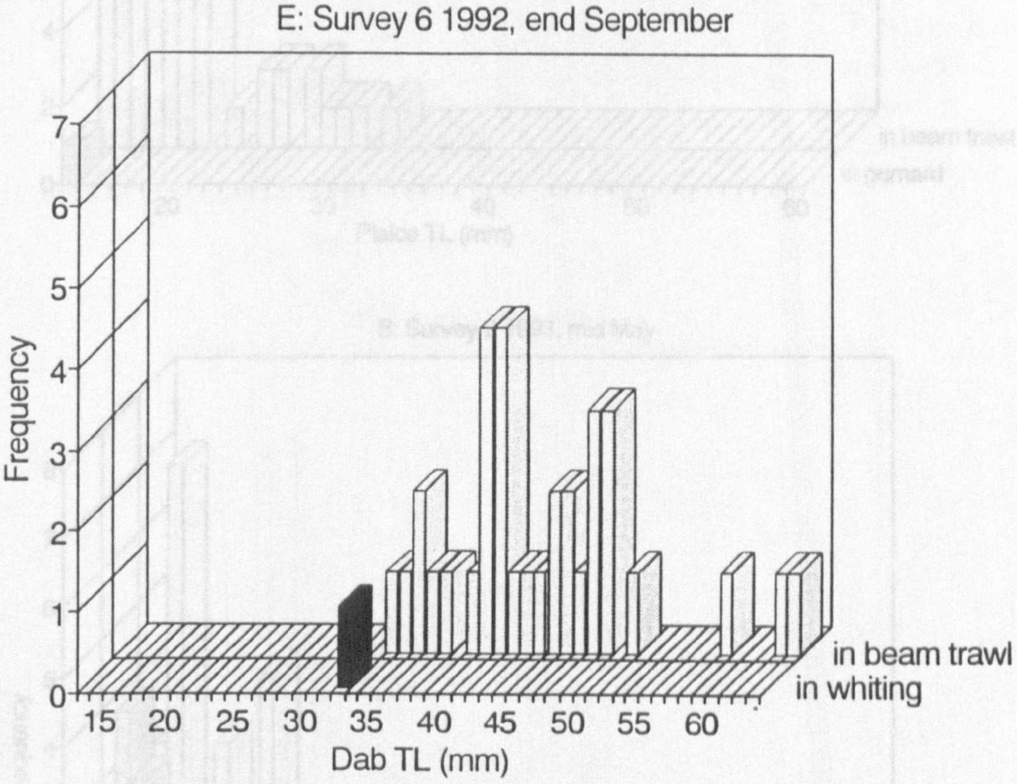
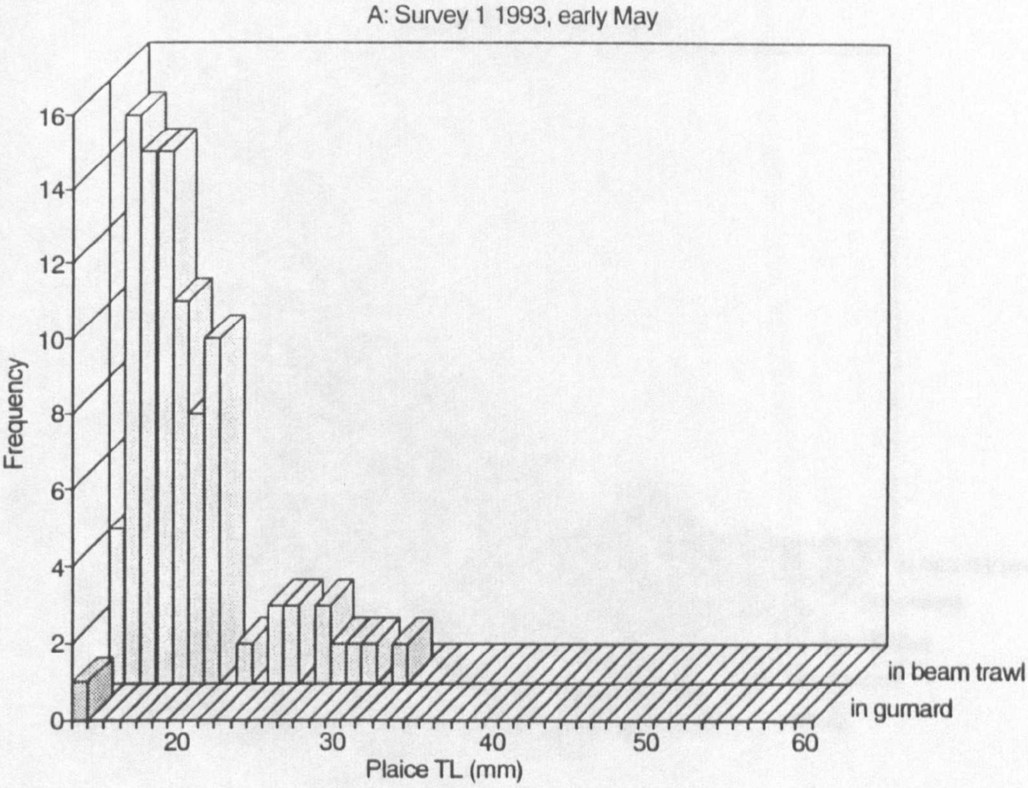


Figure 6.1 (continued): Length frequency distributions of dabs recovered from gadoid stomachs, and dab population on Tralee beach in 1992. E: 24/9/92. Length distributions of dab population from beam trawl samples.



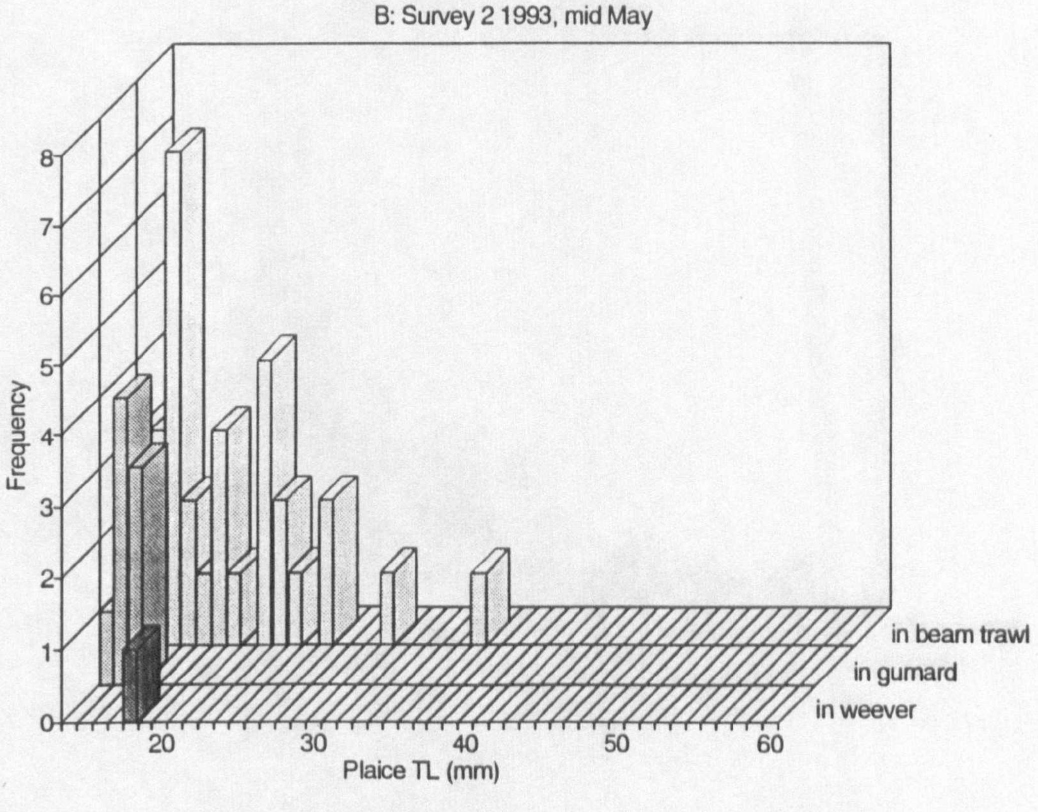
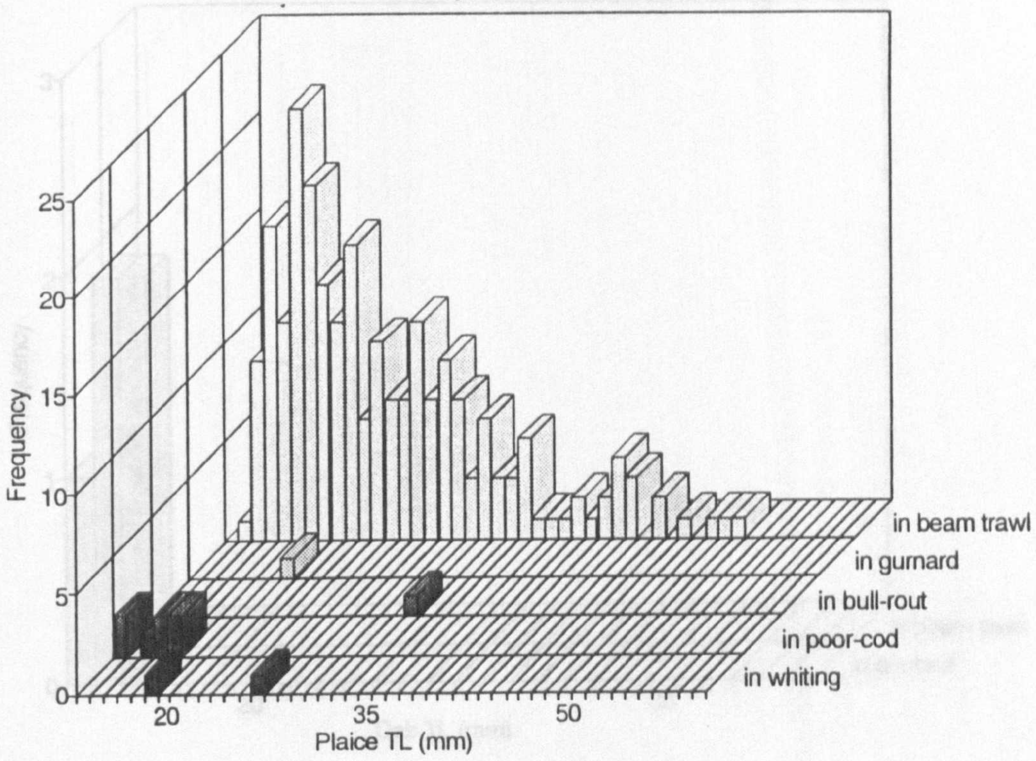


Figure 6.2: Length frequency distributions of plaice recovered from fish stomachs, and plaice population on Tralee beach in 1993. A: 6/5/93; B: 19/5/93. Length distributions of plaice population from beam trawl samples.

C: Survey 3 1993, early June



D: Survey 4 1993, mid June

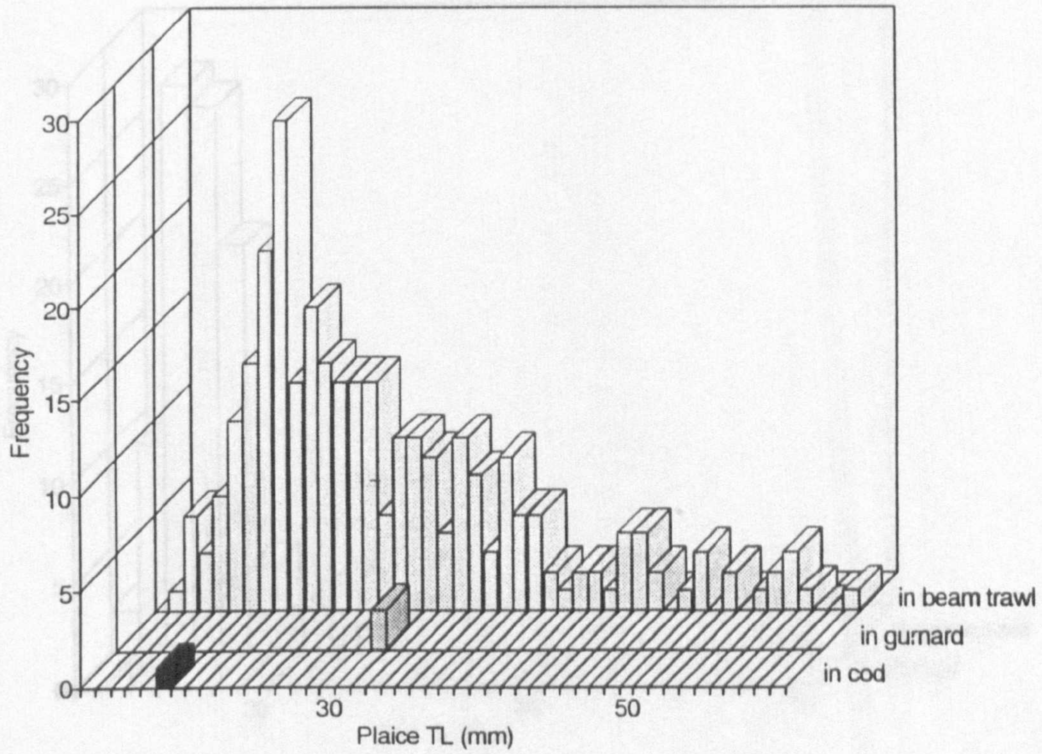
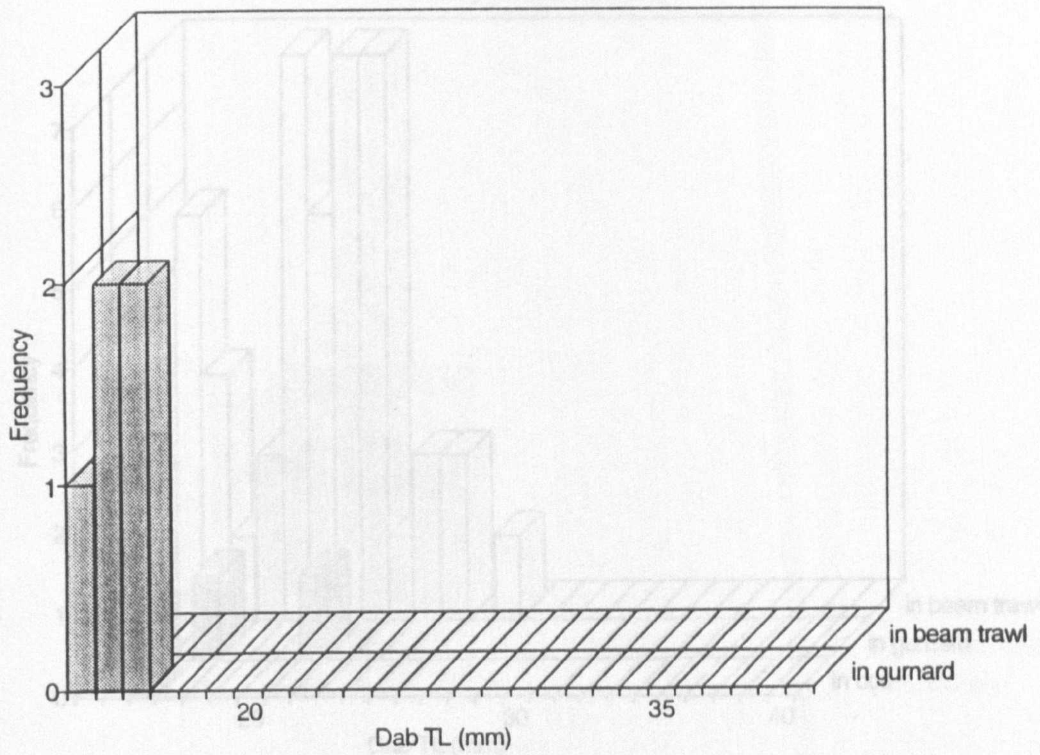
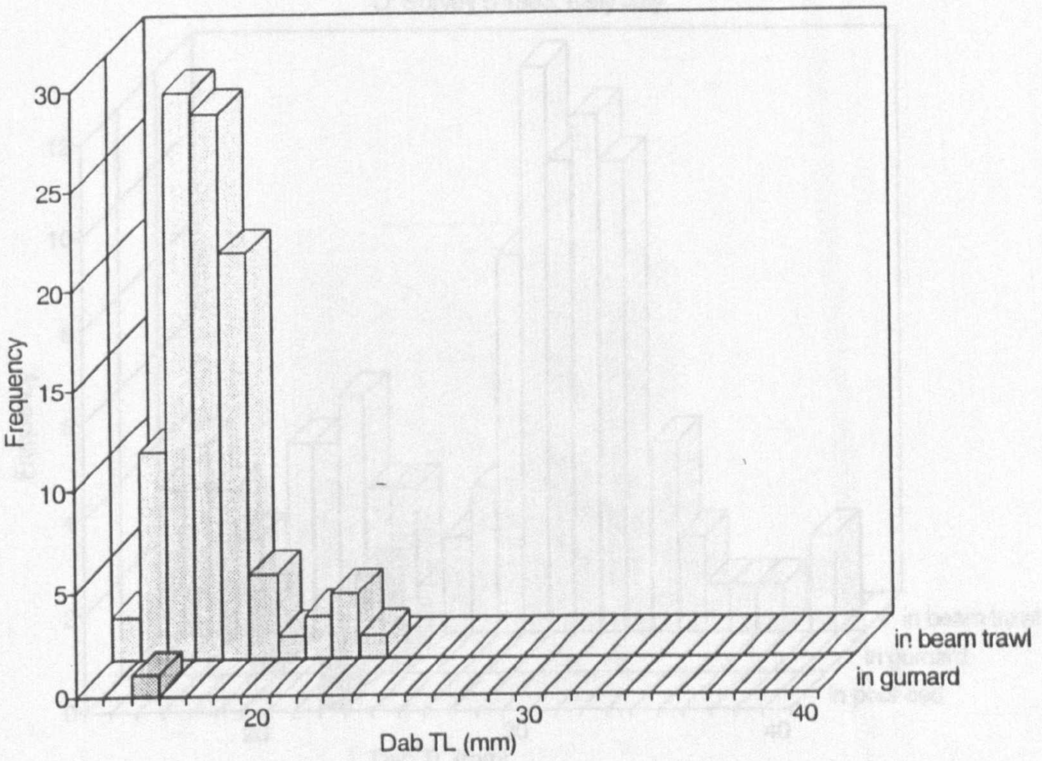


Figure 6.2 (continued): Length frequency distributions of plaice recovered from fish stomachs, and plaice population on Tralee beach in 1993. C: 2/6/93; D: 16/6/93. Length distributions of plaice population from beam trawl samples.

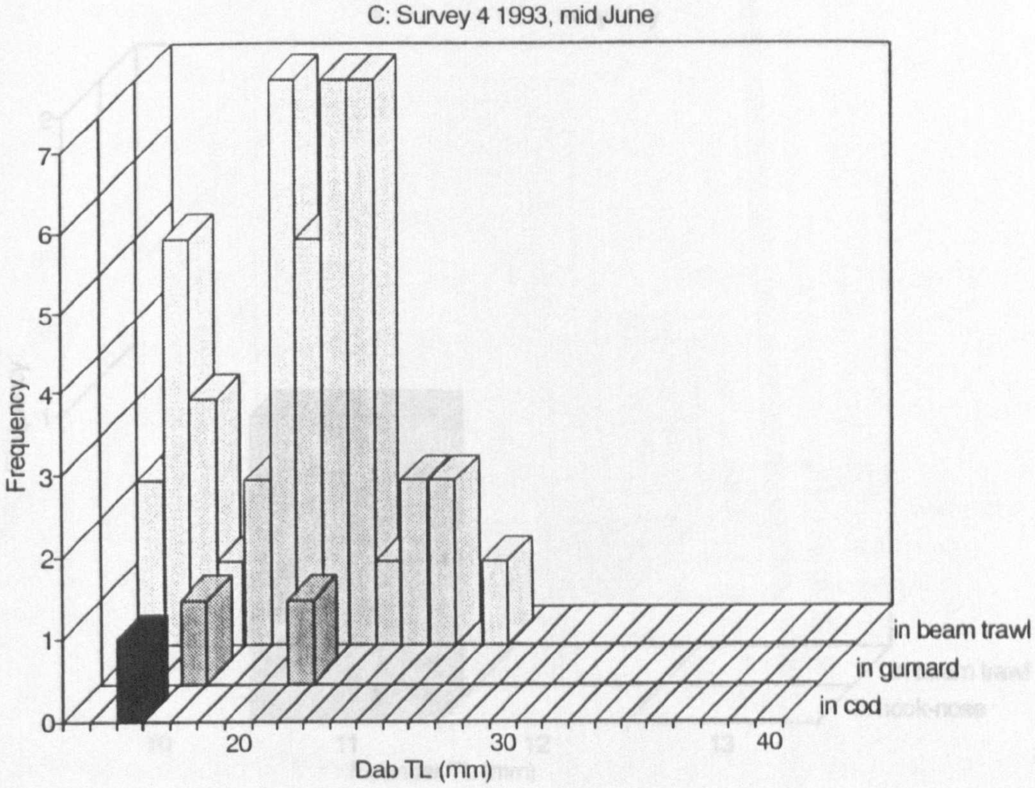


A: Survey 2 1993, mid May



B: Survey 3 1993, early June

Figure 6.3: Length frequency distributions of dab recovered from fish stomachs, and dab population on Tralee beach in 1993. A: 19/5/93; B: 2/6/93. Length distributions of dab population from beam trawl samples.



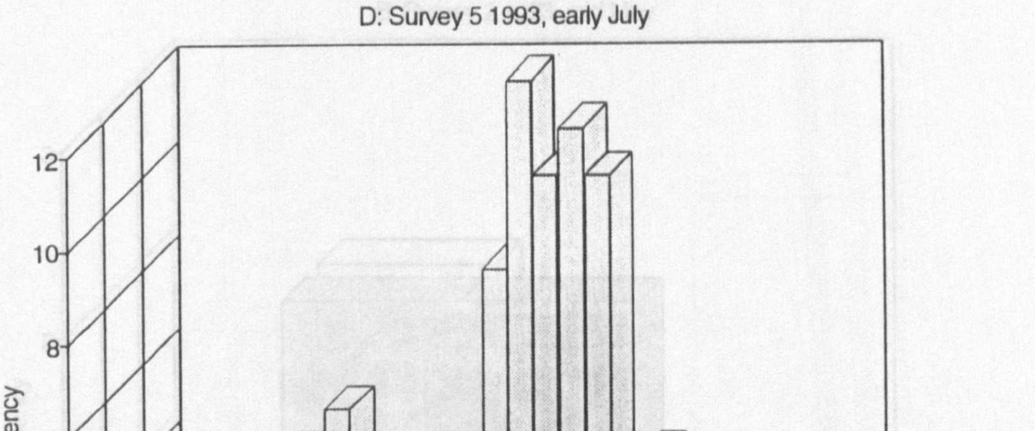
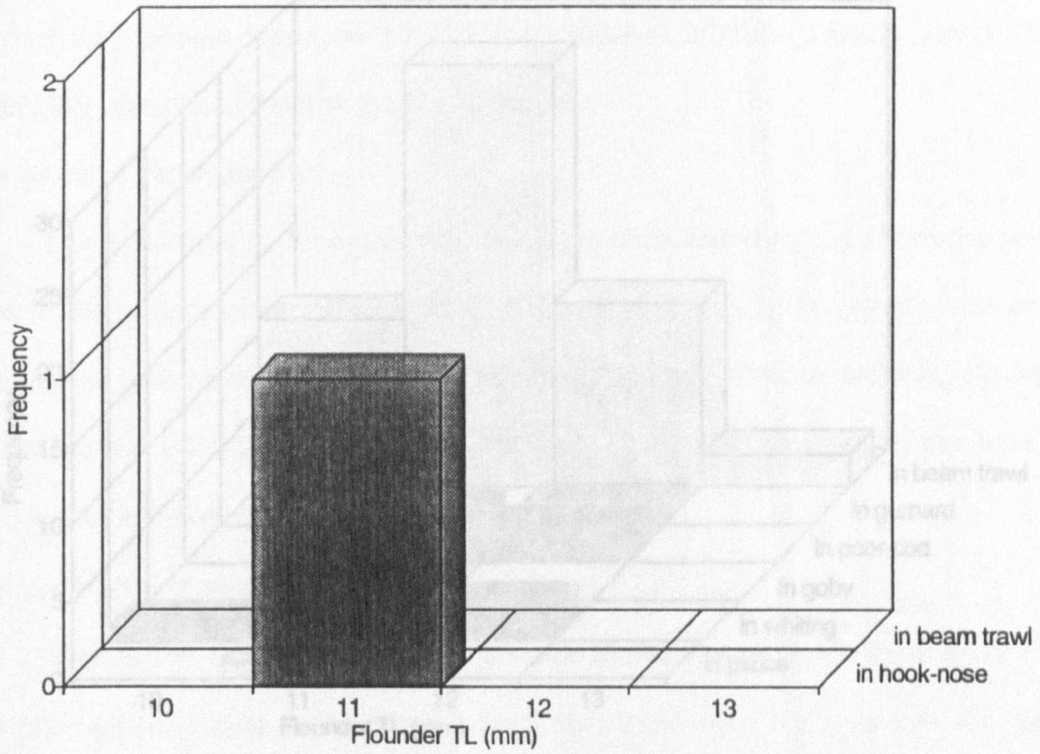


Figure 6.3 (continued): Length frequency distributions of dab recovered from fish stomachs, and dab population on Tralee beach in 1993. C: 16/6/93; D: 1/7/93. Length distributions of dab population from beam trawl samples.

A: Survey 1 1993, early May



B: Survey 2 1993, mid May

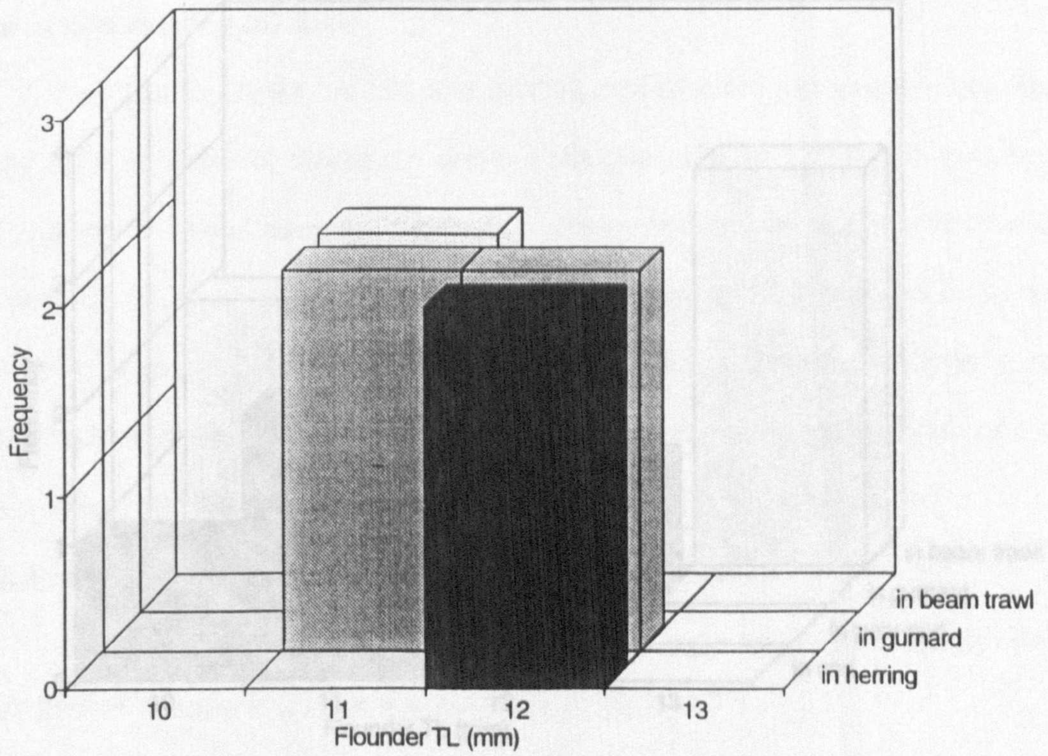
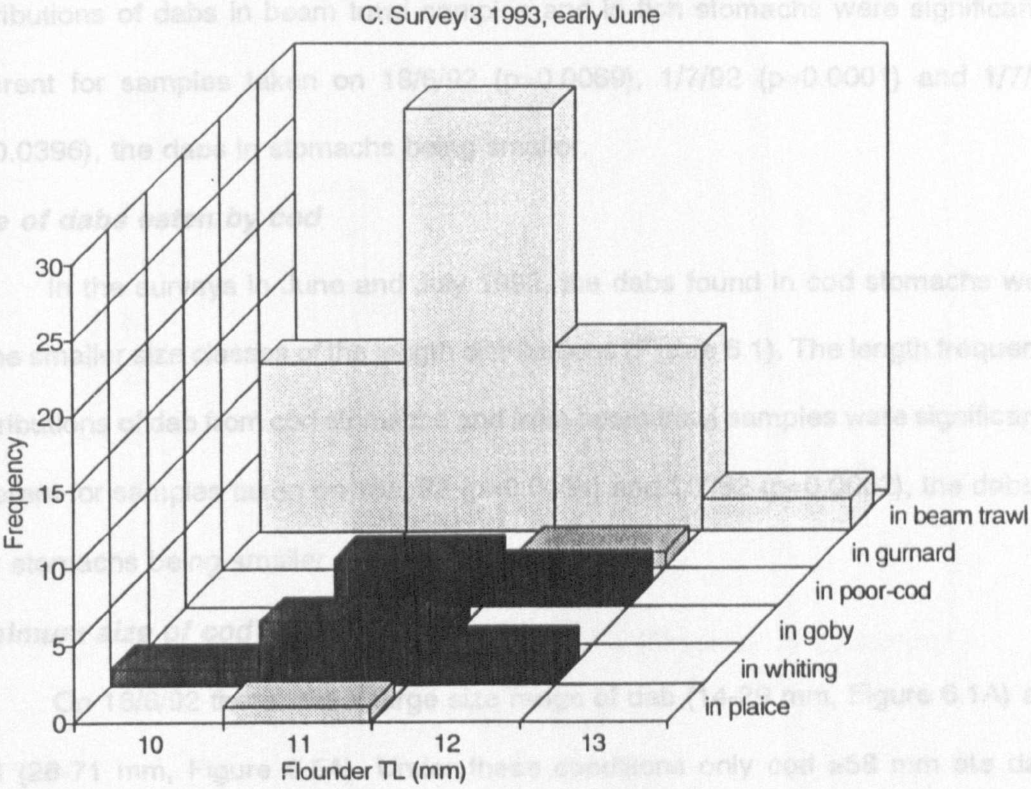


Figure 6.4: Length frequency distributions of flounder recovered from fish stomachs, and flounder population on Tralee beach in 1993. A: 6/5/93; B: 19/5/93. Length distributions of flounder population from beam trawl samples.



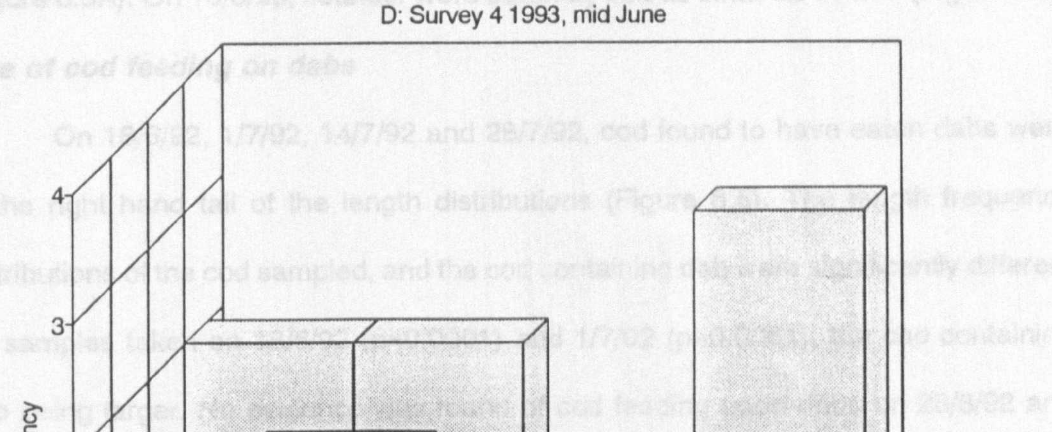


Figure 6.4 (continued): Length frequency distributions of flounder recovered from fish stomachs, and flounder population on Tralee beach in 1993. C: 2/6/93; D: 16/6/93. Length distributions of flounder population from beam trawl samples.

distributions of dabs in beam trawl samples and in fish stomachs were significantly different for samples taken on 18/6/92 ($p=0.0069$), 1/7/92 ($p=0.0001$) and 1/7/93 ($p=0.0396$), the dabs in stomachs being smaller.

Size of dabs eaten by cod

In the surveys in June and July 1992, the dabs found in cod stomachs were in the smaller size classes of the length distributions (Figure 6.1). The length frequency distributions of dab from cod stomachs and from beam trawl samples were significantly different for samples taken on 18/6/92 ($p=0.0034$) and 1/7/92 ($p=0.0002$), the dabs in cod stomachs being smaller.

Minimum size of cod eating flatfish

On 18/6/92 there was a large size range of dab (14-29 mm, Figure 6.1A) and cod (28-71 mm, Figure 6.5A). Under these conditions only cod ≥58 mm ate dabs (Figure 6.5A). On 16/6/93, flounder were eaten by cod as small as 51 mm (Figure 6.6).

Size of cod feeding on dabs

On 18/6/92, 1/7/92, 14/7/92 and 28/7/92, cod found to have eaten dabs were in the right hand tail of the length distributions (Figure 6.5). The length frequency distributions of the cod sampled, and the cod containing dab were significantly different for samples taken on 18/6/92 ($p=0.0001$) and 1/7/92 ($p=0.0061$), the cod containing dab being larger. No evidence was found of cod feeding upon dabs on 28/8/92 and 24/9/92. On 16/6/93, the single plaice and dab were found in cod in the right hand tail of the length distribution (Figure 6.6).

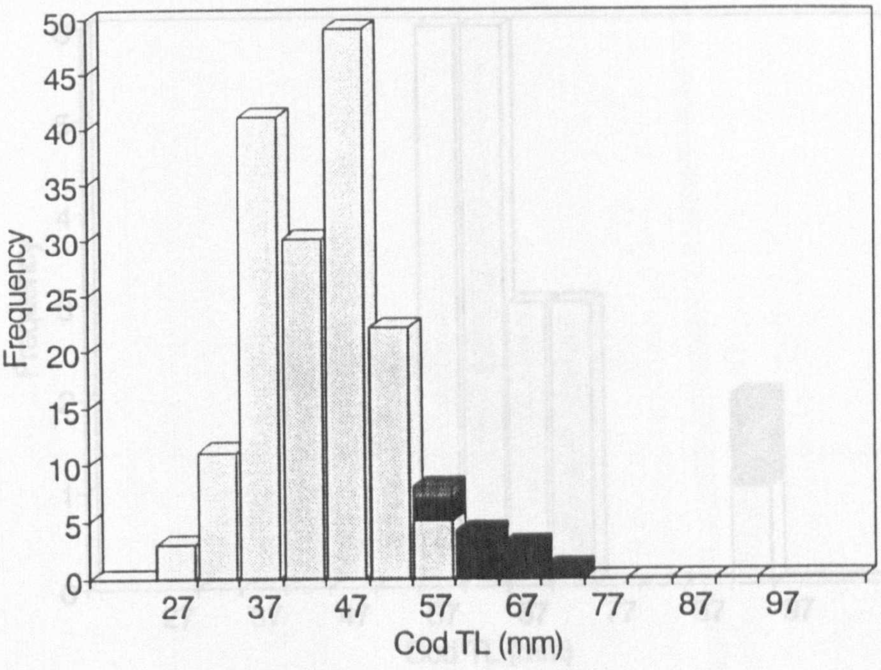
Relationship between cod size and number of dabs eaten

On 18/6/92, all cod ≥59 mm contained dabs. Larger cod were found with more dabs in their stomachs (Figure 6.7; $r_s=0.729$, $n=10$, $p<0.05$).

Relative lengths of the dab, plaice and cod populations in 1992

The ratio (Q_1:Q_3) of the lower quartile of the dab length distribution (Q_1) to the upper quartile of the cod population (Q_3), increased between 18/6/92 and 28/7/92 (Table 6.1). The smaller dabs were therefore apparently growing faster than the larger

A: Survey 1 1992, mid June.



B: Survey 2 1992, early July

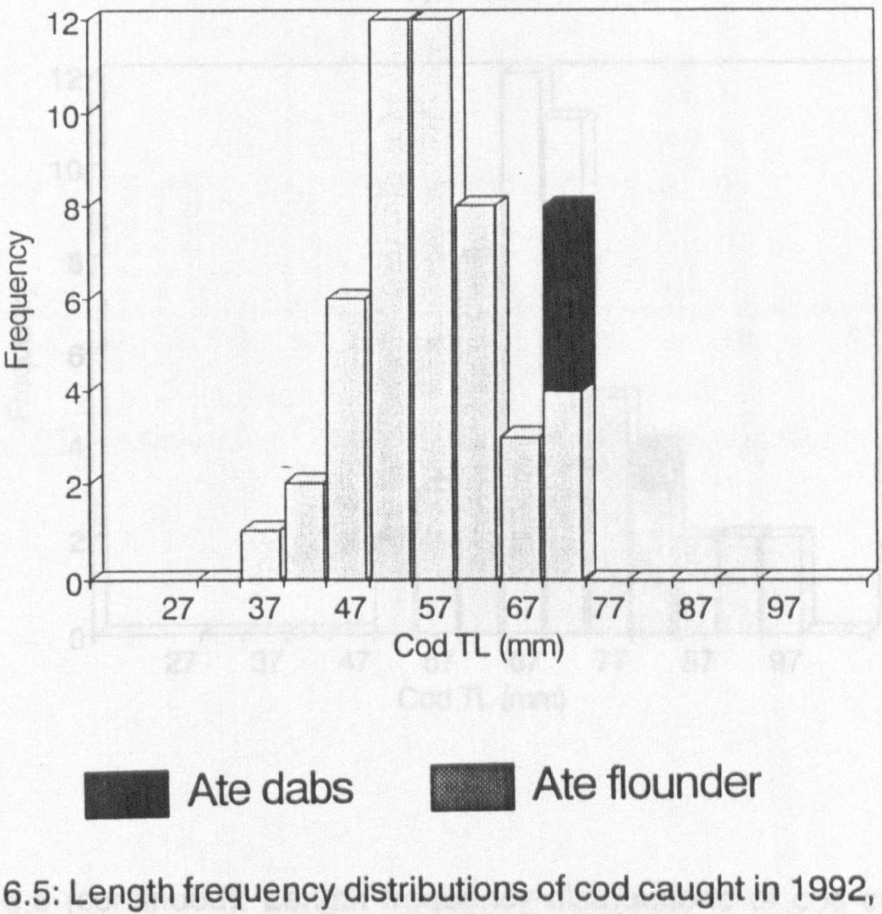
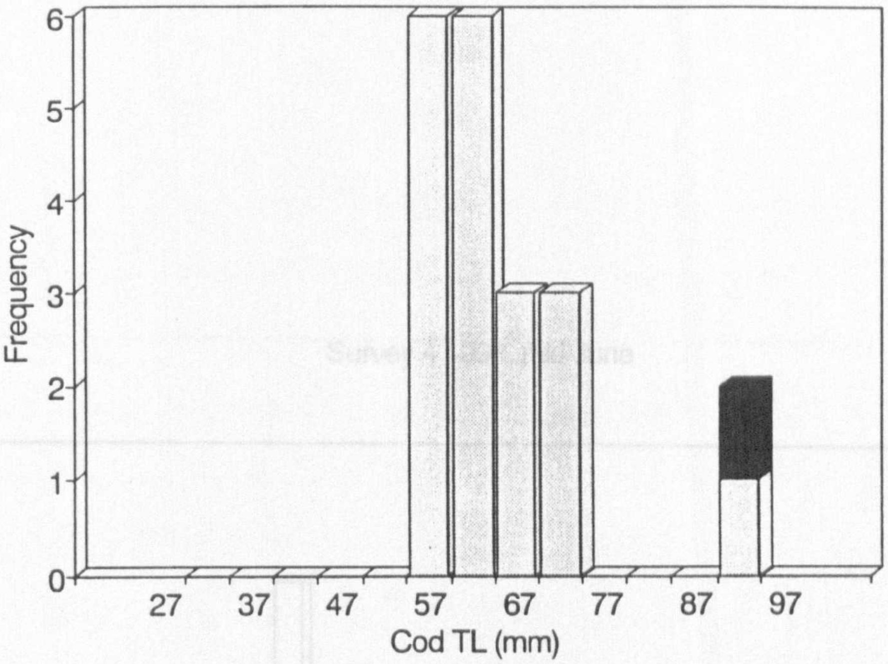


Figure 6.5: Length frequency distributions of cod caught in 1992, showing sizes eating flatfishes. A: 15 & 18/6/92; B: 1/7/92.

C: Survey 3 1992, mid-July



D: Survey 4 1992, end July

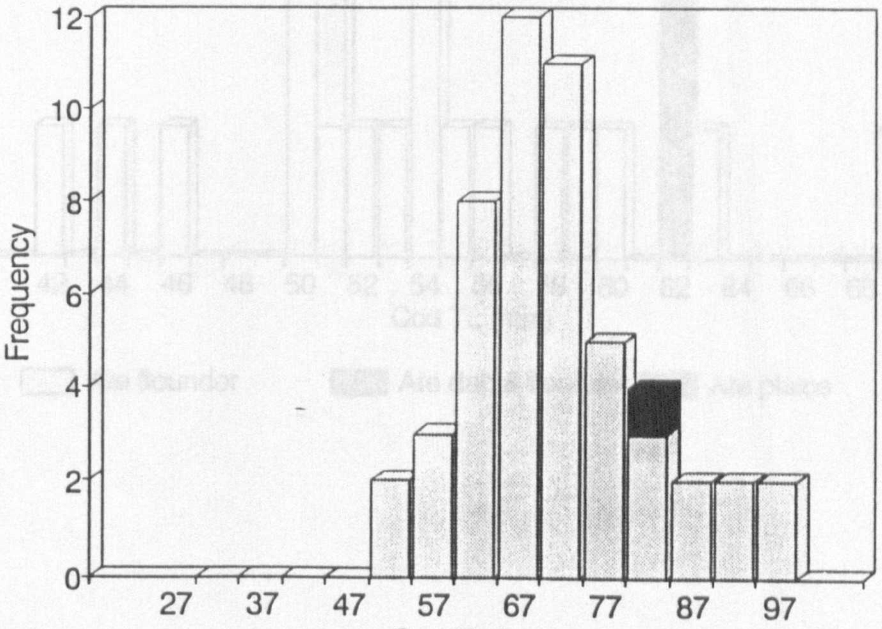


Figure 6.5 (continued): Length frequency distributions of cod caught in 1992, showing sizes eating flatfishes. C: 14/7/92; D: 28/7/92.

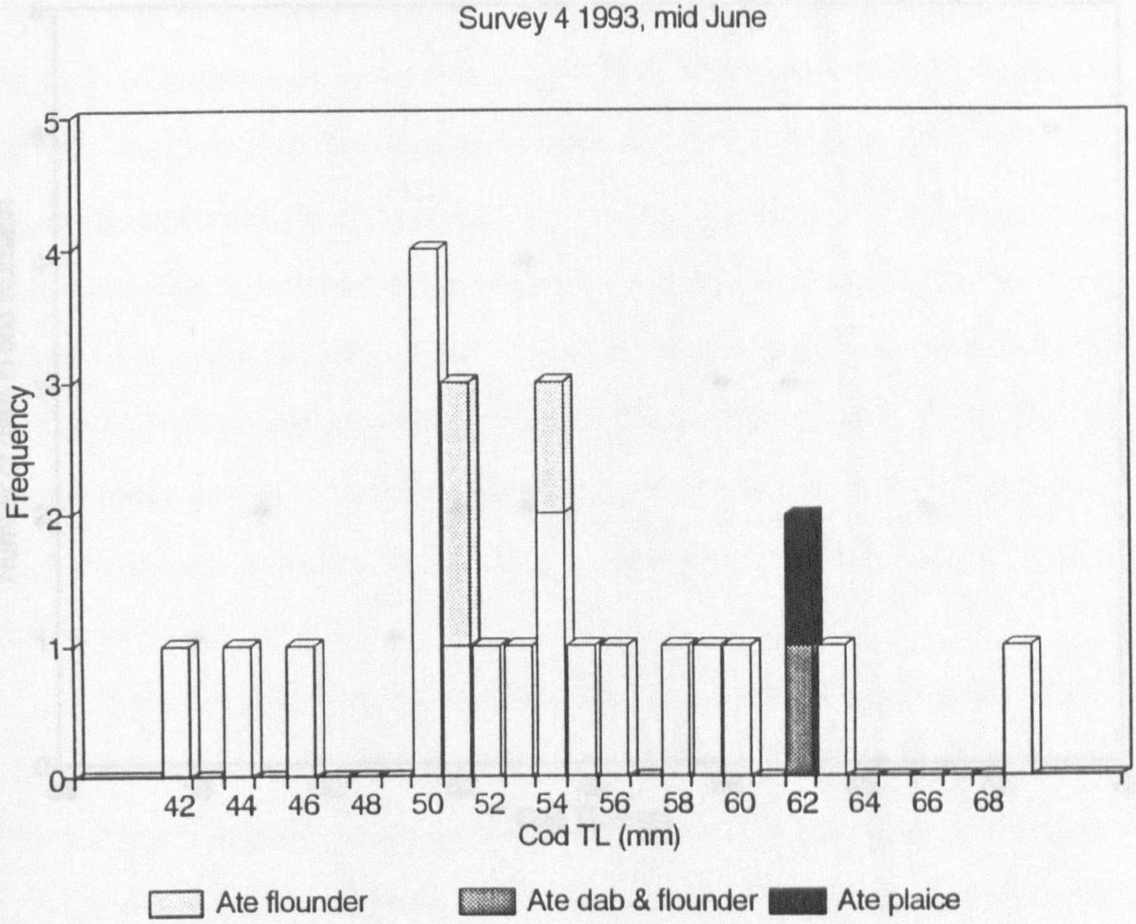


Figure 6.6: Length frequency distribution of cod caught on 16/6/93, showing sizes eating flatfishes.

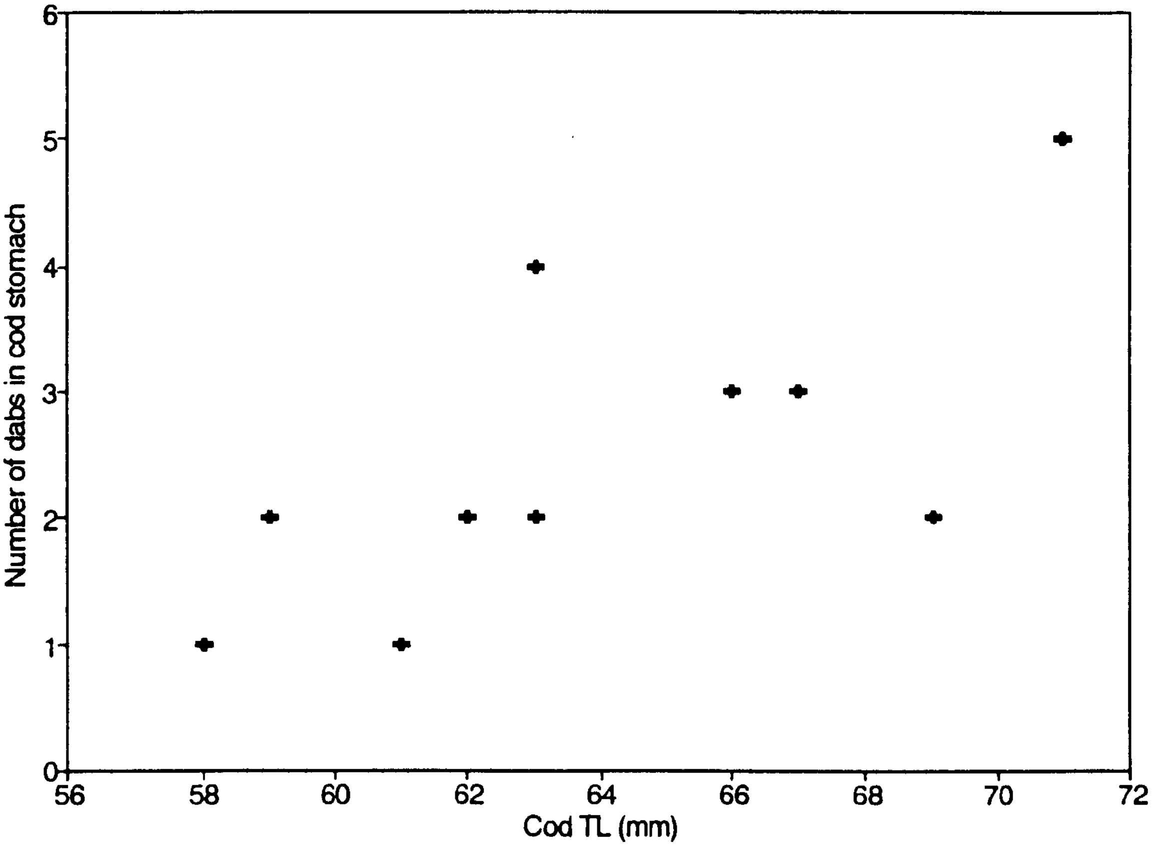


Figure 6.7: Number of dabs found in individual cod stomachs caught on 18/6/92.

cod. The Q_1 of the plaice population was always larger than that of the dabs, and the Q_1:Q_3 ratio for plaice:cod was high (Table 6.1).

DISCUSSION

Flatfish size greatly affected the predation rate on flatfishes (see Figures 6.8 & 6.9). Predation rates on plaice increased with an increase in density in 1993 (early May to early June), but then fell markedly as mean plaice size increased (mid June to early July), despite an increase in plaice density (Figure 6.9). Although the density of dab was lower than that of plaice in early July 1993, dab were eaten and plaice were not, presumably because of the smaller size of the dab (Figure 6.9). Despite low densities, flounder suffered high predation rates, presumably due to their small size (Figure 6.9). Flounder were subject to predation from a greater taxonomic range of predators (see Chapter 5), and a greater size range of predators, e.g. cod, than the larger plaice or dab. VAN DER VEER *et al.* (1991) noted that flounder suffered a higher mortality rate than plaice, and attributed this, in part, to a small size at settlement.

Selective predation on the smaller size classes of plaice was demonstrated in 1993, and on the smaller size classes of dab in 1992 and 1993. VAN DER VEER & BERGMAN (1987) demonstrated that shrimp ate smaller plaice, but size-selective predation on 0-group flatfishes by fishes has not previously been described in the field.

VAN DER VEER & BERGMAN (1987) showed that in the laboratory plaice >30 mm have a refuge in size from predation by shrimp *Crangon crangon*. Similar size relationships have been found for other crangonid shrimps predating juvenile pleuronectids (SEIKAI *et al.*, 1993; WITTING & ABLE, 1993). R. GIBSON (*pers. comm.*) has shown in laboratory experiments that shrimp *Crangon crangon* were more likely to catch small plaice.

Predation by both fishes and shrimp on 0-group flatfishes will therefore be size-selective, concentrated on the smaller size-classes. Fishes and shrimp are assumed

Table 6.1: Comparison of lengths of smaller plaice, smaller dab, and larger cod in populations in surveys 1-6, 1992. Lower quartiles (Q_1) of plaice and dab length distributions and upper quartiles (Q_3) of cod length distributions.

Survey	Plaice Q_1 (mm)	Dab Q_1 (mm)	Cod Q_3 (mm)	Ratio plaice Q_1/cod Q_3	Ratio dab Q_1/cod Q_3
1	28	18	49	0.57	0.37
2	50	28	63	0.80	0.45
3	47	34	70	0.67	0.49
4	53	41	76	0.70	0.54
5	61	39	102	0.60	0.38
6	65	41	106	0.61	0.38

Table 6.2: Mean lengths of cod, plaice and dab populations and occurrence of flatfishes in cod at Firemore Bay in 1965 (EDWARDS, 1968; STEELE & EDWARDS, 1970) and at Tralee in 1990 (R. GIBSON, *pers. comm.*), 1992 and 1993.

			Mid June	Early July	Mid July	End July	End August	End September
Cod	Firemore 1965	Mean TL (mm)	79					
		Occ. plaice	50%					
	Tralee 1990	Mean TL (mm)	42					
		Occ. Flatfishes	5.8%					
	Tralee 1992	Mean TL (mm)	45	57	66	71	91	99
		Occ. dab	6.4%	7.7%	5.0%	2.0%	0%	0%
	Tralee 1993	Mean TL (mm)	54	58				
		Occ. plaice	4%	0%				
		Occ. dab	4%	0%				
Plaice	Firemore 1965	Mean TL (mm)	24	28	37	44	49	61
	Tralee 1990	Mean TL (mm)	33					
	Tralee 1992	Mean TL (mm)	33	54	51	59	69	71
	Tralee 1993	Mean TL (mm)	29	42				
Dab	Tralee 1990	Mean TL (mm)	22					
	Tralee 1992	Mean TL (mm)	20	30	36	44	50	45
	Tralee 1993	Mean TL (mm)	20	26				

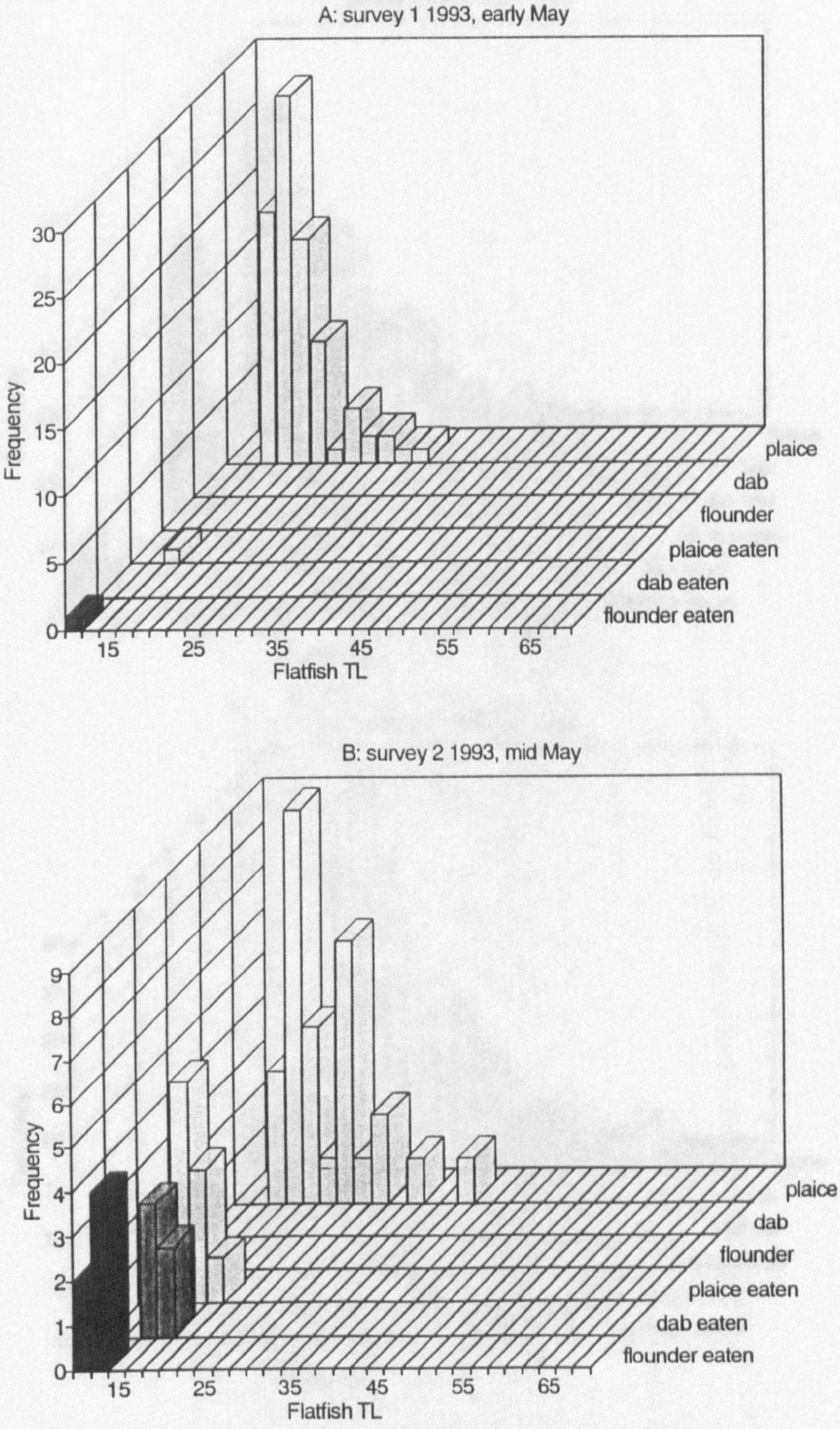
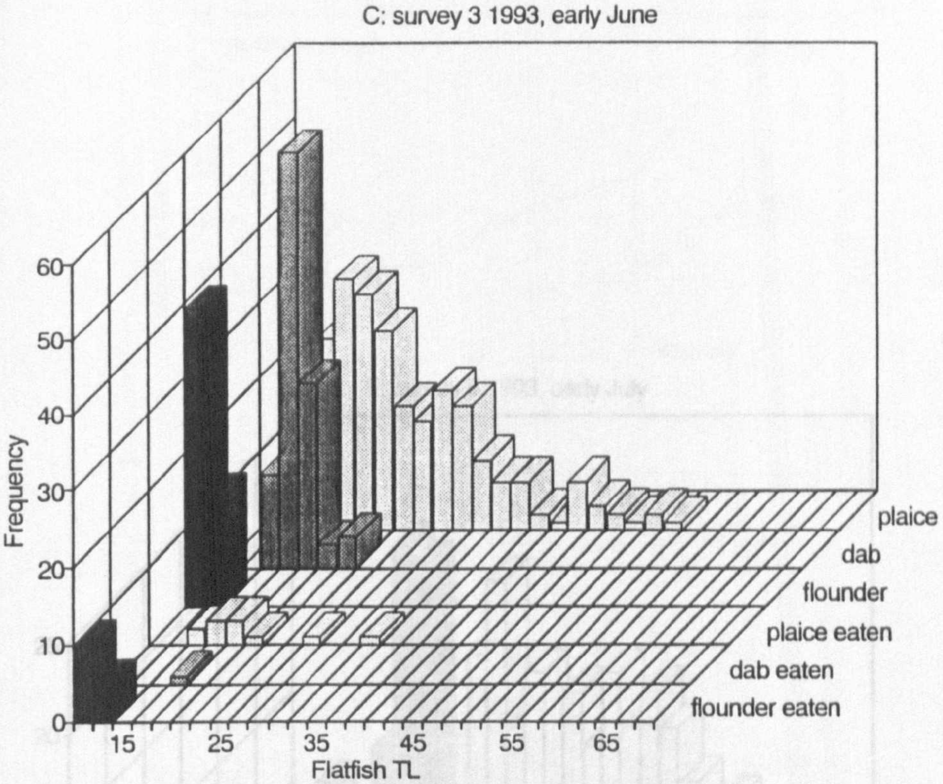


Figure 6.8: Length frequency distributions of flatfishes recovered from fish stomachs, and flatfish populations on Tralee beach in 1993. A: 6/5/93; B: 19/5/93. Length distributions of flatfish populations from beam trawl samples.



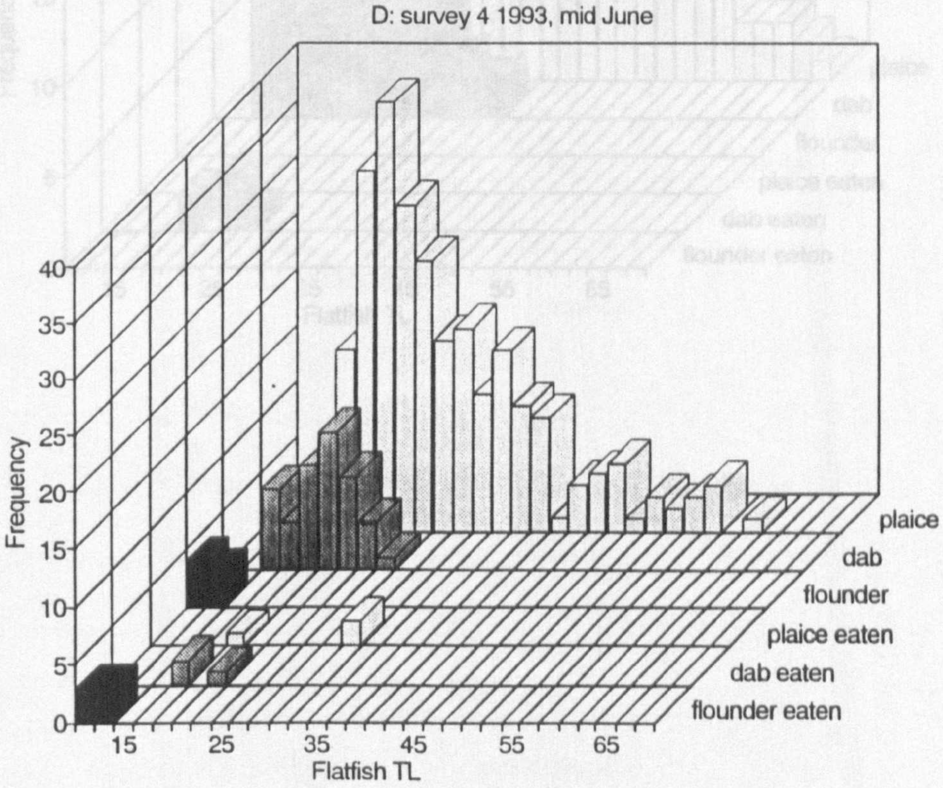


Figure 6.8 (continued): Length frequency distributions of flatfishes recovered from fish stomachs, and flatfish populations on Tralee beach in 1993. C: 2/6/93; D: 16/6/93. Length distributions of flatfish populations from beam trawl samples.

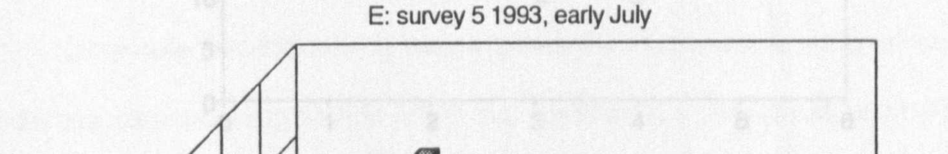


Figure 6.8 (continued): Length frequency distributions of flatfishes recovered from fish stomachs, and flatfish populations on Tralee beach in 1993. E: 1/7/93. Length distributions of flatfish populations from beam trawl samples.

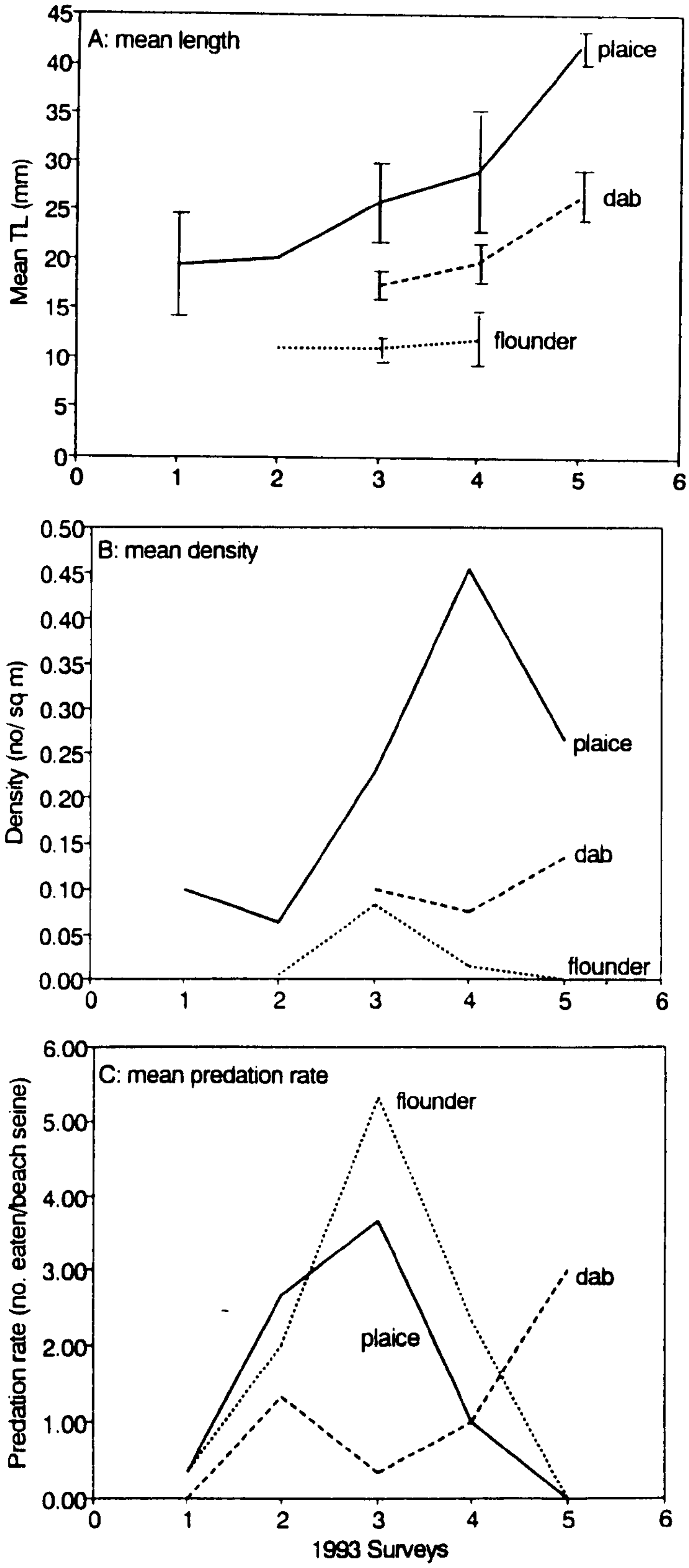


Figure 6.9: Plots to show change in mean length (A), mean density (B), and mean predation rate (C), and differences between plaice, dab and flounder, in 1993 surveys. Survey 1: 6/5/93; survey 2: 19/5/93; survey 3: 2/6/93; survey 4: 16/6/93; survey 5: 1/7/93. Predation rate expressed as mean number of flatfishes found in fish stomachs per beach seine.

to be the major predators of flatfishes on nursery grounds, and predation is assumed to be the main cause of mortality of 0-group flatfishes (VAN DER VEER *et al.*, 1990). Mortality will therefore be size-selective. STEELE & EDWARDS (1970) and RILEY (1973) found evidence that the mortality rate of small 0-group plaice was higher than that of larger plaice. Size-selective mortality of 0-group dab populations has not been demonstrated.

Size-selective mortality is very important with respect to population dynamics. For density-dependent growth to affect the numbers in a year-class, mortality must be size-selective (see Chapter 1). Also, if mortality is size-selective, then growth rates estimated from changes in population mean length will be biased (OTTERA, 1992). HOVENKAMP (1991) suggested that size-selective predation explained why growth estimated from mean lengths exceeded that predicted by models for laboratory conditions with unlimited food. Agreement between such estimates of growth rate in the field and modelled growth rate under optimum food conditions have been used as evidence against density-dependent growth (ZIJLSTRA & WITTE, 1985; BERGMAN *et al.*, 1988; VAN DER VEER *et al.*, 1990). EDWARDS *et al.* (1969) found that growth under laboratory conditions underestimated growth in the field. Therefore, the evidence against density-dependent growth of 0-group plaice needs reviewing. COLMAN (1966), and more recently VAN DER VEER & WITTE (1993), used comparative studies to show that food availability does affect the growth of 0-group plaice. Food limitation is the first step in demonstrating density-dependent growth. However, VAN DER VEER & WITTE (1993) found no evidence that density-dependent competition for food affected growth.

0-group cod as a predator of 0-group flatfishes

The size of 0-group cod was important in determining predation on 0-group flatfishes. On 18/6/92, all cod ≥59 mm were found to have eaten dab, showing that dab are a common food item when of a suitable size at sufficient densities. The minimum size of cod found to eat flounder was 51 mm, and the minimum size found to have eaten dabs was 58 mm. These may be the minimum sizes at which cod can pursue, capture and handle flatfishes in the field.

This minimum size may be very important in determining the effect of 0-group cod predation on the flatfish populations. On 18/6/92, 58 mm was in the right hand tail of the length distribution (Figure 6.5A), and therefore only the largest cod were eating dabs. Also the larger cod ate more dabs. If the modal length of the cod population had shifted towards 58 mm, then the occurrence of dabs in cod stomachs, and the number eaten, would have been higher.

Additionally, predation was concentrated on the smallest dabs. If the mode of the dab length distribution was smaller, then a greater proportion of the population would have been vulnerable to cod predation.

Between 18/6/92 and 28/7/92, the smaller dabs were apparently growing relatively faster than the larger cod (Table 6.1), although size-selective predation will have affected the length frequency distributions. The dabs were seemingly outgrowing the cod, which could account for the decrease in their occurrence in cod stomachs (see Chapter 5), although there will have been additional density effects.

In summary, it can be hypothesised that the relative sizes of cod and dab will affect the extent of predation. The sizes will be dependent upon the times of settlement, sizes at settlement and subsequent growth rates. This hypothesis can be extended to include the plaice-cod interaction. In 1992 there was no evidence of cod feeding on plaice. In 1993 only one cod was recorded containing a plaice (Figure 6.6). Plaice settle before dabs (Figure 6.9; EDWARDS & STEELE, 1968) and plaice settlement started before mid April in 1992 and 1993 (*pers. obs.*). The majority of plaice therefore had a refuge in size when the 0-group cod recruited to the beach, mainly in mid to late June, in 1992 and 1993.

It could be argued that the relative lengths of the cod, dab and plaice populations will be affected by the same processes in the pelagic and demersal phases and remain constant from year to year. However, the mean lengths of plaice in 1965 (from Figure 5 of STEELE & EDWARDS, 1970), at Loch Ewe on the west coast of Scotland, were smaller than those at Tralee (Table 6.2) in 1992 ($p<0.001$) and 1993 ($p<0.001$). Also the mean cod length from samples in June and July 1965 (79 mm, EDWARDS, 1968) was larger than all samples taken during that period at Tralee (Table 6.2) in 1992 ($p<0.001$) and 1993 ($p<0.001$). The larger cod and smaller plaice in 1965 may explain the high occurrence (>50% in some samples) of plaice in cod in 1965 (STEELE & EDWARDS, 1968) compared to 0% in 1992 at Tralee, and 4% in 1993 (Table 6.2).

The effect of time of recruitment to nurseries on survival within a year-class

It was shown that predator-prey relationships are greatly affected by body size, and it was hypothesised that the time of recruitment would, therefore, affect mortality. STEELE & EDWARDS (1970) noted that a late settling "sub-cohort" of plaice suffered very high mortality. The effect of time of recruitment to nurseries on survival of flatfishes has only recently attracted more specific interest (e.g. VAN DER VEER, 1985; AL-HOSSAINI *et al.*, 1989; HOVENKAMP, 1991; VAN DER VEER *et al.*, 1991). VAN DER VEER (1985) suggested that early recruitment would lessen the extent of coelenterate predation on the late larval stages of plaice and flounder. VAN DER VEER *et al.* (1991) suggested that in the demersal phase, early settlement would favour survival due to low predation pressure as predator abundance and temperature would be low. Conversely, AL-HOSSAINI *et al.* (1989) and HOVENKAMP (1991) suggested that late recruitment of plaice would favour survival. HOVENKAMP (1991) cited the higher growth rate and shorter duration at vulnerable sizes, as the potential cause of lower mortality for later recruits. Mortality rates will reflect predation pressure, affected by a complex of factors which change over time, e.g. flatfish size and growth rate, and the size, abundance and temperature-dependent feeding activity of predators (HOVENKAMP, 1991; VAN DER VEER *et al.*, 1991). The abundance of alternative prey for predators has been overlooked in studies of predation on 0-group plaice but will change over time and affect mortality rates (see BAILEY & HOUDE, 1989).

As both early and late settlement are thought to affect mortality, there may be an "optimal" time for settlement, when conditions promote the survival of late stage larvae and newly settled fish. The time of peak spawning of plaice on a single spawning ground varies very little between years, but does differ between grounds (see Chapter 2 for references). Spawning may therefore be synchronised to a "time window" for larval recruitment to nurseries.

The effect of size at time on mortality: a comparison between year-classes and nurseries

The effect of the time of recruitment of plaice to nurseries on body size has been established (VAN DER VEER *et al.*, 1990). The size of plaice at any one time is a result of the time of recruitment and growth, and these factors result in differences in mean lengths between years and nurseries (VAN DER VEER *et al.*, 1990). Size greatly affects vulnerability to predation within a season, so differences in size between years and nurseries may cause differences in mortality.

The hypothesis that differences in size at time between years and nurseries affect the mortality rate of 0-group plaice populations was tested using published data. Mortality rates of 0-group plaice populations (Table 6.3) were taken from ILES & BEVERTON (1991). Mean TL on 1 July was taken to represent size and was estimated by interpolation from the sources listed in Table 6.3. Mortality rate was negatively correlated with size (Table 6.4; Figure 6.10A), showing larger sizes on 1 July are correlated with lower mortality rates.

Negative correlations between density and size, which were once taken as evidence for density-dependent growth (e.g. STEELE & EDWARDS, 1970), are now thought to be explained by the time of recruitment and subsequent growth (ZIJLSTRA & WITTE, 1985; BERGMAN *et al.*, 1988; VAN DER VEER *et al.*, 1990). Low temperatures enhance the survival of pelagic stages, but increase development time (BERGMAN *et al.*, 1988). Late recruitment to the nursery reduces the growing season, and results in a smaller size at the end of the season (see Figure 6.11).

Table 6.3: Maximum densities (D_{max}: number/1000 m^2) and daily instantaneous mortality rates (Mort) of O-group plaice on different nurseries taken from ILES & BEVERTON (1991) and grouped according to BEVERTON & ILES (1992b). Mean TL on 1 July estimated from sources listed. Mean lengths were not always available (N/A) from published studies.

Region	Nursery	Year	D_{max}	Mort	Mean TL (mm) on 1 July	Source for TL
SCOTTISH COASTS	Firemore Bay	1965	736	.0198	28	1
		1966	354	.0204	33	1
		1967	313	.0195	40	1
		1968	153	.0109	42	1
	Ardmucknish Bay	1972	1525	.0164	40	2
		1986	3547	.0122	33	2
		1987	33	.0069	45	2
		1988	211	.0218	59	2
		1989	1586	.0165	43	2
	Irvine Bay	1973	797	-	N/A	-
		1974	717	.0239	45	3
	Ayr Bay	1974	700	.0243	42	4
FILEY BAY		1968	20	.0206	19	5
		1969	1173	.0299	19	5
		1972	274	.0106	N/A	-
		1973	147	.0172	N/A	-
IRISH SEA	Port Erin Bay	1963	718	.0161	N/A	
		1964	121	.0132	32	6
		1965	532	.0232	35	6
	Red Wharf Bay	1964	104	.0142	40	7
		1965	55	.0189	33	7
	Dinllaen Bay	1964	47	.0141	N/A	-
		1965	53	.0122	N/A	-

Table 6.3 (continued): Maximum densities (D_{max}: number/1000 m^2) and daily instantaneous mortality rates (Mort) of O-group plaice on different nurseries taken from ILES and BEVERTON (1991) and grouped according to BEVERTON & ILES (1992b). Mean TL on 1 July estimated from sources listed. Mean lengths were not always available (N/A) from published studies.

Region	Nursery	Year	D_{max}	Mort	Mean TL (mm) on 1 July	Source for TL
WADDEN SEA		1973	500	.0101	52	8
		1975	137	-	59	8
		1976	191	.0089	58	8
		1977	202	.0070	59	8
		1978	519	.0085	53	8
		1979	320	.0075	53	8
		1980	164	.0105	N/A	-
		1981	360	.0248	N/A	-
		1982	297	.0138	N/A	-
SWEDISH COAST	Gullmar Bay	1977	600	.0127	N/A	-
		1978	1340	.0209	47	9
		1979	2400	.0347	44	9
		1980	300	-	32	9
		1981	800	.0108	44	9
		1982	2700	.0515	44	9
	Laholm Bay	1985	525	.0131	N/A	-
NORTH FRISIAN ISLANDS	Norstrander Bay	1981	70	.0019	39	10
		1982	115	.0126	51	10

Sources for mean TL on 1 July:
1. STEELE & EDWARDS (1970) Fig 5
2: R. GIBSON (pers. comm.)
3: POXTON *et al.* (1983) Fig 3
4: POXTON *et al.* (1983) Fig 5
5: ZIJLSTRA *et al.* (1982) Fig 4
6: COLMAN (1966) Fig 10
7: MACER (1967) Fig 5
8: ZIJLSTRA *et al.* (1982) Fig 4
9: VAN DER VEER *et al.* (1990) Fig 7
10: BERGHAHN (1987) Fig 4 medians

Table 6.4: Spearman rank correlation coefficients for relationships between size (TL), maximum density (D_{max}) and daily instantaneous mortality rate (M). Size was represented by mean TL on 1 July. The data (see Table 6.3) were analyzed four times to exclude points which may exert significant leverage, following BEVERTON & ILES (1992b). Probabilities were derived from one-tailed tests.

Data from Table 6.3	Correlation coefficients (r_s)		
	M & D_{max}	M & TL	TL & D_{max}
All	0.409 n=38 $p<0.01$	-0.383 n=28 $p<0.025$	-0.038 n=30 $p>0.25$
All excluding Gulmar 1982	0.367 n=37 $p<0.025$	-0.419 n=27 $p<0.025$	-0.049 n=29 $p>0.25$
All excluding Filey 1968	0.469 n=37 $p<0.0025$	-0.371 n=27 $p<0.05$	-0.146 n=29 $p>0.1$
All excluding Gulmar 1982 & Filey 1968	0.431 n=36 $p<0.005$	-0.403 n=26 $p<0.025$	-0.161 n=28 $p>0.1$

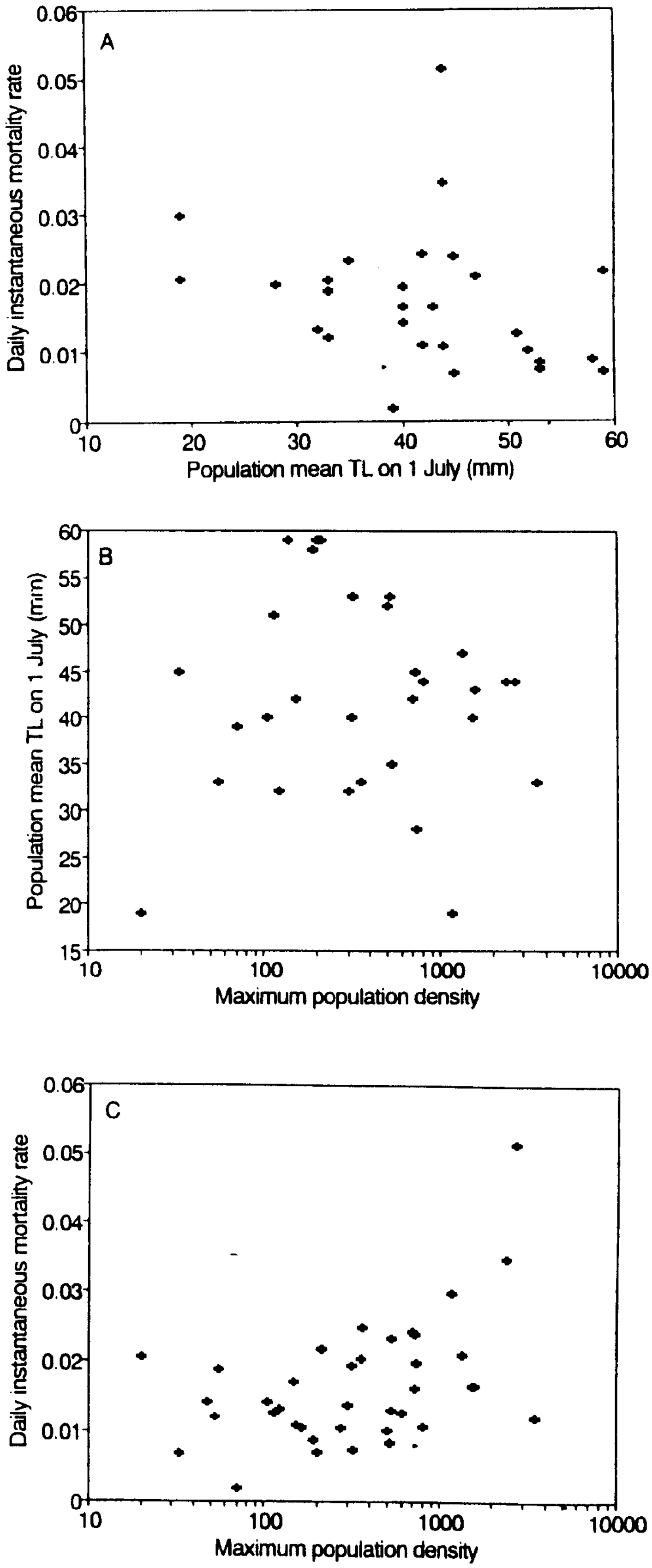


Figure 6.10: Scatter plots of data in Table 6.3. Note maximum population density (number/10^{3}m^2) plotted on logarithmic scale.

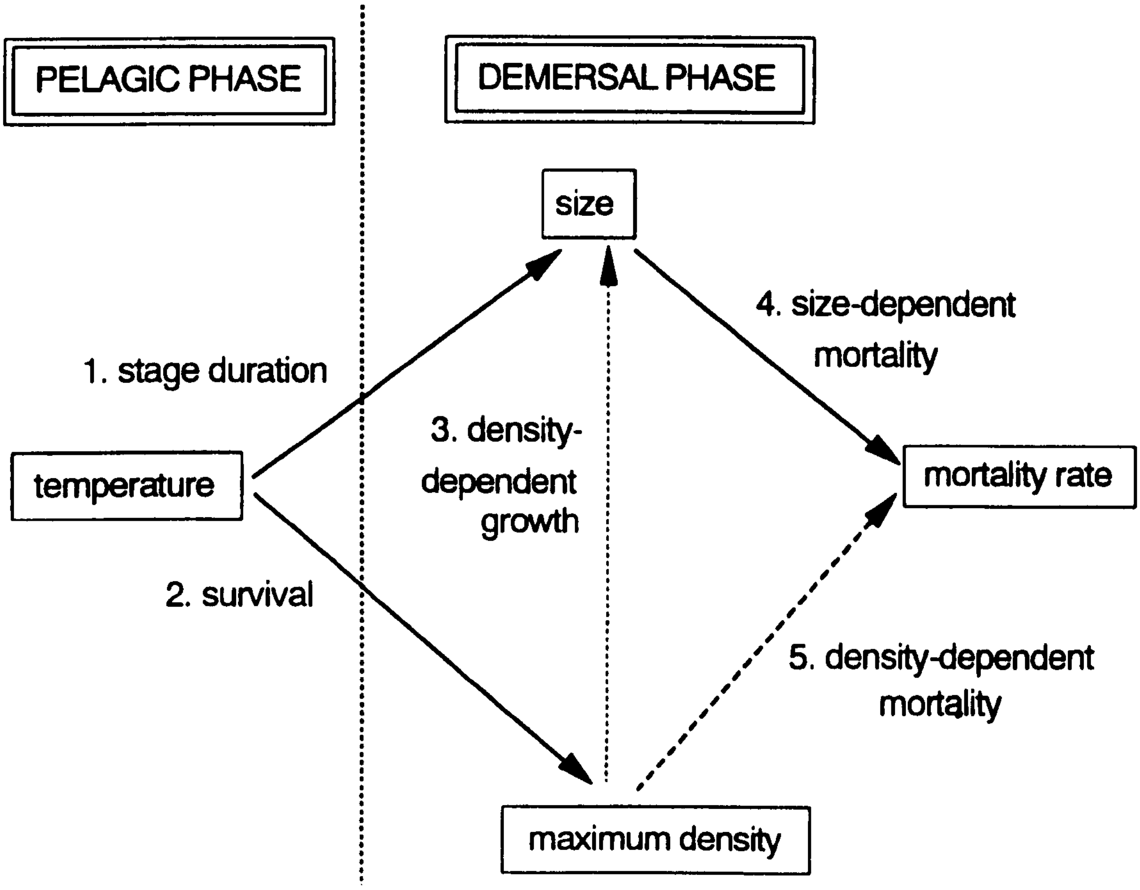


Figure 6.11: Schematic diagram to show relationships between size, density and mortality rate of 0-group plaice on nursery grounds.

Development time (1) and survival (2) in the pelagic phase are temperature-dependent. Size and density in the demersal phase are negatively correlated, not because of density-dependent growth (3), but because both factors are dependent upon temperature during the pelagic phase. Mortality rate and size are negatively correlated, due to size-dependent mortality (4). Density and mortality may then be positively correlated, but not because of density-dependent mortality (5).

A negative correlation between density and size, and a negative correlation between size and mortality rate would result in a positive correlation between density and mortality (see Figure 6.11). Positive correlations between density and mortality (see Figure 6.10C; Table 6.4) have been taken as evidence for density-dependent mortality (LOCKWOOD, 1980; VAN DER VEER, 1986; BEVERTON & ILES, 1992b). Despite the fact that size is likely to have a stronger effect on mortality rate than density, the effect of size has been overlooked.

BEVERTON & ILES (1992b) did recognise that correlation does not prove cause and effect, and stated that other factors which vary in a similar way to density across space and time may be responsible for the relationship with mortality rate. Density, time of recruitment, growth rate, size and temperature will all vary systematically to a certain extent, as may alternative food for predators. For example, there is a relationship between temperature and mortality in 0-group plaice populations (VAN DER VEER *et al.*, 1991).

The hypothesis that size-dependent mortality could produce apparent density-dependent mortality, was tested using data in Table 6.3. The effects of size and density on mortality rate were analyzed using multiple regression analysis. Regression analysis assumes linear relationships between dependent and independent variables (ZIJLSTRA & WITTE, 1985). BEVERTON & ILES (1992b) assumed a linear relationship between mortality rate and $\log_e$ of maximum density (D_{max}). Mortality rate was also assumed linear with respect to $\log_e$ of mean TL.

The data was analyzed four times (Table 6.5) following BEVERTON & ILES (1992b) to exclude points which may exert a significant leverage. Although density had a significant effect on mortality in all four analyses, size was only significant in one. However, a strong positive relationship between density and mortality rate would be as expected, as they are not independent. When the effect of size was significant, it made a larger contribution to the variance of mortality rate than did density.

The major problem with the analysis is the necessity to pool data for all

Table 6.5: Results of regression analyses of daily instantaneous mortality rate against ln D_{max} and ln mean TL (data in Table 6.3). The data was analysed four times to exclude points which may have exerted a significant leverage, following BEVERTON & ILES (1992b).

Data set	Source of variance	Sum of squares	d.f.	F	p	r^2	Contribution of factor to variance in mortality rate
All data	Regression	0.00091	2	6.28	0.0062	0.33	
	ln D_{max}	0.00063	1	8.74	0.0067		69%
	ln Mean TL	0.00028	1	3.82	0.0620		31%
	Residual	0.00182	25				
Excluding Gulmar 1982	Regression	0.00056	2	6.97	0.0041	0.37	
	ln D_{max}	0.00025	1	6.19	0.0202		45%
	ln Mean TL	0.00031	1	7.74	0.0103		55%
	Residual	0.00097	24				
Excluding Filey Bay 1968	Regression	0.00096	2	6.57	0.0053	0.36	
	ln D_{max}	0.00086	1	11.76	0.0022		90%
	ln Mean TL	0.00010	1	1.38	0.2512		10%
	Residual	0.00176	24				
Excluding Gulmar 1982 and Filey 1968	Regression	0.00055	2	6.69	0.0051	0.37	
	ln D_{max}	0.00039	1	9.35	0.0056		70%
	ln Mean TL	0.00017	1	4.03	0.0565		30%
	Residual	0.00095	23				

nurseries because of the lack of long time series for single nurseries. Different nurseries will all have different predatory characteristics, and there is good evidence that predators differ between nurseries (Chapter 5; EDWARDS & STEELE, 1968; VAN DER VEER *et al.*, 1990). The effects of nursery and region were tested using ANOVA, but the effects were non-significant in all the analyses. Also the $\log_e$ transformations of both independent variables will greatly influence their relative effects. A confounding problem is the difficulty in obtaining reliable estimates of population parameters.

It must be recognised that there is a complex interaction of different processes affecting mortality rate, e.g. time of recruitment, temperature and size, which produce compensatory mortality independently of density. For example VAN DER VEER (1985) suggested that coelenterate predation resulted in density-dependent mortality in the late larval phase of plaice. Similarly VAN DER VEER & BERGMAN (1986) suggested that lethal abiotic conditions (high temperatures and low oxygen levels) soon after settlement would produce density-dependent mortality. However, both mechanisms were based solely upon the time of recruitment and were independent of plaice density. Such mechanisms would therefore result in compensatory mortality, but not density-dependent mortality.

CHAPTER 7:

PREDATOR BEHAVIOUR:

PREY HANDLING TIME
AND PREY SELECTION
OF 0-GROUP FLATFISHES
BY 0-GROUP COD

INTRODUCTION

It was shown in Chapter 6 that predation on 0-group flatfishes was size-selective, concentrated on the smaller individuals. Raptorial feeding consists of four consecutive processes, and selection of prey types or sizes can occur at the encounter, pursuit, capture, or ingestion stage (see GARDNER, 1981 and HUGHES & SEED, 1981). Encounter rates depend upon the density, visibility, activity and behaviour of prey. The visibility (O'BRIEN *et al.*, 1976) and activity of larger prey will be greater, so selection for smaller size-classes will probably occur after the encounter stage of feeding.

Size-selection at the pursuit stage implies a behavioural decision of the predator, either to pursue a prey item once encountered or to continue searching (GARDNER, 1981). Selection of smaller prey can also occur at the capture stage as the escape speed of small prey will be lower (KISLALIOGLU & GIBSON, 1975). Size selection at the ingestion stage will depend upon the morphological constraint of mouth gape (HAMBRIGHT, 1991), and a behavioural decision, to ingest or return to searching (HUGHES & SEED, 1981).

Morphologically mediated selection of smaller prey will therefore occur at the capture and/or ingestion stages, and behavioural selection at the pursuit and/or ingestion stages. Optimal Foraging Theory (HUGHES, 1980) and the Basic Prey Model (STEPHENS & KREBS, 1986) provide a basis for predicting the behavioural selection of prey, in terms of the rate of energy gain. A behavioural basis to prey selection by predators is assumed because economical foraging would confer a selective advantage (WERNER & HALL, 1974; HUGHES, 1980). There is, however, some discussion on the value of optimal foraging theory (see PIERCE & OLLASON, 1987 and STEARNS & SCHMID-HEMPLE, 1987).

The prey size which provides the highest return of energy per unit time is termed the "optimal" prey (KISLALIOGLU & GIBSON, 1976). The Basic Prey Model predicts that a predator will always pursue "optimal" prey when encountered

(STEPHENS & KREBS, 1986). As the density of optimal prey decreases, less profitable prey will be included in the diet in rank order (STEPHENS & KREBS, 1986).

The time considered when predicting prey selection is termed "handling time". Handling time is the time spent in pursuit, capture and ingestion, and hence lost from searching for alternative prey (STEPHENS & KREBS, 1986). Ingestion consists of intake into the buccal cavity, manipulation within the buccal cavity, and conveying the prey to the stomach (WANKOWSKI, 1979). Handling time is influenced by the morphology (HOYLE & KEAST, 1987; HAMBRIGHT, 1991) and size (WERNER, 1974) of the prey, the size (WERNER, 1974), satiation (WERNER, 1974; KISLALIOGLU & GIBSON, 1976) and experience (see HUGHES *et al.*, 1992) of the predator, and temperature (BERGMAN, 1987).

Handling times have proved useful in predicting the size-selection of prey by fishes in the laboratory (e.g. WERNER & HALL, 1974; BENCE & MURDOCH, 1986; HART & GILL, 1992) and field (KISLALIOGLU & GIBSON, 1976; HOYLE & KEAST, 1987). The purpose of the experiments detailed here was to estimate the handling times of 0-group flatfishes by 0-group cod and hence provide a basis for predicting prey size selection. Predicted selection was then compared to that observed in laboratory experiments and in the field (Chapter 6).

MATERIALS AND METHODS

0-group cod were captured in June and July 1992 by trawling from *R.V. Seol Mara* during the day in 4-10 m depth off Tralee beach (see Chapter 5). The cod were maintained in a stock tank and the sea-water inflow passed through a "de-saturator column" as cod are vulnerable to supersaturated oxygen (R. BATTY, *pers. comm.*). Cod were fed every second day, on both live food (mysids and shrimp *Crangon crangon*) and dead food (pieces of fish and pelleted salmon food). 0-group plaice and dabs were caught from Tralee beach with a 1.5 m push-net (RILEY, 1971) at low water. They were maintained in the laboratory on a diet of fresh mysids.

Feeding of live flatfishes to cod was conducted under Personal Home Office Licence No. PIL 60/04325. Feeding experiments were conducted in compartments (60 x 33 x 31 cm) of two Perspex tanks. The water level was 26 cm and there was a constant flow through the tanks. A mesh lid prevented the cod jumping out. The tanks were illuminated from above by fluorescent lighting. Light intensities above the tanks and in mid-water were $2.55\text{-}3.6\times10^{15}$ and $0.26\text{-}0.44\times10^{15}$ quanta $cm^{-2}s^{-1}$ respectively. Experiments were not performed in temperature controlled conditions, and water temperatures differed slightly between experiments (13-16°C, mean 14.5°C).

Experiments were filmed using VHS video equipment. The video camera (J.V.C. TK-S310EG) was mounted on a tripod and connected to a video cassette recorder (J.V.C. BR-S410E) via a time code generator (FOR.A VTG-33). Experiments were filmed from the side. To achieve a large image of the cod, the camera was placed close (c. 1.5 m) to the tank. As the whole compartment was not in view, the camera was moved by hand during the experiment to keep the cod in the field of view.

Cod History

Cod were selected from the stock tank, placed singly in the compartments of the experimental tanks, and left to adjust for at least three days before experimentation. Satiation is known to affect handling time (WERNER, 1974; KISLALIOGLU & GIBSON, 1976) so hunger level was standardised by feeding cod daily in the experimental tanks. Cod have a capacity to learn from experience, as they have been found to show a conditioned response to baited hooks (LOKKEBURG *et al.*, 1989). Experience of prey affects handling time (HUGHES *et al.*, 1992), so cod were fed flatfish at least twice before experimentation.

Handling Time Experiments: procedure

Plaice or dabs of a single size were selected from stock tanks for each experiment, and placed individually into small tubs containing a little sea water. The V.C.R. was started, and approximately 1 min later the first flatfish was introduced into the experimental tank containing the cod by submersing the tub beneath the surface of the water, and allowing the flatfish to swim out. If it was eaten another of the same size was introduced, and so on. If the cod showed no interest in feeding, additional flatfish were added to encourage feeding. Experiments lasted for approximately 30 min. The length of cod used in successful experiments was measured after lightly anaesthetizing the cod with benzocaine.

Handling time experiments: analysis

Cod capture prey by suction (see FUIMAN & BATTY, 1994). Handling times were for ingestion only and measured from the time the cod first captured the flatfish to when it was judged to have been conveyed to the stomach (KISLALIOGLU & GIBSON, 1976; HOYLE & KEAST, 1988). Pursuit times were not included. Handling times were estimated to 0.5 s from the times generated by the time code generator on the video tapes. Cod would sometimes capture the prey, and then release and recapture it. If handling was continuous, the first handling was included in the handling time. If the cod lost interest in the prey, but subsequently ate it, the first handling time was not included.

Judging the end of handling, i.e. when the prey had been conveyed to the stomach, often proved difficult. For small prey there was often very little sign and, as handling appeared instantaneous, times of 0.5 s were assumed. For larger prey a characteristic swallowing action was evident (Figure 7.1), and distension of the stomach region could sometimes be seen. The clarity of these features would depend upon the orientation of the cod to the camera.

Handling time and profitability data were analyzed with the generalised linear model procedure (GLM) using the SAS statistical package (SAS Institute Inc.). Profitability was measured as the wet weight gained per unit handling time (mg s^{-1}). Handling time, profitability, cod TL and flatfish TL were $\log_e$ transformed for analysis.

Length-weight relationships

Wet weights (in mg) of flatfishes were estimated from total length (in mm) using the following relationships, derived by functional regression (see RICKER, 1973) for

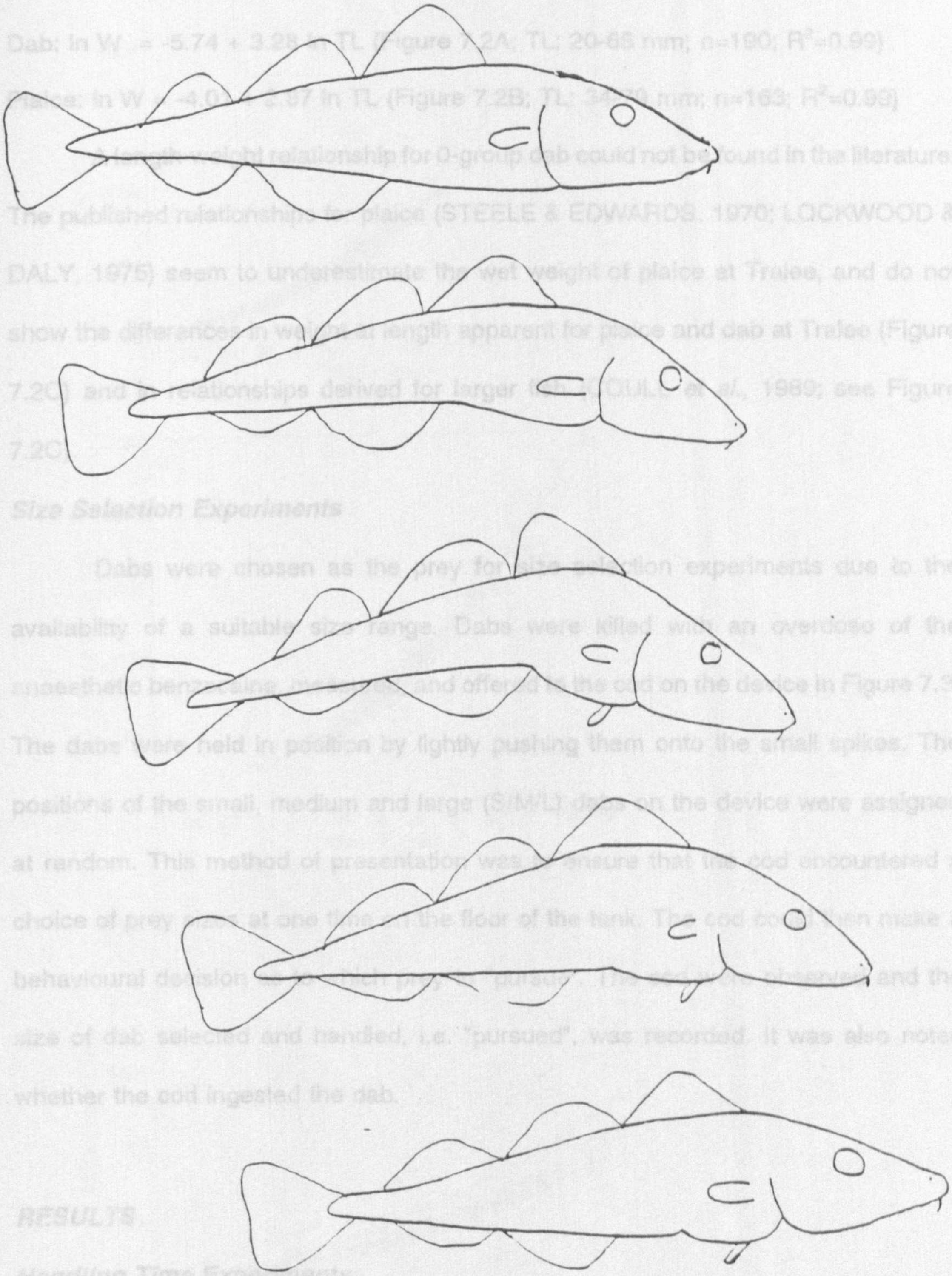


Figure 7.1: Diagrammatic representation of swallowing action of cod consuming a large prey item. Note distension in region of stomach.

plaice and dab caught from Tralee.

Dab: $\ln W = -5.74 + 3.28 \ln TL$ (Figure 7.2A; TL: 20-65 mm; n=190; R^2=0.99)

Plaice: $\ln W = -4.01 + 2.87 \ln TL$ (Figure 7.2B; TL: 34-79 mm; n=163; R^2=0.99)

A length-weight relationship for 0-group dab could not be found in the literature. The published relationships for plaice (STEELE & EDWARDS, 1970; LOCKWOOD & DALY, 1975) seem to underestimate the wet weight of plaice at Tralee, and do not show the differences in weight at length apparent for plaice and dab at Tralee (Figure 7.2C) and in relationships derived for larger fish (COULL *et al.*, 1989; see Figure 7.2C).

Size Selection Experiments

Dabs were chosen as the prey for size selection experiments due to the availability of a suitable size range. Dabs were killed with an overdose of the anaesthetic benzocaine, measured, and offered to the cod on the device in Figure 7.3. The dabs were held in position by lightly pushing them onto the small spikes. The positions of the small, medium and large (S/M/L) dabs on the device were assigned at random. This method of presentation was to ensure that the cod encountered a choice of prey sizes at one time on the floor of the tank. The cod could then make a behavioural decision as to which prey to "pursue". The cod were observed and the size of dab selected and handled, i.e. "pursued", was recorded. It was also noted whether the cod ingested the dab.

RESULTS

Handling Time Experiments

It was not possible to discern the alignment of small flatfishes during capture and ingestion due to the speed of ingestion. Of the 77 occasions when the orientation was discernable, 77% were ingested tail first, and 23% were ingested head first. This reflects the orientation of capture, as most flatfishes were captured by the tail. During ingestion of large prey, or prey caught in an oblique orientation, the cod would adjust

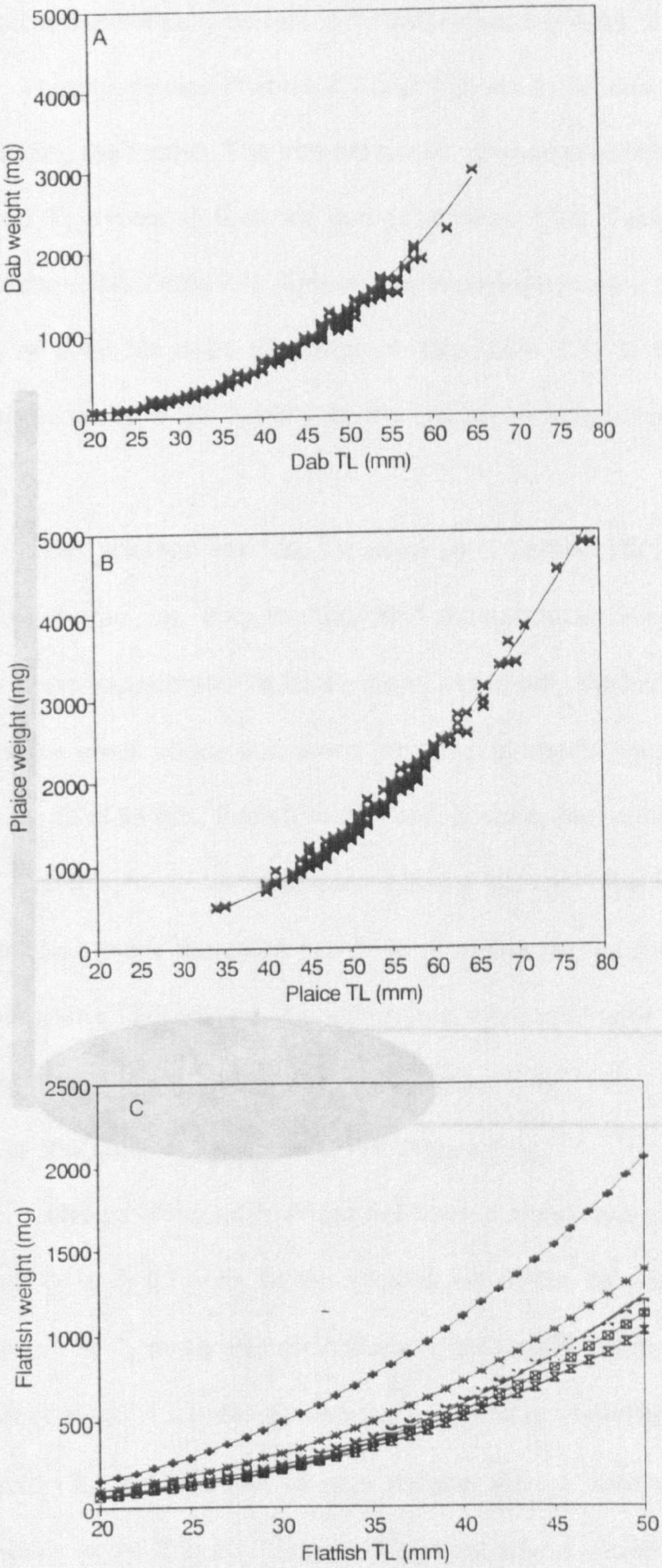


Figure 7.2: Length weight relationships for dab and plaice.
A: dab from Tralee; B: plaice from Tralee; C: -◆- plaice COULL *et al.* (1989); -✱- plaice Tralee; -⧓- plaice LOCKWOOD & DALY (1975); — dab Tralee; -⊠- dab COULL *et al.* (1989); -⧗- plaice STEELE & EDWARDS (1970).

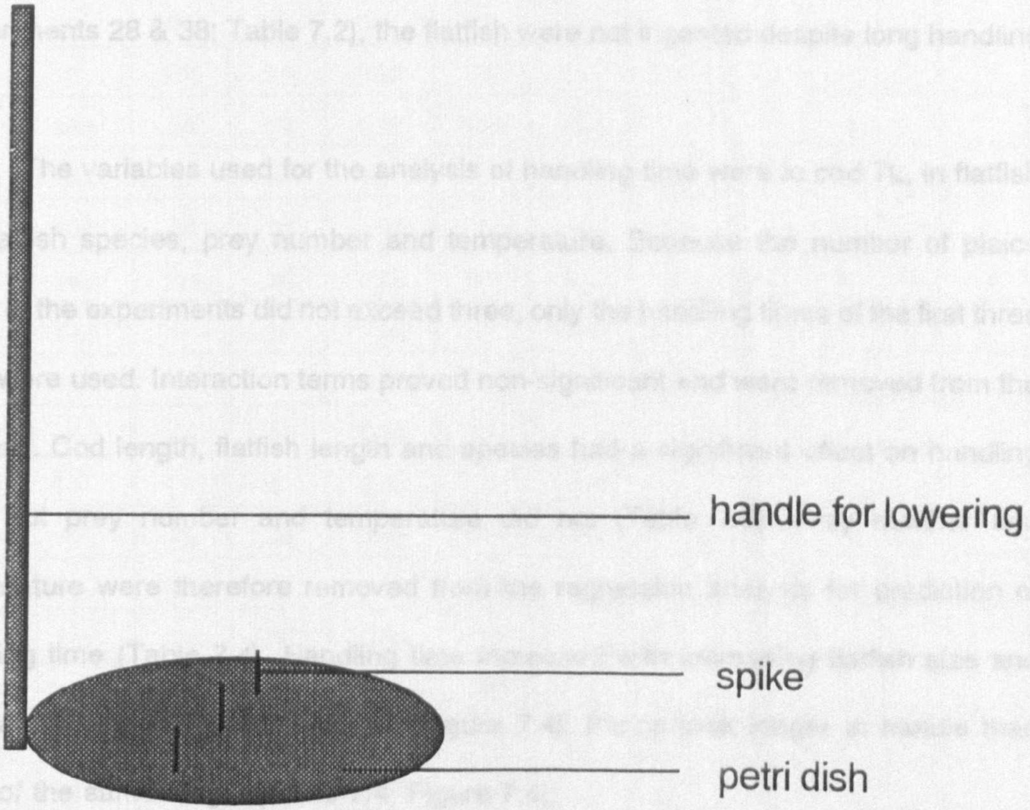


Figure 7.3: Presentation device used for offering dabs to cod in laboratory size selection experiments.

the position of the prey by releasing and re-seizing it, as observed by BRAWN (1969).

Handling times (Tables 7.1 and 7.2) are indicative of the difficulty the cod had in ingesting the flatfish. The longest handling times preceding ingestion were for flatfish TL: cod TL ratios of 0.44 for dab (Experiment 22: Table 7.1) and 0.39 for plaice (Experiment 36: Table 7.2). These prey were ingested tail first. At prey:predator length ratios of 0.49 for dabs (Experiment 19: Table 7.1) and 0.42 and 0.40 for plaice (Experiments 28 & 38: Table 7.2), the flatfish were not ingested despite long handling times.

The variables used for the analysis of handling time were ln cod TL, ln flatfish TL, flatfish species, prey number and temperature. Because the number of plaice eaten in the experiments did not exceed three, only the handling times of the first three dabs were used. Interaction terms proved non-significant and were removed from the analysis. Cod length, flatfish length and species had a significant effect on handling time, but prey number and temperature did not (Table 7.3). Prey number and temperature were therefore removed from the regression analysis for prediction of handling time (Table 7.4). Handling time increased with increasing flatfish size and decreased with increasing cod size (Figure 7.4). Plaice took longer to handle than dabs of the same length (Table 7.4; Figure 7.4).

Although prey number did not have a significant effect in the analysis for prey number (1 to 3) for both flatfish species, when the data for dab were analyzed (prey numbers 1 to 7), there was an indication that handling times did increase as more prey were ingested. The estimates for the regression coefficients for prey number (i.e. the correction for the intercept as prey number was a class variable) increased as more prey were eaten (Figure 7.5). Handling time would therefore increase with increasing numbers of prey eaten, although the effect was again non-significant ($p=0.0651$).

Profitability data were analyzed similarly to the handling time data. Interactions were not significant and removed from the analysis. Cod size and flatfish size affected profitability, but species and prey number did not (Table 7.5). There was no indication

Table 7.1: Handling times of dabs by cod. h_i is the handling time of the *ith* dab ingested.

Exp. No.	Temp (°C)	Cod TL (mm)	Dab TL (mm)	TL ratio	Handling times of dabs (secs)						
					h_1	h_2	h_3	h_4	h_5	h_6	h_7
4	13.5	65	20	0.31	4	21	15				
5	13.5	81	30	0.37	4	211					
6	13.5	65	27	0.42	390						
9	14	96	30	0.31	15	26					
10	13	106	23	0.22	0.5	0.5	5.5	-	-	2	
11	13.5	65	25	0.38	409	169					
12	13.5	81	30	0.37	854						
13	13.5	96	26	0.27	7	4	11				
14	14.5	111	26	0.23	0.5	0.5	6	10.5	5	6	10
15	14.5	70	28	0.40	51	692					
16	14.5	102	29	0.28	1	9	9				
17	14.5	86	33	0.38	17						
18	14	111	37	0.33	11	146					
19	14	70	34	0.49	1064: Not ingested						
20	14	86	37	0.43	473						
21	14	102	36	0.35	13						
22	14	70	31	0.44	1308						
23	15	114	32	0.28	0.5	5.0	5.0	24.0	27		
24	14.5	104	30	0.29	10	7.5	7	10	8.5		
25	15	89	32	0.36	34	254					
26	15	74	29	0.39	86	256					
34	14.5	107	43	0.40	258						
35	14.5	80	33	0.41	445						
76	15	144	29	0.20	0.5	0.5					
77	15	135	38	0.28	8	9	29.5				
78	16	144	33	0.23	0.5	0.5					
89	15	140	43	0.31	14.5	8.5					
90	15	147	42	0.29	14	9.5					
91	15	121	42	0.35	38						
92	15	144	47	0.33	30						
93	15	152	45	0.30	25	10.5					

Table 7.2: Handling times of plaice by cod. h_i is the handling time of the *ith* plaice ingested.

Exp. No.	Temp. (°C)	Cod TL (mm)	Plaice TL (mm)	TL Ratio	Handling times of plaice (secs)		
					h_1	h_2	h_3
27	14.5	116	32	0.28	11		
28	14.5	76	32	0.42	1248: not ingested		
30	14.5	106	32	0.30	12	22	10
31	14.5	80	28	0.35	97		
36	14.5	76	30	0.39	1339		
38	15	93	37	0.40	405: not ingested		
39	15	122	36	0.30	50	153	
41	16	85	25	0.29	7	14	
42	16	113	35	0.31	12	6	60
44	15	116	41	0.35	323		
45	15	86	30	0.35	229		
46	15	122	33	0.27	0.5		
47	15	119	29	0.24	1.5	2.5	
49	15	96	32	0.33	9		
50	15	119	32	0.27	14	3.5	
51	15	87	32	0.37	917		
54	15.5	133	41	0.31	222		
57	15.5	134	34	0.25	4	4	2.5
58	16	124	39	0.31	7		
59	15	135	43	0.32	18		
60	15	125	41	0.33	53		
62	14.5	139	35	0.25	5	0.5	1
63	15	139	37	0.27	9	8	6.5
64	15	130	35	0.27	10	7	7
68	15	140	44	0.31	29	16	
69	15	132	41	0.31	13.5		
70	16	134	37	0.28	1	5	35
71	15.5	143	36	0.25	1	1	4.5
80	15	138	38	0.28	20.5		
82	16	147	44	0.30	10.5		
83	15	138	43	0.31	44		
85	15	147	43	0.29	15		
86	15	147	42	0.29	15		
88	15	140	43	0.31	24		

Table 7.3: Generalised Linear Model analysis of effects on ln handling time of dab and plaice by cod.

Source	GLM RESULTS			
	df	SS	F	p
ln Cod TL	1	213.65	166.49	0.0001
ln Flatfish TL	1	121.25	94.49	0.0001
Species	1	8.95	6.97	0.0096
Prey number	2	44.41	2.11	0.1271
Temperature	6	7.33	1.22	0.4617
Error	99	127.04		

Table 7.4: Regression estimates from Generalised Linear Model of ln handling time of dab and plaice by cod. Cod and flatfish TL were included as continuous variables, and species as a class variable. The estimates relating to cod TL and flatfish TL are therefore coefficients, while the estimates for species modify the intercept.

Parameter		Estimate	p	S.E.
ln Cod TL		-9.57	0.0001	0.65
ln Flatfish TL		9.07	0.0001	0.80
Intercept		15.69	0.0001	2.44
Flatfish Species	Plaice	0.50	0.0374	0.24
	Dab	0.00		

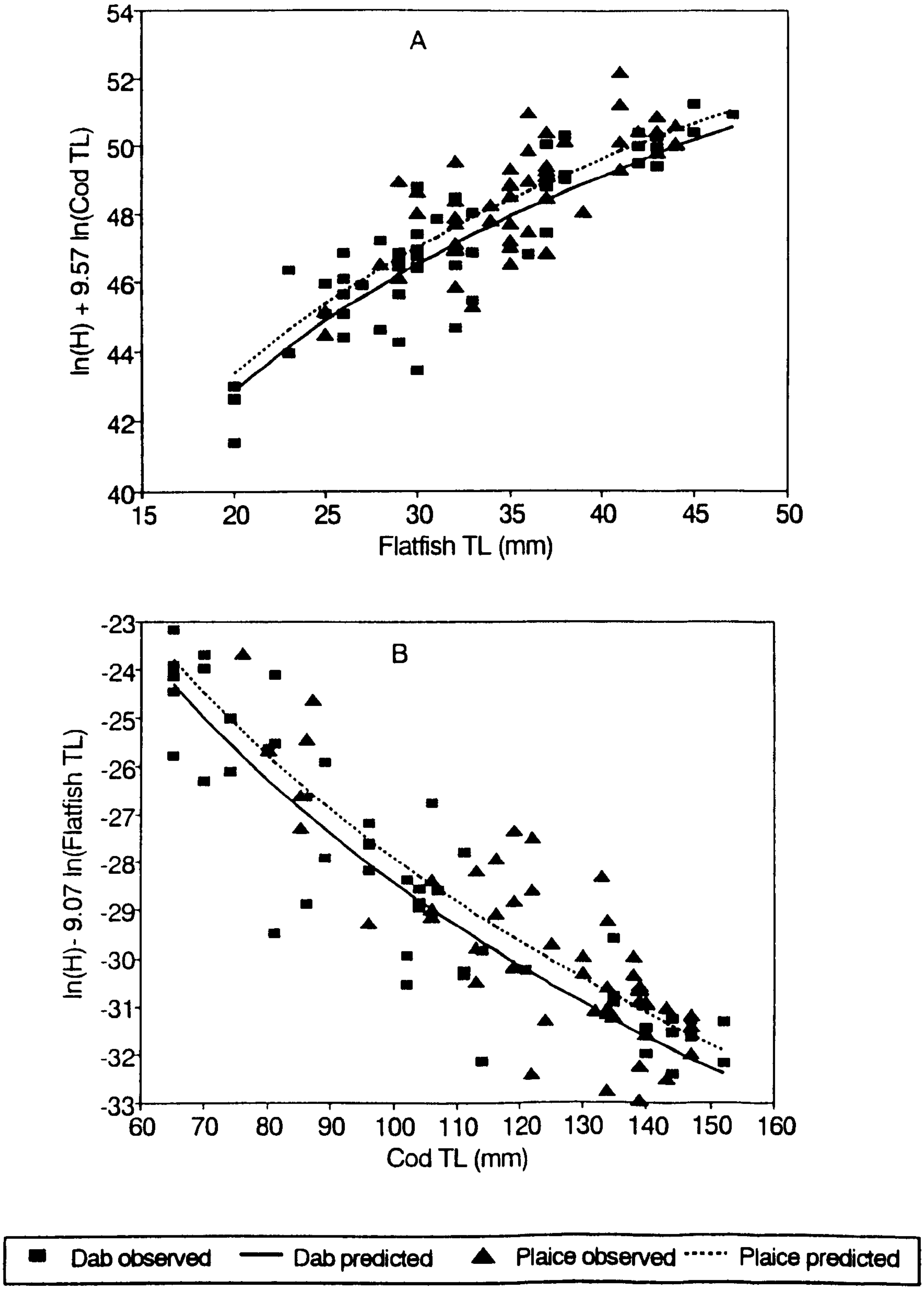


Figure 7.4: Handling times of flatfishes by cod, showing the effect of flatfish TL (A), cod TL (B) and flatfish species (A & B). The observed handling times were standardised for cod TL (A) and flatfish TL (B) using the regression relationships. The regression relationships are also shown.

ln H = 15.68 - 9.57 ln(cod TL) + 9.07 ln(dab TL)

ln H = 15.68 - 9.57 ln(cod TL) + 9.07 ln (plaice TL) + 0.50 (see Table 7.4).

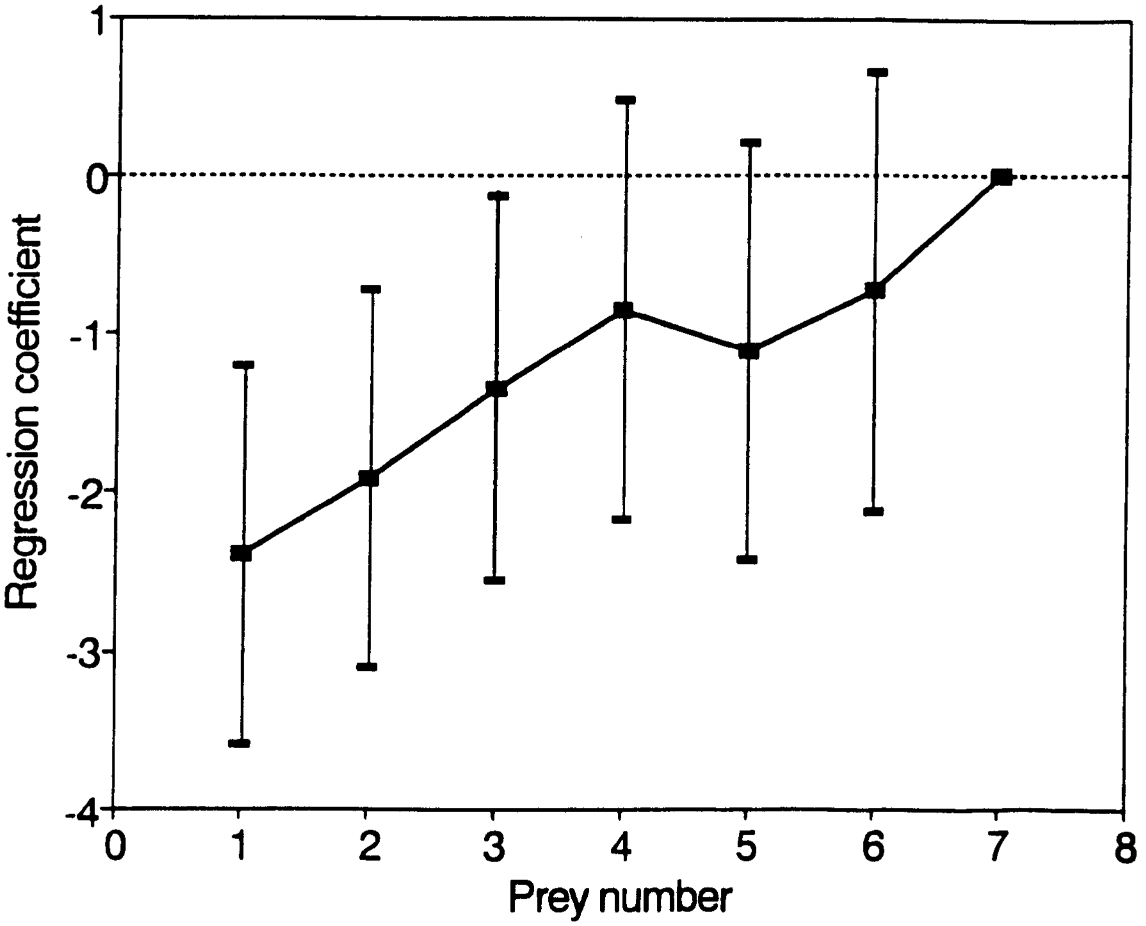


Figure 7.5: Regression coefficients for the effect of prey number on the handling time of dab by cod. Prey number refers to when the prey item was eaten within an experiment. The regression coefficient is the modification to the intercept when predicting the handling time for that prey number. The effect of prey number was not significant (p=0.0651). However, a trend of increasing coefficients is apparent, implying longer handling times for prey eaten later in a sequence.

of a peak in profitability for the range of prey sizes offered. Profitability decreased with increasing flatfish size and increased with increasing cod size (Figure 7.6; Table 7.6).

Size Selection Experiments

The sizes of cod, and the sizes of the dead dab offered, selected and ingested are given in Table 7.7. The frequencies of "pursuit", i.e. selection of the small, medium and large sized dabs were compared using χ^2 tests. The cod did not select for a particular size of dab at the "pursuit" stage (Table 7.8). The frequencies of ingestion and rejection of the small, medium and large sized dabs, once "pursued", were compared using χ^2 tests (contingency tables). The cod showed selection for small dabs at the ingestion stage (Table 7.8), but the result must be interpreted with caution because of low expected frequencies.

DISCUSSION

Morphological limitations of prey size

Cod were only observed to ingest flatfishes whole. Cod are attracted to the feeding activity of conspecifics (LOKKEBURG *et al.*, 1989) and food may be torn to pieces by cod seizing the same prey item (BRAWN, 1969). Such activity would allow cod to eat flatfish larger than the theoretical maximum size. This probably does not occur in the field as no dab remains were found larger than the predicted maximum size (Figure 7.7). The prey length: cod length ratio for maximum prey size of dabs (c. 0.44) was larger than for plaice (c. 0.39). Cod can ingest longer dab than plaice, because plaice are deeper for their length than dab (NORMAN, 1934).

Large flatfish (relative to cod size) were only seen to be ingested into the mouth horizontally. The diameter of the oesophagus probably does not restrict prey size as it is highly distensible, and does not restrict the prey size of larval cod (ECONOMOU, 1991a). The morphological limits that restrict prey size will therefore be the body depth of the prey and horizontal mouth gape (see HAMBRIGHT, 1991). ROBB & HISLOP (1980) found an isometric relationship between mouth gape (calculated from jaw

Table 7.5: GLM analysis of effects on profitability of cod size, flatfish size, flatfish species and prey number. Profitability was expressed as wet weight of flatfish gained per second handling time, and log transformed for analysis.

Source	GLM RESULTS			
	df	SS	F	p
In Cod TL	1	272.17	211.42	0.0001
In Flatfish TL	1	73.39	57.01	0.0001
Species	1	1.30	1.01	0.3170
Prey number	2	4.44	1.72	0.1834
Error	105	135.17		

Table 7.6: Regression estimates from GLM for predicting In profitability to cod of different sized plaice and dab. The estimates relating to cod TL and flatfish TL are coefficients.

Parameter	Estimate	p	S.E.
In Cod TL	9.39	0.0001	0.63
In Flatfish TL	-5.95	0.0001	0.80
Intercept	-20.09	0.0001	2.26

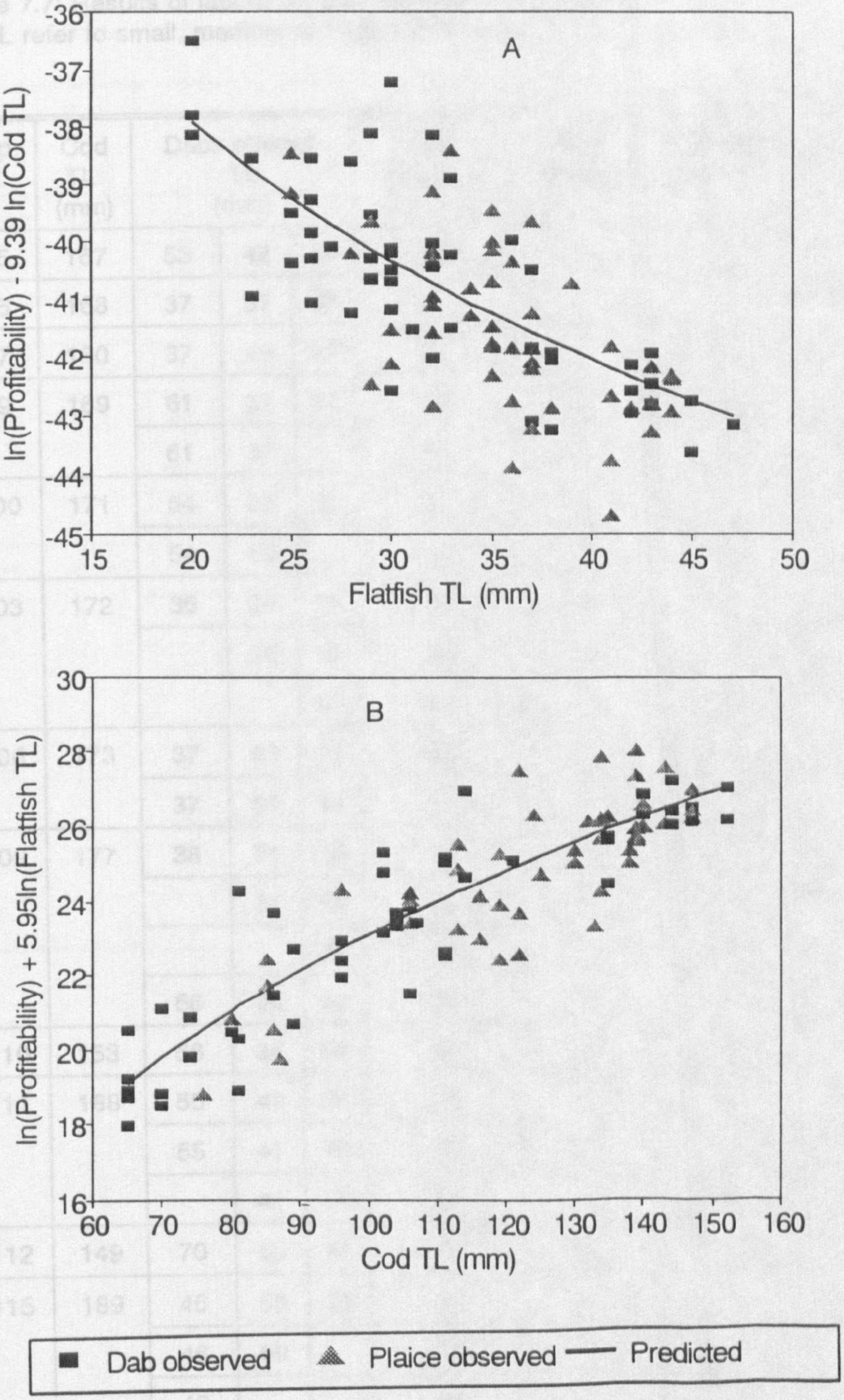


Figure 7.6: Profitability of flatfish prey to cod, showing the effect of flatfish TL (A) and cod TL (B). Profitability expressed as wet weight gained per unit handling time (mg s^{-1}). The observed profitabilities were standardised for cod TL (A) and flatfish TL (B) using the regression relationships. The regression relationships are also shown.

ln (Profitability) = -20.09 + 9.39 ln(cod TL) - 5.95 ln(flatfish TL) (see Table 7.6).

Table 7.7: Results of laboratory size selection experiments.
S/M/L refer to small, medium or large fish selected.

Exp. No.	Cod TL (mm)	Dabs offered TL (mm)			Dab selected TL (mm)	Size (S/M/L)	Ingested Yes/No	Dab TL/ Cod TL
95	167	53	42	35	35	S	Y	0.21
96	168	37	57	47	57	L	Y	0.34
97	150	37	49	47	49	L	N	0.33
99	169	61	37	54	54	M	Y	0.32
		61	37		61	L	N	0.36
100	171	54	63	37	37	S	Y	0.21
		54	63		54	S	Y	0.31
103	172	36	26	59	36	M	Y	0.21
			26	59	26	S	Y	0.15
				59	59	-	Y	0.34
106	173	37	53	61	53	M	Y	0.31
		37	51	61	61	L	Y	0.35
109	177	38	71	56	38	S	Y	0.21
			71	56	71	L	N	0.40
				56	56	-	Y	0.32
		56	35	65	56	M	N	0.32
110	153	56	35	65	56	M	N	0.37
111	188	55	41	70	70	L	N	0.37
		55	41	70	55	M	Y	0.29
			41	70	70	L	N	0.37
112	149	70	53	41	70	L	N	0.47
115	189	46	59	38	38	S	Y	0.20
		46	59		59	L	Y	0.31
		46			46	-	Y	0.24
		29	52	40	52	L	N	0.28
		29	52	40	29	S	Y	0.15
			52	40	52	L	Y	0.27
				40	40	-	Y	0.21

Table 7.7 (continued): Results of laboratory size selection experiments. S/M/L refers to small, medium or large fish selected.

Exp. No.	Cod TL (mm)	Dabs offered TL (mm)			Dab selected TL (mm)	Size (S/M/L)	Ingested Yes/No	Dab TL/ Cod TL
116	150	47	37	64	47	M	Y	0.31
			37	64	64	L	N	0.43
			37	64	37	S	Y	0.25
118	146		37	64	37	S	Y	0.25
120	151	60	43	33	33	S	Y	0.22
		60	43		60	L	N	0.40
		60	43	35	35	S	Y	0.23
125	197	37	61	45	45	M	Y	0.22
		37	61		61	L	N	0.31
		37	61		37	S	Y	0.19
			61		61	-	N	0.31
126	154	43	58	37	37	S	Y	0.24
		43	58		43	S	Y	0.28
			58		58	-	N	0.38
			59	42	59	L	N	0.38

Table 7.8: Summary of results of laboratory size selection experiments, with results of χ^2 analysis. Note expected frequencies < 5 for χ^2 analysis of ingestion.

	3 dabs offered						2 dabs offered			
Size selected	S		M		L		S		L	
Observed	8		8		6		6		9	
Expected	7.3		7.3		7.3		7.5		7.5	
χ^2	0.35 (df=1; p>0.75)						0.60 (df=1; p>0.25)			
Ingested	Y	N	Y	N	Y	N	Y	N	Y	N
Observed	8	0	6	2	2	4	6	0	2	7
Expected	5.8	2.2	5.8	2.2	4.4	1.6	3.2	2.8	4.8	4.2
χ^2	7.72 (df=2; p<0.025)						8.75 (df=1; p<0.005)			
Proportion eaten	1.0		0.75		0.33		1.0		0.22	

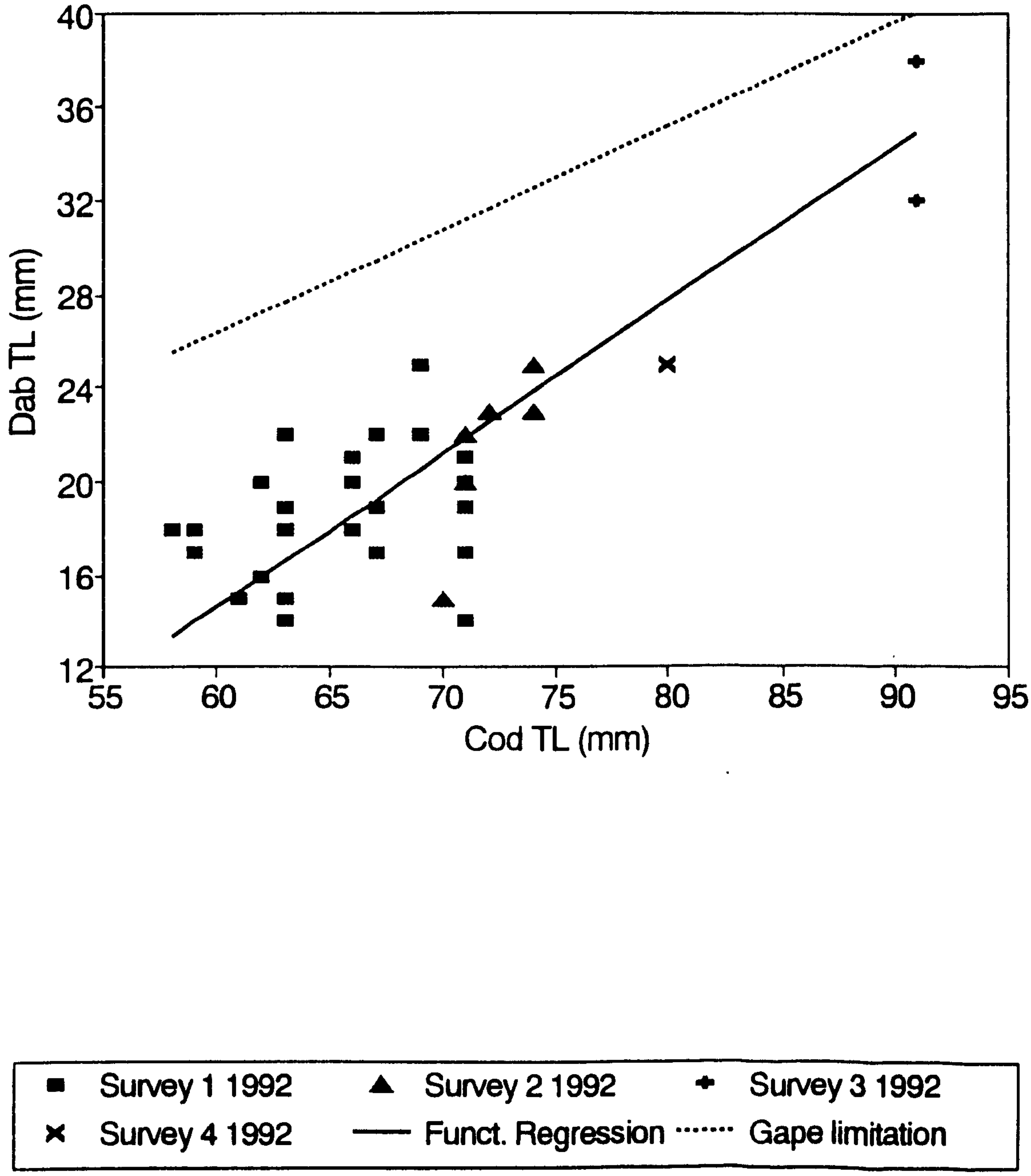


Figure 7.7: Sizes of dab eaten by cod in surveys 1-4 1992 with functional regression line fitted to the data. The upper size limit due to gape limitation is also indicated.

dimensions) and length for pelagic 0-group cod (20-84 mm). The ratios for maximum prey size will therefore probably apply over the range of cod sizes used here, provided that the relationships between body depth and length for the flatfish are also isometric.

Despite the ability to ingest larger dabs, the cod sampled in surveys 1 and 2 had selected dabs from the smaller, less abundant, size classes (Figure 7.7; Chapter 6). The largest ratio for dab TL: cod TL found in the field was 0.41 (Figure 7.7). Cod will therefore catch and eat prey close to the upper size limit in the field. It is predicted that this would result in a long handling time (248 s from regression relationships). Extended periods of handling may make fish more vulnerable to predators (KISLALIOGLU & GIBSON, 1976).

Handling times

Handling times decreased with increasing cod size. This is to be expected because mouth gape will increase and facilitate the ingestion of prey. Handling times increased with flatfish size. This is also to be expected because body depth increases with flatfish size, making larger flatfish more difficult to ingest. Handling times were longer for plaice than dab of the same length. This is because the body depth of plaice is greater than that of dabs. Prey morphology therefore affected handling time.

Handling times have been recorded to increase with satiation (KISLALIOGLU & GIBSON, 1976). Prey number did not significantly affect handling time, although there was an indication that handling time did increase with the number of prey ingested. The cod were eating prey large in proportion to their own size. The numbers of prey consumed was therefore low, particularly for larger prey, and may have made the effect, if present, difficult to demonstrate.

Profitability and "Optimum Prey Size"

The profitability of flatfishes increased with cod size. This could account for the occurrence of flatfishes in the larger cod in the field (Chapter 6). Profitability decreased with increasing flatfish size, over the range of predator and prey sizes used in the experiments (Figure 7.6). There was no evidence of a peak in profitability corresponding to an "optimum" prey size. Such monotonically decreasing profitabilities curves have previously been noted (HUGHES, 1980; HUGHES & SEED, 1981; DAVIDSON, 1986; BENCE & MURDOCH, 1986) and may be explained by a normal distribution truncated to the left of the mode (HUGHES, 1980). The optimal prey size is therefore smaller than the smallest prey sizes used.

A mean prey size eaten in the field may approximate to the "optimal" prey size (KISLALIOGLU & GIBSON, 1976). A mean dab size for cod size was estimated from field data by functional regression (R^2= 0.64; n=35; Figure 7.7). Mean dab size tended towards the maximum dab size for larger cod. The mean length ratio (dab size: cod size) therefore changed over the range of cod sizes which suggests cod were eating prey larger than a true optimal size. DEKKER (1983) applied the Andersen consumption model to estimate prey size preference of North Sea cod. He recorded a mean dab weight:cod weight ratio of 0.00641. This ratio was obtained from a large range of cod sizes (see DAAN *et al.*, 1990) and the fit was good (R^2=0.86; DEKKER, 1983). This weight ratio corresponds to a mean length ratio of 0.19 (using condition factors assumed by DEKKER, 1983). This prey length:predator length ratio was much lower than those used in the handling time experiments (Table 7.1).

Both the profitability analysis and DEKKER's (1983) ratio suggest that for 0-group cod feeding on flatfishes, the optimal prey size is below the minimum size available. The smallest flatfishes available will therefore always be the most profitable, which could account for the size-selective predation on dab in 1992, and the feeding on the small flounder in 1993 (Chapter 6). DEKKER's (1983) prey length to predator length ratio is smaller than the size ratio of 0-group plaice and dab and 0-group cod recorded at Tralee in 1992 and 1993. Predation by 0-group cod on flatfishes would therefore always be expected to be size-selective, as cod would show selection for the smaller size-classes. The degree to which cod concentrate on the smaller individuals will depend upon their density, and the encounter rates with, and profitabilities of, non-flatfish prey.

Dab and plaice of the same length are of similar profitabilities. Although plaice take longer to handle than dabs, they are heavier for their length. If plaice and dab were of the same size range and density, then cod would be expected to feed equally on both species. However dabs recruit to nurseries later than plaice (Chapter 6; EDWARDS & STEELE, 1968) and are therefore smaller at any one time. 0-group cod would therefore be expected to select dabs in preference to plaice, as dabs would be more profitable. Whether cod feed upon plaice would depend upon the profitabilities of, and encounter rates with, plaice and other prey.

Is there a behavioural component to prey selection?

Behavioural selection of prey size can occur at the pursuit stage (either pursue or continue searching) or ingestion stage (either ingest or resume searching) of feeding. The size-selection experiments gave no indication that cod selected at the pursuit stage for the smaller, more profitable, dab. This could be due to the experimental conditions, e.g. food availability, lack of complete information (STEPHENS & KREBS, 1986) or hunger level (HART & GILL, 1992). HART & ISON (1991) found that sticklebacks did not conform to the Basic Prey Model under laboratory conditions.

It could be argued that if cod feed at night in the field (see Chapter 5), at low light intensities, then they cannot visually judge prey size, and behavioural decision-making at the pursuit stage would not occur. Although the details of encounters of cod with flatfish in the field are unknown, there may be alternative sensory cues, e.g. mechanical or olfactory, for prey location (see ANSELL & GIBSON, 1993) and size determination enabling behavioural selection. Movement of food stimulates feeding behaviour in cod (BRAWN, 1969) and inactive food on the bottom is detected by chemo-reception as the barbel and pelvic fins are trailed on the substratum (BRAWN, 1969; LOKKEBURG *et al.*, 1989).

Behavioural selection of prey can also occur at the ingestion phase (see HUGHES & SEED, 1981; HART & ISON, 1991), although this is not emphasised in the literature. Predators may not handle prey for longer than a threshold "persistence" time, which may be a function of hunger (HUGHES & SEED, 1981). In the size-selection experiments, although there was no selection before the ingestion stage, cod were more likely to ingest small prey. This implies a behavioural decision at the ingestion stage, but the lack of data means no firm conclusions can be drawn.

The selection of larger and/or more prey: path analysis

If size-selection of small prey is independent of behavioural "decisions", then it will result solely from morphological parameters such as the ability to capture and ingest prey. Larger cod would then be expected to include larger dabs in the diet. If behavioural decisions are involved, then larger cod would be expected to exclude larger dabs from the diet, and maintain feeding on the more profitable small dabs. The number of dabs eaten would have then have to increase to keep food intake in proportion to body size.

Field data from 18/6/92 was used to examine the effect of prey size and number on the intake of dabs by cod. This was when the largest number of cod were caught containing dabs (see Figure 7.7) and it could be assumed that all cod encountered the same size distribution of prey. The variables under consideration were cod TL, the number of dabs, weight of dabs and total weight of dabs ingested (Table 7.9). There was a highly significant positive relationship between cod TL and weight of dabs ingested (Table 7.10).

It was desired to quantitatively assess the relative effects of prey number and prey size on the total weight of dabs ingested. Path analysis (KERLINGER & PEDHAUZUR, 1973; see BURROWS & HUGHES, 1991 for examples) is a method for quantitatively assessing the relative effects of causal variables on dependent variables. The relationships between variables are organised analytically as a path diagram (Figure 7.8) where arrows connect causal (independent) and effect (dependent) variables. Exogenous and endogenous variables are influenced by causes outside and inside the system respectively. The path coefficient (ρ_{ji}) relates the degree of change

Table 7.9: Data for cod caught in survey 1 1993, used in path analysis model. TL of dabs estimated in Chapter 6, and weights estimated from length-weight relationship.

Cod TL mm	No. of Dab	Dabs recovered from cod stomach										Mean W mg	Total W mg
		1		2		3		4		5			
		TL mm	W mg	TL mm	W mg	TL mm	W mg	TL mm	W mg	TL mm	W mg		
58	1	18	43									42.8	43
59	2	18	43	17	36							39.2	78
61	1	15	24									23.5	24
62	2	20	61	16	29							44.8	90
63	2	19	51	15	24							37.4	75
63	4	22	83	18	43	15	24	14	19			42.0	168
66	3	21	71	20	61	18	43					58.2	174
67	3	22	83	17	36	19	51					56.5	169
69	2	25	126	22	83							104.4	209
71	5	14	19	19	51	17	36	21	71	20	61	47.4	237

Table 7.10: Correlation (r) and regression (b) coefficients used as path coefficients in path analysis model. See text for explanation.

	Variables		r	b	p	Path coefficient
Spearman rank correlation	Cod TL	Total weight of dabs	0.875		<0.005	
Correlations of N scores	Cod TL	ln number of dabs	0.758		<0.005	ρ_{21}
	Cod TL	ln mean dab weight	0.596		<0.05	ρ_{31}
	ln number of dabs	ln mean dab weight	0.410		>0.10	ρ_{32} & ρ_{23}
Regression of N scores against N scores of ln total weight of dabs ingested	ln number of dabs			0.625	0.001	ρ_{42}
	ln mean dab weight			0.559	0.001	ρ_{43}

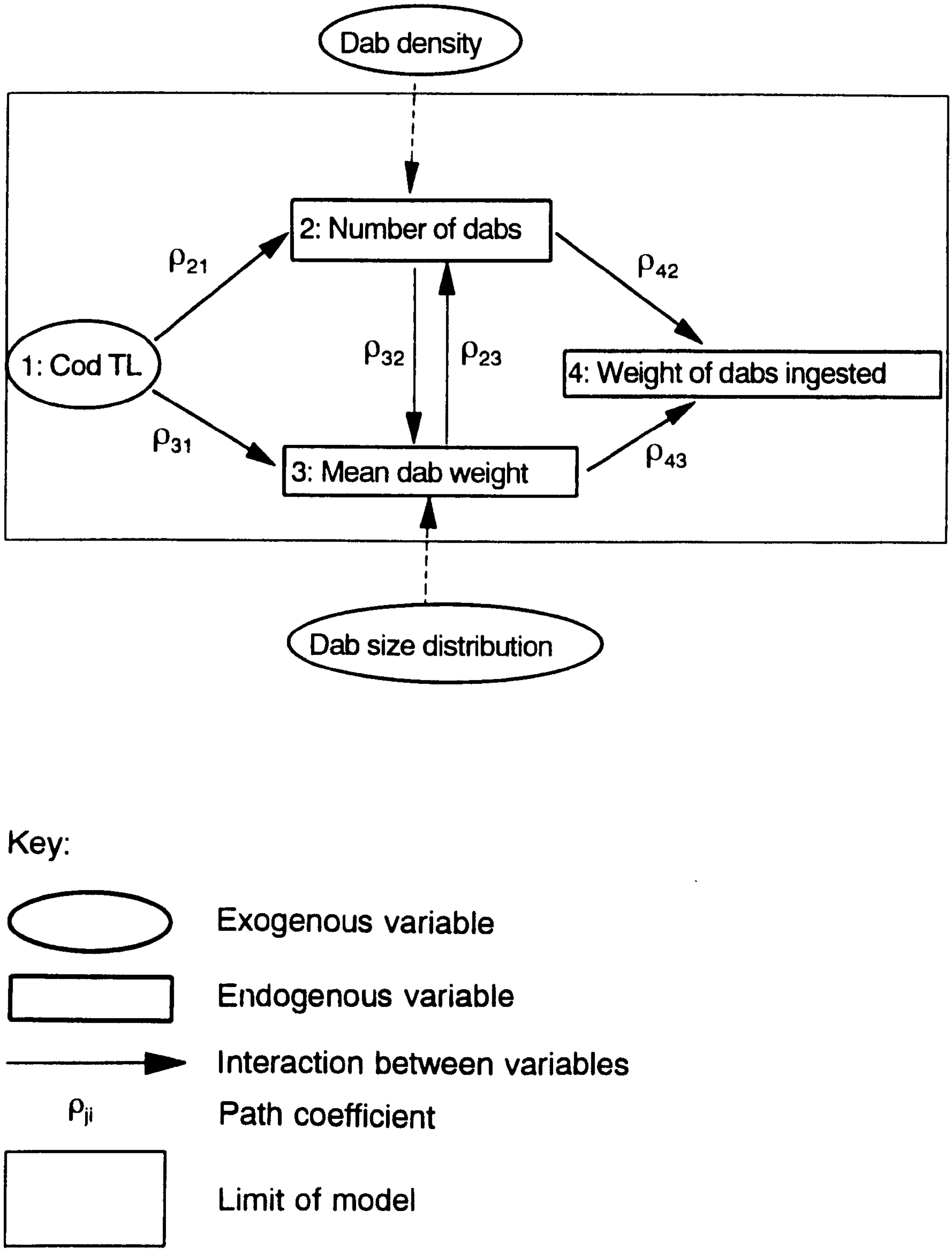


Figure 7.8: Path analysis diagram.
The weight of dabs eaten by cod is a product of the number of dabs and mean size eaten, and both factors will change with cod size.

in the effect variable to change in the causal variable. The path coefficient is equal to the correlation coefficient (of the N scores, i.e. normal deviates, see ZAR, 1984) for a variable dependent on a single cause. For variables dependent on two causes, the path coefficients are equal to regression coefficients (β) of the N scored data (see KERLINGER & PEDHAUZUR, 1973).

The weight of dabs ingested is a product of the number and size:

Total weight of dabs ingested = number of dabs x individual weight

Path analysis assumes that relationships between variables are linear. These data were therefore $\log_e$ transformed:

$$\ln(W) = b_1 \ln(\text{mean } W) + b_2 \ln(\text{number of dabs}) + c$$

The variables used in the path analysis model were

1: N scores Cod TL

2: N scores ln(Number of dabs)

3: N scores ln(mean weight)

4: N scores ln(Total weight of dabs ingested)

The path coefficients (Table 7.10) for both number and size were significant, showing both factors affect the total weight of dabs ingested. The relative importance of number and size can be assessed from:

ρ_{41} (via 2) = $\rho_{21} \times \rho_{42} = 0.758 \times 0.625 = 0.474$

ρ_{41} (via 3) = $\rho_{31} \times \rho_{43} = 0.596 \times 0.559 = 0.333$

ρ_{41} (via 2 and 3) = $\rho_{21} \times \rho_{23} \times \rho_{43} + \rho_{31} \times \rho_{32} \times \rho_{42}$

$$= (0.758 \times 0.410 \times 0.559) + (0.596 \times 0.410 \times 0.625) = 0.326$$

The path via the number of dabs (2) was more important than the path via dab size (3). This is evidence for behavioural selection of prey.

Prediction of Size Selection in the field

Prey selection in the field on 18/6/92 (see Figure 7.7) was compared to that predicted by the Basic Prey Model algorithm (after STEPHENS & KREBS, 1986).

$$\frac{\sum_{i=1}^{j} \lambda_i W_i}{1+\sum_{i=1}^{j} \lambda_i h_i} > \frac{W_{j+1}}{h_{j+1}}$$

where λ = encounter rate (no. s^{-1}) W = dab weight (mg)

h = handling time (s)

The Prey Algorithm predicts whether a prey item is included in, or excluded from, the diet. Prey items are incorporated into the algorithm in order of decreasing profitability (i=1 to j). If the right hand side of the algorithm is greater than the left hand side, then prey item $j+1$ is included in the diet, if not, then it is excluded.

Handling times of different sized dab by different sized cod were estimated from the regression relationship (Table 7.6). The sea temperature at Tralee in mid June (12°C, M. BURROWS, *pers. comm.*) was similar to laboratory temperatures at which handling times were measured. Weight was taken to represent energy content, and derived from the length/weight relationship. Encounter rate (no. s^{-1}) was predicted from the density of dabs (no. m^{-2}) and the search rate of cod (m^2s^{-1}). The encounter rate with different sized dabs was assumed to be directly proportional to the density, which assumes differences in visibility, activity or behaviour between size classes are insignificant. Movement stimulates feeding by cod, and the reactive distance of cod increases with prey size (BRAWN, 1969) which will favour encounter with larger dab. Densities of the different size-classes of the dab population were calculated as in Chapter 5. The search rate of the cod was unknown. Search rate (m^2s^{-1}) is the product of reactive distance (m) and foraging speed (ms^{-1}). Both reactive distance and foraging speed were assumed proportional to TL. The search rate of cod was therefore assumed proportional to TL^2, i.e.

$$\text{Search rate of cod} = c.\text{TL}^2 \ (\text{m}^2\text{s}^{-1})$$

The algorithm predicted that the smaller size-classes of dab would always be eaten as they are the most profitable. The upper limit of size eaten was predicted by changing "*c*" for the search area to obtain the plots shown in Figure 7.9. The algorithm predicted that the range of prey sizes eaten increased with increasing cod size (Figure 7.9), due to the increase in profitability of the larger dabs. Also when the encounter rate was increased by increasing *c*, then the range of prey sizes eaten decreased.

However to fit the predicted size range eaten to the observed sizes eaten in the field, the search rate had to be set unrealistically high, (c=12), i.e. the cod searched an area of 12 times the square of the body length each second. If the cod were foraging optimally, then either the encounter rates with prey, and/or the handling times were greatly underestimated.

In the handling time experiments cod did not always resume normal activity following the completion of handling of large prey, but would remain lethargic. There may be a recovery time following ingestion which would need to be included in the handling time (c.f. BEGON *et al.*, 1986, p. 323). Also handling times were simply the times for ingestion following capture. Strictly for the basic prey model handling times should include pursuit and ingestion times (HART & ISON, 1991). Although pursuit time (from encounter to capture) is thought to be negligible for swift-striking piscivores (HOYLE & KEAST, 1987), it is probably important for cod feeding on flatfishes. In addition, morphologically mediated size-selective processes are probably operating at the capture stage. The speed of the escape response of 0-group flatfishes increases with size (S. GIBSON, *pers. comm.*) which would favour selection of small dabs. Handling times should therefore be corrected to incorporate the probability of capture.

Most studies concerning the behavioural selection of prey by predators have used microphagous fishes or invertebrates feeding on sessile prey, as such species are amenable to laboratory experimentation. In the literature to date, the importance of the escape of prey (see HEATH, 1993), pursuit time and recovery time is not stressed, as these factors are not significant. The application of the basic prey model has revealed the probable importance of such factors to macrophagous cod.

The encounter rates with food will also have been underestimated because the

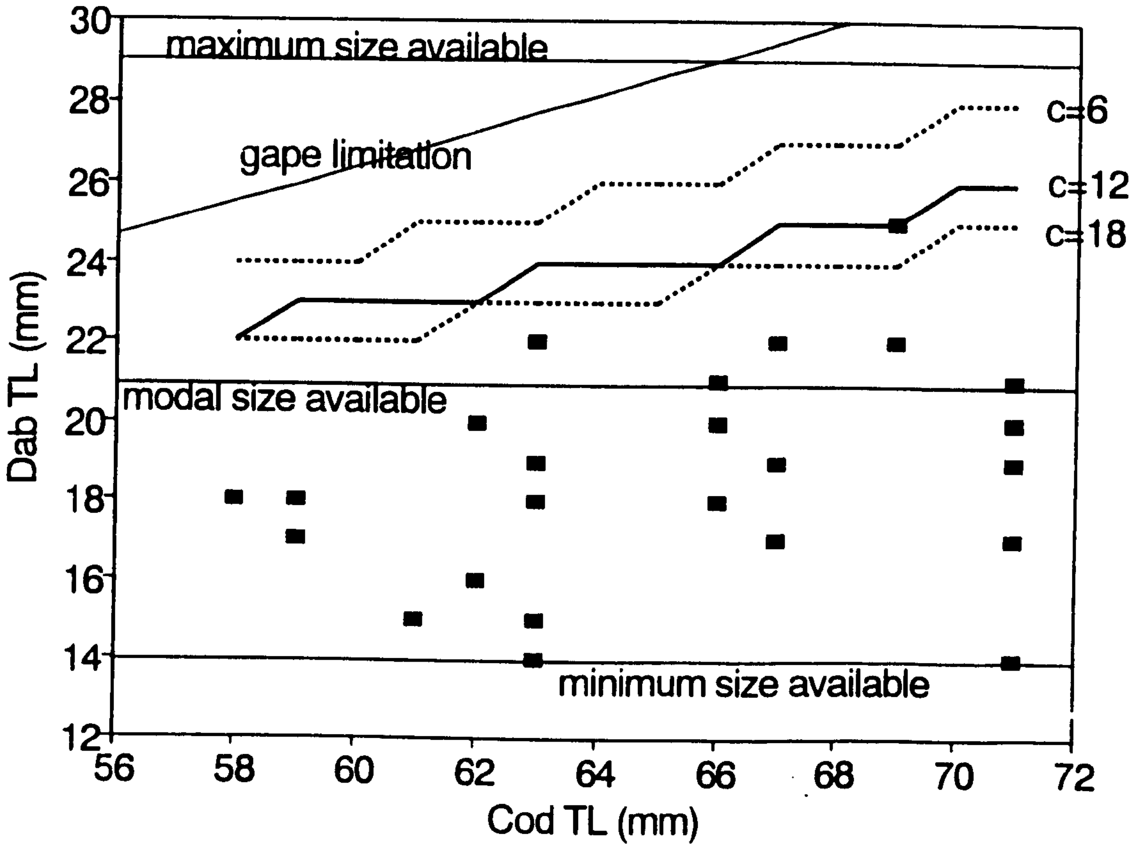


Figure 7.9: Sizes of dab eaten by cod in field survey 1 1992.
The minimum, modal and maximum sizes of dab available are also indicated. The maximum prey size that could be ingested due to gape limitation was predicted from the prey:predator length ratio of 0.44.
The upper prey size limit was predicted using the Basic Prey Model. The search rate (m^2sec^{-1}) of cod was unknown, but input into the model as c.cod TL^2. The effect of changing c on the upper size of dabs selected is shown. See text for further explanation.

presence of alternative food, other than dabs, was ignored in the analysis. In addition, the Basic Prey Model ignores the fact that foraging may be constrained by factors other than prey encounter rates and profitabilities, e.g. the risk from predation (see LIMA & DILL, 1990). Strong selection for small profitable prey with short handling times may have been the optimal strategy if the cod themselves were at risk from predation.

A DISCUSSION OF FEEDING BEHAVIOUR IN RELATION TO DENSITY-DEPENDENT MORTALITY

If the compensatory mortality observed in 0-group plaice populations (LOCKWOOD, 1980; VAN DER VEER, 1986; BEVERTON & ILES, 1992b) is truly density-dependent (see Chapter 6), then it will be due either to the feeding behaviour of predators, or the behaviour of the plaice. Behavioural mechanisms with the potential for producing density-dependent mortality are presented below. It has been assumed that density-dependent predation will produce density-dependent mortality (CUSHING, 1974). However predation rate would always be expected to increase as prey density increases. Density-dependent mortality will only occur if a larger proportion of the population is eaten at higher densities (LOCKWOOD, 1980; VAN DER VEER & BERGMAN, 1987), so the mortality rate increases. Mechanisms 5, 6 and 7 below would increase predation rate at higher densities, but whether density-dependent mortality would result is unknown, but could be resolved by modelling studies.

1. Numerical response of predators

A numerical response occurs when the number of predators increases as prey density increases, due to reproduction or immigration (SOLOMON, 1949). The time scale for a response to plaice density excludes the possibility of a reproductive response (VAN DER VEER & BERGMAN, 1987). Certain predatory fishes (LOCKWOOD, 1980) and *Crangon crangon* (VAN DER VEER & BERGMAN, 1987) have been suggested to migrate to nursery areas at times of high plaice density. However such migration responses are dubious when plaice form a limited part of predators' diets (see Chapter 5).

The response proposed by LOCKWOOD (1980) was direct proportionality in numbers of predators and prey at low plaice densities, and he recognised such a response would result in density-independent mortality. VAN DER VEER & BERGMAN (1987) also proposed a response of direct proportionality, but a population of predators would be resident in the nursery when plaice were absent (see Figure 7.10A). They assumed such a response could produce positive density-dependent mortality. However, if the number of prey eaten by each predator remained constant, then such a response would produce negative density-dependent mortality, as the proportion of the population eaten would decrease with increasing plaice density.

For a numerical response to produce positive density-dependent mortality without additional effects, it would have to be sigmoidal. Such a response could be caused by predators "switching" foraging micro-habitat and aggregating on patches of prey. For predators to remain aggregated, there would have to a continual production or recruitment of new prey.

2. Functional response of predators

VAN DER VEER & BERGMAN (1987) reported a functional response in predation rate of plaice by *Crangon crangon* in laboratory experiments, i.e. the predation rate increased as plaice density increased, and suggested such a response would produce density-dependent mortality. However, the response in predation rate only occurred at densities far above those they observed in the field, and no response was apparent at natural densities.

The shapes of functional responses vary, and responses may be "type 1", "type 2" or "type 3" (see BEGON *et al.*, 1986). The functional response observed by VAN DER VEER & BERGMAN (1987) is a type 2 response. Predation rate increased with prey density, but the rate of increase decreased until "predator saturation" occurred and predation rate levelled off (see Figure 7.10B).

The shape of a functional response is a product of the encounter rate and

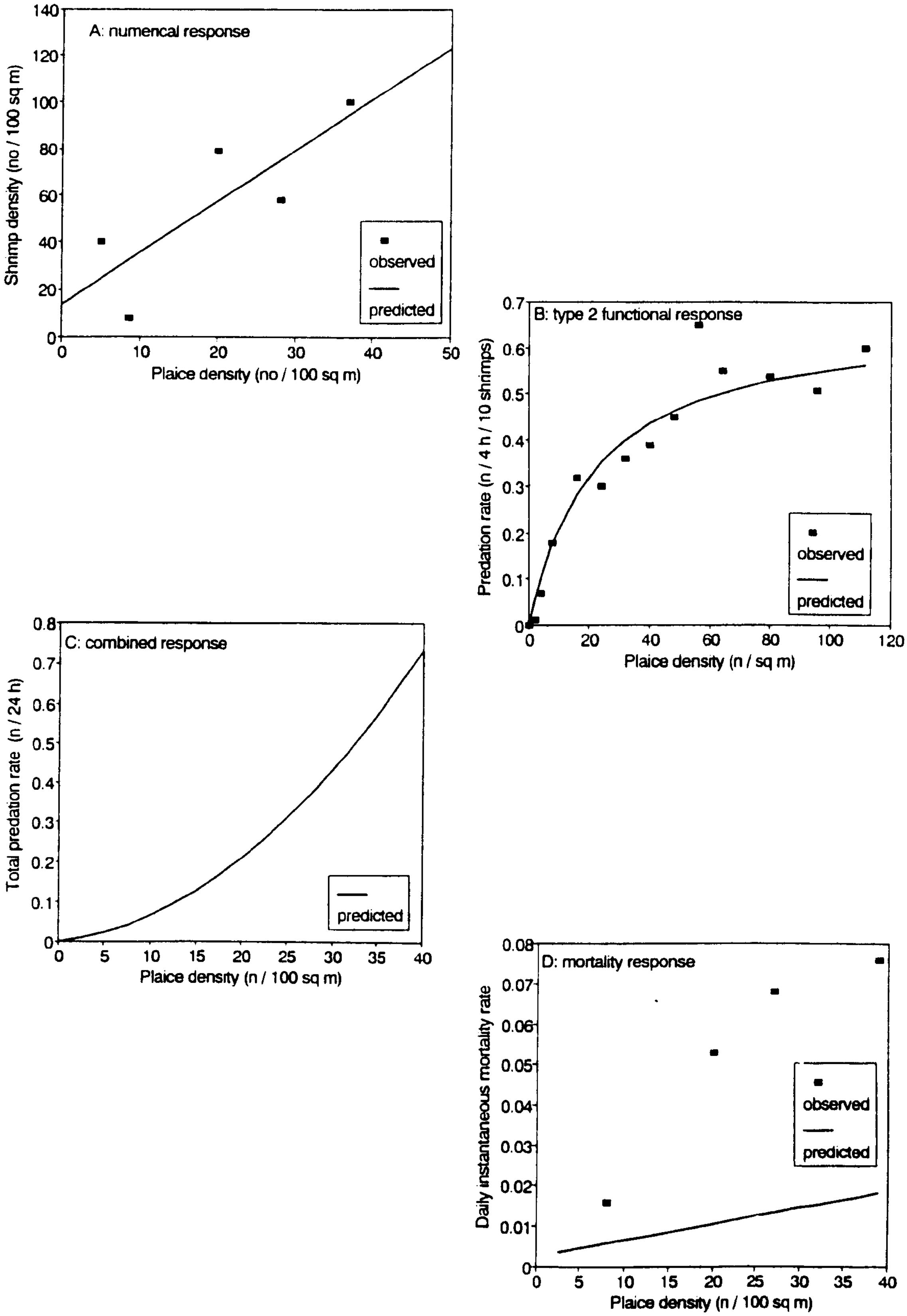


Figure 7.10: Illustration of a numerical response (A), a functional response (B), the combination of a numerical and functional response (C), and the effect of the combined response on mortality (D). Data for shrimp predating plaice, taken from VAN DER VEER & BERGMAN (1987).

handling time, and both factors can be predicted from a type 2 functional response using Holling's disc equation (from BEGON *et al.*, 1986)

$$P = (a'N) / (1 + a'hN)$$

where P: predation rate

a': searching efficiency or attack rate

N: prey density

h: handling time

This can be rearranged into the form of a straight line, i.e.

$$1 / P = 1 / (a' N) + h$$

Handling time and attack rate can therefore be derived from the regression of the reciprocal of predation rate against the reciprocal of prey density. Using VAN DER VEER & BERGMAN's (1987) data (Figure 7.10B) handling time (the intercept) was predicted by regression (n=12; R^2=0.96) at approximately 40 h. As their experiments only lasted approximately 36 h, the shape of the response must be considered dubious.

LOCKWOOD (1980) also proposed a type 2 response of migrant fish predators to plaice density, although he did not use such terminology. He suggested that search time would decrease as plaice density increased, i.e. the encounter rate would increase. As encounter rate increases, a larger proportion of the predators time is spent in handling prey rather than searching and produces a type 2 response. In type 2 responses, the rate of increase in predation rate decreases with increasing density. A type 2 functional response will therefore result in negative density-dependent mortality over all prey densities.

Only a type 3 functional response will produce positive density-dependent mortality (BEGON *et al.*, 1986) without additional effects occurring. This occurs when predation rate shows a "S-shaped" response to prey density (BEGON *et al.*, 1986). The rate of increase of predation rate increases at low prey densities producing positive density-dependent mortality. A type 3 response occurs when predators "switch" prey within a habitat in relation to prey density. Switching is due to experience when learning increases recognition, capture and/or handling efficiency (HUGHES, 1980; HUGHES *et al.*, 1992) and learning will be density-dependent.

3. A combination of a functional response and a numerical response

LOCKWOOD (1980) recognised that although density-dependent mortality would not result solely from a type 2 functional response or a numerical response of direct proportionality, a combination of the two responses would produce positive density-dependent mortality. Total predation rate (the product of individual predation rates and the number of predators) will increase exponentially (see Figure 7.10C) until the asymptote of either response is reached. However, such a process for producing strongly density-dependent mortality is dependent on predator numbers increasing greatly with only small increases in plaice density. In fact the combination of the numerical and functional responses proposed by VAN DER VEER & BERGMAN (1987) could not account for the density-dependent mortality observed in the field (Figure 7.10D).

4. Size-selective predation by predators and density-dependent growth

Predation on plaice by fishes (Chapter 6) and shrimp *Crangon crangon* (VAN DER VEER & BERGMAN, 1987) is size-selective, concentrated on the smaller size classes. Size-selective mortality is a possible cause of density-dependent mortality (SHEPHERD & CUSHING, 1980). If growth is density-dependent, due to either parasite load (see Chapter 1) or competition, and mortality is size-selective, then cumulative mortality will be density-dependent. Nevertheless, growth of 0-group plaice does not appear to be density-dependent (ZIJLSTRA & WITTE, 1985; VAN DER VEER & WITTE, 1993). However, the evidence needs to be reviewed (see Chapter 6).

5. Density-dependent consumption of smaller size-classes

A novel alternative explanation for increasing predation rate at higher densities is based upon size-selective predation. The encounter rate of predators with plaice will be density-dependent. If predation is size-selective, as encounter rates increase predators should concentrate on the more profitable, i.e. smaller, prey (HUGHES, 1980). The mortality of the larger, less profitable prey, would therefore be negatively density-dependent. However, for predators to reach satiation they would have to consume a larger number of small prey. The proportion of small prey eaten would therefore increase with increasing density, i.e. mortality of small prey would be positively density-dependent. Whether this could result in positive density-dependent mortality of the whole population is unknown.

6. Patch residence time of predators

LOCKWOOD (1980) suggested that the density of plaice would determine the time migrant fish predators spend on nurseries. According to the patch model (STEPHENS & KREBS, 1986), the time predators spend within a patch of prey will depend upon the energy gain function (proportional to food density) and the average travel time between patches. The energy gain function would depend upon the density of prey. "Migrant" predators would therefore be expected to remain feeding in plaice populations longer at higher plaice densities, but only if plaice form an important part of the diet.

7. Behavioural response of plaice

The potential for plaice behaviour to be modified by density and affect predation rate has been overlooked. There is evidence for food limitation in 0-group plaice populations, but not density-dependent growth (VAN DER VEER & WITTE, 1993). Foraging activity may increase at high plaice density and affect the encounter rate with predators and hence predation rate.

Conclusions

To conclude, the mechanisms (1, 2 & 3) currently proposed in the literature (LOCKWOOD, 1980; VAN DER VEER & BERGMAN, 1987) to produce positive density-dependent mortality of juvenile plaice populations are disputable. Factors other than plaice density could be responsible for apparent numerical responses (see Chapter 5). Compensatory mortality could occur without being truly density-dependent (Chapter 6). If true density-dependent mortality does occur in the demersal phase, then other mechanisms may be responsible, and density-dependent growth has to be a strong possibility.

CHAPTER 8:

GENERAL DISCUSSION

THE EFFECTS OF DENSITY, SIZE AND TIMING ON MORTALITY FROM PREDATION

The results were discussed in each chapter, so they will only be summarised here as the basis for a more general discussion.

A plaice spawning ground on the west coast of the Isle of Man was identified and egg production was estimated (Chapter 2). Although egg production constituted a small proportion of the total production of the Irish Sea plaice stock, sufficient larvae would theoretically be produced to supply local nurseries. Peak spawning was in March, before the spring zooplankton bloom in the Irish Sea.

Sprat and herring were identified as predators of plaice eggs in the Irish Sea (Chapter 3). Sprat were feeding more heavily than herring, probably due to their smaller size. Sprat >80 mm and herring selected plaice eggs from other smaller planktonic fish eggs. Individual sprat ate more plaice eggs than individual herring, and sprat were tentatively proposed as a major predator of plaice eggs in the Irish Sea.

I-group grey gurnards, poor-cod and whiting were identified as the major fish predators of newly settled plaice and dab on a Scottish fjordic nursery ground (Chapter 5). These fishes have not previously been recorded as predators of 0-group flatfishes, so the fish predators of 0-group plaice differ between nurseries. The predation rate of fish predators was quantified and shown to be a significant source of mortality of 0-group flatfishes. Fish predation on flatfishes was size-selective and concentrated on smaller individuals, both within and between species (Chapter 6). It was hypothesised that the timing of settlement would affect vulnerability to predation.

Laboratory experiments with 0-group cod (Chapter 7) were of use in explaining the size-selective predation on smaller flatfishes observed in the field. On the basis of weight of prey gained per unit handling time, the smallest flatfishes available would be the most profitable to 0-group cod. It was suggested that selection of prey by cod was determined by both behavioural and morphological processes, and that behavioural selection of prey may occur at the ingestion stage of feeding, rather than at the pursuit stage.

Density-dependent mortality has been a common theme for discussion in this thesis. It is generally accepted that density-dependent processes must operate in fish populations (ROTHSCHILD *et al.*, 1989), and that strong density-dependent processes regulate year-class strength in the first year of life when mortality rates are high and can be regulated to a sufficient degree (SHEPHERD & CUSHING, 1980). SHEPHERD & CUSHING (1980) argued that strong density-dependent mortality must occur in the egg or larval stages. CUSHING (1974), SHEPHERD & CUSHING (1980) and CUSHING (1983) directed attention to the larval phase, suggesting density-dependent growth would produce density-dependent mortality. However, in 1984 Beverton suggested that the extent of variation in recruitment (reflecting the strength of density-dependent processes) was inversely related to the degree of concentration in the juvenile phase (see VAN DER VEER *et al.*, 1990). This has become known as "the concentration hypothesis" (BEVERTON, 1993).

The current thinking is that density-independent processes (generating variation in year-class strength) occur in the egg and larval phases of marine fishes, and density-dependent processes (reducing the variation) occur in the juvenile stage (see BAILEY & HOUDE, 1989). Plaice is considered to be a good example, as there is evidence for density-independent mortality in the egg stage (ZIJLSTRA & WITTE, 1985) and density-dependent mortality in the juvenile stage on the nursery ground (LOCKWOOD, 1980; VAN DER VEER, 1986; VAN DER VEER & BERGMAN, 1987; BEVERTON & ILES, 1992b).

However, the evidence for density-dependent mortality in the juvenile phase of plaice, derived by correlating mortality rates with population densities from different nurseries (LOCKWOOD, 1980; BEVERTON & ILES, 1992b) is weak. The statistical problem of correlating dependent variables, i.e. density and the mortality rate estimated from densities, cannot be overlooked. Pooling data from different nurseries implies a single common mortality process, but predators differ between nurseries (VAN DER VEER *et al.*, 1990; Chapter 5). Factors other than plaice density, which may be correlated with density (e.g. plaice size), are likely to have a stronger effect on mortality rate than density itself (Chapter 6). Compensatory mortality could occur in the early demersal phase without density-dependent processes occurring (see Chapter 6). Also, the predatory mechanisms suggested for producing density-dependent mortality of 0-group plaice (LOCKWOOD, 1980; VAN DER VEER & BERGMAN, 1987) are dubious (see Chapter 7).

Arguably the most convincing evidence in support of the theory that density-dependent mortality occurs on the nursery ground is the reduction in the coefficient of variation in abundance (CoV) between settlement and July recorded by VAN DER VEER (1986). However the CoV (standard deviation/mean) will be affected by the scale of sampling (BAILEY, 1994) and the number of observations. The CoVs in the pelagic phase in VAN DER VEER (1986) are inversely related to the number of observations. Also the CoV of late stage eggs is similar to the CoV at recruitment (see VAN DER VEER, 1986). This is surprising if density-independent factors operating in the egg stage generate variability in year-class strength, as suggested by ZIJLSTRA & WITTE (1985). The CoV in recruitment of plaice is very similar in the North Sea (35% at age 2, VAN DER VEER, 1986) and Irish Sea (32% at age 1, see Chapter 1), despite the fact that predation mortality on Irish Sea nurseries is likely to be density-independent (VAN DER VEER *et al.*, 1990; Chapter 5). The CoVs can therefore be used as evidence that density-dependent mortality occurs before the nursery stage, in the egg stage.

BRANDER & HOUGHTON (1982) provided equivocal evidence that density-dependent mortality occurs, and is complete, before the late egg stages of North Sea plaice. COOMBS *et al.* (1990) estimated plaice egg mortality over short periods of time, and the rates were higher than previous estimates derived for longer time periods. They sampled around the time of peak egg production, i.e. at times of high egg density, so mortality may have been high due to density-dependent mortality.

BAILEY & HOUDE (1989) concluded that the mortality of plaice eggs was density-independent. However the mortality rates they used were calculated from all egg stages (see HARDING *et al.*, 1978) and density-dependent mortality would only be expected at high egg densities, i.e. for newly spawned eggs. Unfortunately, density-dependent mortality is difficult to show if it is masked by stronger density-independent processes (BAILEY & HOUDE, 1989).

It was proposed in Chapter 3 that density-dependent mortality is likely to occur in the early egg stages of plaice. Plaice spawn when there is little alternative food for predators and plaice eggs are large and selected for by predators. Plaice eggs may then locally form a significant part of predators diets as they are a "profitable" prey item. Plaice eggs are concentrated over specific spawning grounds, so they may provide a "patch" of food for predators.

The effects of patchiness and dispersal on density-dependent processes of pelagic stages of fish eggs and larvae have been the subject of recent discussion (CUSHING, 1983; MCGURK, 1986; GULLAND, 1987; MCGURK, 1987; ROTHSCHILD, *et al.*, 1989; ECONOMOU, 1991b). Similarly, spatial heterogeneity and density-dependence has attracted recent interest from insect ecologists (see HASSELL, 1987; MOUNTFORD, 1988). MCGURK (1986) proposed that the predation mortality of fish eggs and larvae was high due to aggregation in high density patches, although he did not classify the process as density-dependent. HUNTER (1984) also suggested that clupeid predation on plaice eggs was more intense than on cod eggs, because of the higher density of plaice eggs.

Mortality will only be density-dependent if the principal predators respond to patches of prey. Planktivorous fishes are thought to be the major predators of pelagic eggs and larvae (see reviews by HUNTER, 1984 and BAILEY & HOUDE, 1989) and BAILEY & HOUDE (1989) indicated future research should be directed towards such predators.

Of the potential mechanisms for producing density-dependent mortality of pelagic eggs (see Chapters 1 and 7), switching from alternative prey to feeding on plaice eggs is the most probable cause. Herring show opportunistic switching behaviour to feeding on patches of fish larvae (HOPKINS, 1989) and herring and sprat switch to feeding on plaice eggs when egg density exceeds a minimum level (DAAN, 1976).

Prey switching by a population of predators may result from the proportion of specialists in the population increasing rather than individual consumers gradually changing prey preference (BEGON *et al.*, 1986). Individual herring, sprat, anchovy and sandeel do feed exclusively on plaice eggs at times of high egg density (Chapter 3; GARROD & HARDING, 1981). Such exclusive selection for individual prey items by sympatric individuals has been used as circumstantial evidence for prey switching (see HUGHES, 1980).

Switching of prey in relation to prey density occurs either because predators change selection for prey within a habitat, or change the micro-habitat where they forage (BEGON *et al.*, 1986). Although GARROD & HARDING (1981) suggested that planktivorous fishes (herring, sprat, anchovy and sandeel) showed such responses when feeding on plaice eggs, they did not recognise that such behaviour could produce density-dependent mortality.

Theoretical discussion by fishery ecologists of the effects of patchiness on density-dependent mortality has focused on micro-habitat switching (GULLAND, 1987; MCGURK, 1987). This occurs when predators aggregate on patches of prey, i.e. show a numerical response, and is the most common mechanism for prey switching (BEGON *et al.*, 1986). GULLAND (1987) argued that a patchy distribution of fish eggs and larvae would only increase mortality if predators aggregate on patches and do not become satiated. Planktivorous fishes are highly motile and numerous, and therefore could aggregate on patches of food and consume large numbers of eggs.

Switching of prey within a habitat (a "type 3" functional response), will also produce density-dependent mortality (see Chapter 7), and has been recorded in fishes (see BAILEY & HOUDE, 1989). Anchovies show such a response when feeding on their own eggs (VALDÉS SZEINFELD, 1991). A type 3 functional response occurs if learning increases efficiency at one of the four stages of raptorial feeding, i.e. encounter, capture, handling or ingestion (HUGHES, 1980; HUGHES *et al.*, 1992). The selection of plaice eggs will lead to density-dependent experience of such prey (see Chapter 3). An increase in the efficiency of capture, handling or ingestion of plaice eggs seems unlikely. Fish eggs are immobile and cannot actively evade predators. The round smooth shape of eggs, and absence of appendages, will facilitate handling and ingestion by raptorial predators (see HAVEL & DODSON, 1984; MCGURK, 1986). Learning at the encounter stage would therefore be the most logical explanation for prey-switching within a habitat to feeding on plaice eggs.

Learning at the encounter stage can occur through the development of a "search image" (HUGHES, 1980). A search image is "a perceptual change in the ability of a predator to detect familiar cryptic prey" (see LAWRENCE & ALLEN, 1983). Fish eggs are cryptic, as they are transparent in the early stages of development to reduce visibility to visual predators (BAILEY & HOUDE, 1989). Search images are formed when predators attend selectively to certain characteristics or stimuli of prey, e.g. size, colour, shape, presence or absence of appendages (CROY & HUGHES, 1991; HUGHES *et al.*, 1992), which enable the predator to distinguish it from the background (LAWRENCE & ALLEN, 1983). The formation of search images by visually feeding planktivorous fishes may be important for predation on early stage fish eggs. CROY & HUGHES (1991) found that experience increased the reaction distance of the fifteen-spined stickleback *Spinachia spinachia* to planktonic prey (*Artemia*), and HUGHES & CROY (1993) found strong evidence in support of the formation of a search image.

ROTHSCHILD *et al.* (1989) and ECONOMOU (1991b) suggested that planktonic dispersal would minimise density-dependent processes, although they only considered competition between larvae for food. It has been suggested that a pelagic dispersal phase carries eggs and larvae from areas of intense predation to areas of lesser predation (see ECONOMOU, 1991b). The local density of eggs will decrease with age due to mortality and diffusive processes (MCGURK, 1987), as pelagic transport carries eggs away from areas of egg production. The mortality rate of eggs may, therefore, decrease with age due to a decrease in density. Data on age and mortality rate of plaice eggs (Table 8.1, from HARDING *et al.*, 1978) support this. Mortality rate does differ between egg stages (Table 8.2) and there is a drop in mortality rate from stage I to stage III eggs (Table 8.1) which could be due to a reduction in density. The increase in mortality for later stage eggs could be due to embryonic development, increasing visibility to visual predators (see Chapter 3).

MCGURK (1986) suggested that mechanisms controlling the spatial patchiness of eggs may influence the year-class strength of fishes. The year-class strength of North Sea plaice is thought to be determined by the mortality rate in the early egg stages (ZIJLSTRA & WITTE, 1985). Density-dependent mortality of newly spawned plaice eggs could account for both the inter-annual differences in year-class strength related to temperature (see ZIJLSTRA & WITTE, 1985), and the difference between the level of recruitment in the North Sea and Irish Sea (see BASIMI & GROVE, 1985).

The relationship between total egg mortality of plaice and temperature appears to be in contradiction to "the stage duration hypothesis" of Houde (see PIHL, 1990). Predation rate would have to be reduced to such a degree by low temperatures (BANNISTER *et al.*, 1974) that despite the extended development time, cumulative mortality is reduced. Low temperatures extend development time, and as density decreases with age, if mortality is density-dependent, then cumulative mortality could decrease with stage duration.

The level of recruitment (fish ha^{-1}) of plaice is lower in the Irish Sea than in the North Sea (BRANDER & DICKSON, 1984). Plaice eggs are dispersed further from the spawning grounds in the North Sea than in the Irish Sea (see SIMPSON, 1959a; 1959b). The mortality rate of plaice eggs in the Irish Sea would therefore be expected to be higher than in the North Sea. The mortality rate between egg stages II and III does seem to be higher in the Irish Sea than in the North Sea (see Table 8.1).

It is proposed that a single process, density-dependent mortality of newly

Table 8.1: Mortality rates of different stages of plaice eggs in Southern Bight and English Channel (from HARDING *et al.*, 1978) and in Irish Sea (from HARDING & TALBOT, 1973).

Region	Year	Daily instantaneous mortality rates between stages				
		I-II	II-III	III-IV	IV-V	I-V
Southern Bight	1947	0.047	0.006	0.058	0.046	0.040
	1948	0.187	0.069	0.128	0.175	0.142
	1950	0.147	0.032	0.040	0.144	0.094
	1951	0.187	0.009	0.073	0.040	0.070
	1952	0.055	-	-	0.022	0.059
	1957	0.068	-	-	0.115	0.102
	1962	0.040	0.024	0.036	0.017	0.081
	1963	0.038	0.002	0.009	0.029	0.020
	1968	0.011	0.103	0.065	0.196	0.105
	1969	0.081	0.018	0.111	0.086	0.075
	1971	0.107	0.076	0.105	0.159	0.116
	Mean	0.088	0.038	0.069	0.094	0.082
E. Channel	1971	0.182	0.092	0.104	0.163	0.134
Irish Sea	1965	0.033	0.214	0.028	0.051	0.095

Table 8.2: Results of generalised linear model testing effects of year and stage on mortality rate of plaice eggs in Southern Bight.

Source	d.f.	Sum of squares	F	p
Year	10	0.0536	3.04	0.011
Stage	3	0.0213	3.82	0.022
Error	26	0.0483		

spawned eggs, may both reduce and cause inter-annual variation in year-class strength of plaice. SHEPHERD & CUSHING (1980) stated that

> "the key to both the density-dependent processes which regulate the size of fish populations, and the stochastic variations which perturb it, is to be found during the egg and larval stages of the life history, when enormous mortalities occur. It seems very possible that both density dependence and variability may arise as modulations of the very processes which produce that mortality."

SHEPHERD & CUSHING (1980) also argued that the variability in recruitment must be generated during or after the period when density-dependence operates. Spawner-recruit models (e.g. Ricker, and Beverton and Holt) are based upon the compensatory mortality of pre-recruits (BAILEY & HOUDE, 1989). Representation of recruitment to fish stocks by such models necessitates that density-dependent mortality occurs at, or before, the stage when the variability in recruitment is generated. ELLIOTT's (eg. 1987) classic work on stock recruitment relationships in brown trout *Salmo trutta* has shown that density-dependent processes occur early in the life history, and density-independent processes act later.

Density-dependent mortality in the egg stage of fishes is probably not unique to plaice. Density-dependent mortality of Pacific salmon eggs has been recorded (see CUSHING & HARRIS, 1973), a species where such processes are amenable to study. VALDÉS SZEINFELD (1991) recorded a type 3 functional response in predation rate of anchovy (*Engraulis capensis*) to the density of anchovy eggs, which would result in density-dependent mortality in the egg stage.

The positive relationship between fecundity and the degree of density-dependence (see CUSHING & HARRIS, 1973) suggests that density-dependent mortality in the early egg stage may be a feature common to many fish stocks. Highly fecund species will produce high density patches of newly spawned eggs (or newly hatched larvae for demersal spawning species) when spawning is concentrated over fixed grounds. It may be no coincidence that both plaice and cod spawn large eggs early in the year (see RUSSELL, 1976) and show a low variability in recruitment (see

Table III in BERGMAN *et al.*, 1988). RIJNSDORP & JAWORSKI (1990) suggested that both plaice and cod eggs are subject to a common mortality process, and clupeids show selection for both these large eggs (DAAN, 1976; DAAN *et al.*, 1985).

The importance of size and timing, and their interaction, in affecting vulnerability to predation became apparent in this thesis (Chapters 3 and 6). A negative relationship between size and mortality rate is well established (see GULLAND, 1987), presumably due to vulnerability to predation (CUSHING, 1974). Size-selective predation on the smaller juvenile flatfish on a nursery ground was recorded in this study, thereby producing size-selective mortality (Chapter 6). However, the concept that larger size favours survival in the pelagic environment, i.e. the "big is better hypothesis", has recently been questioned by LEGGETT & DEBLOIS (1994). They recognised that predators do not always feed on the smaller individuals because larger prey are more obvious and of a greater energy value.

These concepts are well illustrated by clupeid predation on plaice eggs (Chapter 3) and egg mortality rates (RIJNSDORP & JAWORSKI, 1990). Clupeids >80 mm selected for the large plaice eggs, so larger size would appear disadvantageous. However clupeids <80 mm selected against plaice eggs, so larger size was advantageous. What LEGGETT & DEBLOIS (1994) did not consider was that mortality rate is affected by the number (CUSHING, 1974) and feeding activity of predators. The small predators selecting for smaller eggs will presumably be more numerous and be feeding more intensely than the larger predators selecting for the larger plaice eggs. This is borne out by a negative relationship between mortality rate and egg size (RIJNSDORP & JAWORSKI, 1990).

The potential for the timing of events to affect year-class strength was established by Cushing's "match-mismatch hypothesis" (CUSHING, 1972; see CUSHING, 1990b for review), proposed for larval feeding conditions. The importance of timing to predatory conditions seems to have been overlooked until recently (see

VAN DER VEER, 1985; VAN DER VEER *et al.*, 1991; HOVENKAMP, 1991; Chapter 3; Chapter 6). Significant intra- and inter-annual differences in predation mortality can result from (after BAILEY & HOUDE, 1989):

1. variation in abundance of predators,
2. variation in predator and prey distributions (either biologically or physically mediated) causing variation in predator-prey overlap,
3. variation in abundance of alternative prey for predators,

and all these factors vary with time.

The effects of timing on predator abundance, and predator and prey size overlap, was illustrated in Chapter 6. Late recruitment of dab resulted in a small size when 0-group gadoids were abundant and of a size able to eat small flatfishes. In Chapter 3 it was suggested that clupeids concentrated feeding upon fish eggs, particularly plaice eggs, in March because alternative prey was scarce. As there is considerable variability in the timing of the plankton bloom in the Irish Sea (SAVIDGE & CAIN, 1990), there may be great inter-annual variability in the extent of clupeid predation on fish eggs.

Temperature has a significant effect on the year-class strength of plaice and other marine fish species (see THOMPSON & HILDEN, 1989; HENDERSON & SEABY, 1993). Temperature determines the rate of development of fishes and will therefore affect timing of events, and size at time. Timing in relation to predation may be an important factor in determining the year-class strength of many fish species.

The differences in time of spawning between species and stocks, but the regularity within a stock (CUSHING, 1969) implies an optimal time to spawn. Spawning may be synchronised with periods of high food density (CUSHING, 1990b), or low predation pressure (see Chapter 3). Whether there is an optimal time for larval settlement is unknown, but the time of settlement is likely to affect predatory and feeding conditions in the juvenile habitat (CHAMBERS & LEGGETT, 1987; Chapter 6).

The concept of optimal times for spawning and settlement has received attention from marine invertebrate ecologists (see TODD & DOYLE, 1981). Larval development time is seen to bridge the time gap between the optimal times for spawning and settling (the "settlement timing hypothesis"), and be determined by egg size and developmental mode, i.e. planktotrophic or lecithotrophic (TODD & DOYLE, 1981). Pelagic development time of fishes will be influenced by dispersal requirements (CUSHING, 1990a; ECONOMOU, 1991b) and be determined by egg size, development rate and the sizes at hatching and settlement.

The mean size of pelagic eggs changes over the spawning season (e.g. HORWOOD, 1990), which suggests that the optimal size of eggs changes. The size of pelagic eggs is a key factor in life histories, affecting fecundity, development time, dispersal, mortality, larval size and dependency on planktonic production (TODD & DOYLE, 1981; RIJNSDORP & JAWORSKI, 1990; ECONOMOU, 1991b; Chapter 3). For example, the increase in size of plaice between hatching and settlement is less than that of dab (Table 8.3), so plaice are less dependent on planktonic production. Also, as plaice are larger at hatching they can search a larger area, and capture and ingest a wider size range of prey.

Size at settlement will affect vulnerability to predation (see CHAMBERS & LEGGETT, 1992). Flounder are smaller than plaice and dab at settlement (Table 8.3) and suffered higher predation rates from a greater taxonomic variety and size range of fish predators (Chapters 5 & 6). The similarity in size at settlement of plaice and dab (Table 8.3) suggests an optimal size for settlement. Also size at metamorphosis is typically less variable than age at metamorphosis, although plaice may be unusual in this respect (CHAMBERS & LEGGETT, 1987). Plaice in Port Erin Bay complete metamorphosis at 14-18 mm, with only 4% completing metamorphosis at <13 mm (RILEY, 1966b), while in the Wadden Sea >50% of plaice settle at <13 mm (Fig. 7 in VAN DER VEER, 1986). It is these fish (9-13 mm) which are mainly eaten by shrimp (Fig. 13 in VAN DER VEER & BERGMAN, 1987).

The time of spawning, egg size, size at hatching, size at settlement and time

Table 8.3: Comparison of life history strategies of plaice, dab and flounder. Sizes taken from NICHOLS (1971). Spawning periods taken from RUSSELL (1976), and settlement periods taken from VAN DER VEER *et al.* (1991). The period of settlement of dab in the southern North Sea is not cited in the literature, but can be assumed to occur after plaice, as it does in other areas (EDWARDS & STEELE, 1968; *pers. obs.*).

	Plaice	Flounder	Dab
Period of peak spawning in southern North Sea.	late January - early February	February - April	March - June
Egg diameter (mm)	1.66 - 2.20	0.82 - 1.13	0.66 - 0.98
Larval size on hatching (mm)	5.5 - 7.0	2.25	3.0 - 4.0
Size at settlement (mm)	14	10	14
Period of settlement in southern North Sea	March - April	April	Not cited in literature

of settlement differ between species (MILLER *et al.*, 1991; CHAMBERS & LEGGETT, 1992; Table 8.3). Egg size, size at hatching and size at metamorphosis also vary with latitude (MILLER *et al.*, 1991). That life history traits affecting predation differ within and between species, suggests that the processes determining and regulating year-class strength vary not only between species, but also over the geographical range of a species (see MILLER *et al.*, 1991).

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Appendix 1: Numbers of plaice eggs recorded in 1991 survey

	Station	Approx. bottom depth (m)	Volume sampled (m^3)	Number of plaice eggs of stage recorded				
				I	II	III	IV	V
28/2	1	46	82.4	3		1		
	1		73.8	4	1	1		
	2	42	65.9					
	2		88.8					
	3	42	68.6		2			
	3		81.6	1				
	4	41	67.7					
	4		84.0	3				
1/3	5	28	74.2	2				
	5		70.7	3				
	6	73	59.0					
	6		79.4		1			
	7	73	62.6		1			
	7		73.5					
	8	54	78.9	1				
	8		83.4					
6/3	9	31	60.8	1		1		
	9		84.1	1				
	10	69	65.6					
	10		61.7					
	11	47	65.9					
	11		68.6					
	12	29	57.0	1				
	12		76.8	1				

Appendix 1 (continued): Numbers of plaice eggs recorded in 1991 survey

Date	Station	Approx. bottom depth (m)	Volume sampled (m^3)	Number of plaice eggs of stage recorded				
				I	II	III	IV	V
7/3	13	76	66.0					
	13		66.3					
	14	56	76.5					
	14		72.1					
	15	26	75.3	16	1	1		
	15		85.3	9	1	1		
	16	26	77.2	3	1			
	16		71.6	8	1			

Appendix 2: Numbers of plaice eggs recorded in 1992 surveys

Survey	Date	Station	Bottom depth (m)	Volume sampled (m^3)	Number of plaice eggs of stage recorded				
					I	II	III	IV	V
1	13/1	11	51	72.1					
		11		80.65					
		14	65	80.1					
		14		75.2					
		15	30	72.4					
		15		77.6					
		12	35	66.2					
		12		72.9					
	14/1	17	18	76.8					
		17		80.1					
		18	23	79.4					
		18		78.5					
		19	43	71.5					
		19		72.9					
		20	74	73.6					
		20		87.2					
2	6/2	11	59	68.5					
		11		68.0					
		14	69	83.5					
		14		66.6					
		12	33	88.6	1				
		12		83.5	1				
	11/2	15	27	77.6	2				
		15		87.6					
		17	17	79.3	1				
		17		70.5	2				
		18	17	73.0					
		18		83.4	1				

Appendix 2 (continued): Numbers of plaice eggs recorded in 1992 surveys

Survey	Date	Station	Bottom depth (m)	Volume sampled (m^3)	Number of plaice eggs of stage recorded				
					I	II	III	IV	V
2 (cont.)	11/2	19	44	85.6					
		19		75.6					
		20	74	77.9					
		20		82.8					
3	5/3	21	47	78.9					
		21		78.0					
		22	42	78.5					
		22		74.6					
		15	29	81.0	9				
		15		68.6	5				
		16	33	75.2	4				
		16		73.5	1				
		12	33	70.2	2		1		
		12		72.2	2				
	16/3	17	19	73.4	24				
		17		73.1	24				
		18	18	76.6	2				
		18		76.8	3				
		23	36	90.7					
		23		85.4					
		24	44	86.4	3				
		24		87.3	4				
East coast	24/3	25	28	71.0	28	2	2	1	6
		25		76.9	23	5	12	7	5
		26	40	71.5	2		1		1
		26		76.7	1	2			

Appendix 2 (continued): Numbers of plaice eggs recorded in 1992 surveys

Survey	Date	Station	Bottom depth (m)	Volume sampled (m^3)	Number of plaice eggs of stage recorded				
					I	II	III	IV	V
4	3/4	15	34	76.6					
		15		72.1	1				
		17	23	76.1					
		17		78.0					
		18	20	76.7			1		1
		18		80.1			2	1	1
		24	51	84.9		1	2	1	
		24		80.1	1		1		1
	6/4	12	34	80.9			3		
		12		71.5	3		1		1
		21	44	83.7			1		
		21		76.4				1	
		22	43	76.1					
		22		74.7					
		27	38	82.2				1	
		27		88.4	1				

Appendix 3: Numbers of plaice eggs recorded in 1993 surveys

Survey	Date	Station	Bottom Depth (m)	Surface temp (°C)	Volume sampled (m³)	Number of plaice eggs of stage recorded				
						I	II	III	IV	V
1	9/2	24	48	7.3	64.0					
		24			85.8					
		23	38	7.3	80.0					
		23			79.9					
		18	26	7.3	84.3					
		18			79.1					
		28	19	7.3	78.6					
		17	23	7.3	85.2	1				
		17			63.5		1			
	10/2	21	43	7.3	80.4					
		21			90.3					
		22	40	7.2	77.2					
		22			81.5					
		29	26	7.3	87.0	1				
		29			75.2	1				
		15	33	7.3	72.7	1				
		15			88.3					
		12	35	7.3	76.8	1				
		12			76.0					
2	22/2	21	44	7.1	76.7					
		21			78.1	1				
		22	43	7.1	85.0					
		22			98.1					
		29	25	6.9	75.3	1				
		29			77.9	4				
		15	30	6.9	82.2	1		1		
		15			74.2	1				
		12	33	7.1	73.4	1				

Appendix 3 (continued): Numbers of plaice eggs recorded in 1993 surveys

Survey	Date	Station	Bottom Depth (m)	Surface temp (°C)	Volume sampled (m^3)	Number of plaice eggs of stage recorded				
						I	II	III	IV	V
2 (cont.)	23/2	24	48	7.1	85.1					
		24			84.8	1				
		17	23	7.1	85.5	2				
		17			76.5	4				
		28	19	7.1	72.5	1				
		28			73.6	2				
		18	19	7.1	93.3					
		23	35	7.3	98.7					
3	4/3	22	36	6.7	93.6	1				
		22			61.3	3				
		29	23	6.7	90.8	2				
		29			77.2	1				
		15	30	6.7	84.1	1	1		1	
		15			82.9	1				
	5/3	17	20	6.1	74.6	11	1			
		17			71.7	11				
		28	16	6.3	84.9	18	1			
		28			82.1	13	3			
		18	23	6.4	83.8	3				
		18			86.0					
		24	41	6.9	86.6	1				
		12	30	6.6	56.2					
4	9/3	15	34	6.6	76.2	4				
		15			87.4	11				
		29	26	6.8	70.3	5				
		29			77.7	6				
		17	22	6.8	72.3	3				
		17			85.4	8				
		28	16	6.7	76.0	6		2		
		28			84.8	2				

Appendix 3 (continued): Numbers of plaice eggs recorded in 1993 surveys

Survey	Date	Station	Bottom Depth (m)	Surface temp (°C)	Volume sampled (m³)	Number of plaice eggs of stage recorded				
						I	II	III	IV	V
4 (cont.)	9/3	12	31	6.7	81.1	3				
	10/3	18	28	6.8	74.1					
		18			93.9	1				
		23	38	6.9	83.2					
		23			82.3		1			
		24	46	7.1	85.8					
		24			84.9					
		22	44	7.2	98.7					
		22			96.1					
East coast	11/3	25	27	6.6	90.7	7	3			3
		25			99.1	10	5		1	4
East coast	24/3	25	28	6.8	85.7	13	1	7	2	1
		25			72.3	30	2	8	2	2
5	24/3	18	24	7.1	83.1	1				
		28	18	7.4	75.6				1	
		28			75.5					
		17	20	7.6	74.2	6				
		17			79.9	5	1			1
		29	24	7.8	71.2	8	2			
		15	27	7.5	74.0	2	2			
		15			80.7	4			1	
		12	31	7.1	71.9					
6	31/3	18	21	7.2	71.5	1				
		28	16	7.2	97.6	5				
		17	19	7.2	79.8	9				
		17			76.3	15				
		29	22	7.2	86.3	11				
		15	27	7.2	80.8			1		
		15			85.0	1				
		12	31	7.2	88.8					

Appendix 3 (continued): Numbers of plaice eggs recorded in 1993 surveys

Survey	Date	Station	Bottom Depth (m)	Surface temp (°C)	Volume sampled (m^3)	Number of plaice eggs of stage recorded				
						I	II	III	IV	V
6 (cont.)	1/4	23	35	7.2	81.9					
		24	46	7.3	78.6					
		24			84.0					
		22	38	7.4	80.1					
		22			75.9					
		21	43	7.4	74.9					
7	15/4	12	29	7.5	81.9					
		18	21	7.5	80.7				2	
		28	16	7.8	76.7					
		17	16	7.8	78.7					
		17			85.6					
		29	23	7.8	82.3			1		
		29			80.5	2				
		15	26	7.9	74.7					
		15			83.8					