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Plankton Production and Year-class Strength in Fish Populations: an Update of the Match/Mismatch Hypothesis

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I.	Introduction	250
II.	The Original Hypothesis	251
III.	The Member Vagrant Hypothesis	256
IV.	Extension to Waters Equatorward of 40° Latitude	259
	A. Background	259
	B. Events in upwelling areas	261
	C. Lasker events	262
	D. Spawning and food	264
V.	Testing the Hypothesis	265
VI.	Some Examples	265
	A. The original approach	270
	B. The spawning distributions of seven species in the Southern Bight of the North Sea	271
	C. The link between recruitment and larval abundance	273
	D. The Baltic	274
	E. The gadoid outburst	276
	F. The great salinity anomaly of the 1970s	278
	G. Catches of spiny lobsters and the time of onset of the spring outburst off Tasmania	279
	H. Larvae of the Arcto-Norwegian cod	281
VII.	Discussion	285
VIII.	Acknowledgements	285
IX.	References	285

I. Introduction

The degree of match and mismatch in the time of larval production and production of their food has been put forward as an explanation of part of the variability in recruitment to a stock of fish (Cushing, 1974, 1975, 1982). The magnitude of recruitment is not completely determined until the year-class finally joins the adult stock, and the processes involved probably begin early in the life-history of the fish when both their growth and mortality rates are high (Ricker, 1954). Hjort (1914) thought the level of recruitment was established during this period between hatching and first-feeding (the critical period according to Marr, 1956; May, 1974). However, I extended the match mismatch hypothesis to cover the subsequent development through larval life up to metamorphosis, and possibly just beyond. An essential part of my hypothesis was the suggestion of Ricker and Foerster (1948) that under adventitious predation, i.e. without aggregation, well-fed larvae grow quickly and experience less predatory mortality than poorly fed ones at a given stage of development (Cushing and Harris, 1973; Shepherd and Cushing, 1980). Hence, one would expect growth and mortality to be inversely related. Almost as a consequence of match and mismatch, fish in temperate waters should release their larvae during the spring or autumn peaks in the production cycle, when more food is available. Anderson (1988) listed a number of hypotheses regarding the survival of pre-recruits, and he came to the conclusion that the growth mortality hypothesis (as he named it) was most significant. As well as extending my match mismatch hypothesis to cover a longer period in the life-history of fish, it was also more explicitly related to climatic factors and to the Sverdrup (1958) model than Hjort's first hypothesis.

Hjort's (1914) second hypothesis, i.e. that recruitment may be determined by the loss of larvae through advective processes, was revived by Bailey (1981), who found recruitment to the hake stock off the west coast of the U.S.A. to be negatively correlated with an index of upwelling. I decided to examine the effect of upwelling on recruitment in waters equatorward of 40° latitude and, subsequently, I re-examined the data in support of my original hypothesis together with more recent information, including the member vagrant hypothesis.

The match mismatch hypothesis has developed over a number of years in several publications, and I thought it desirable to bring all of the evidence together here. However, it should be noted that although my original hypothesis applied only to recruitment to fish stocks, I now also include spiny lobsters and Dungeness crabs.

II. The Original Hypothesis

The original match mismatch hypothesis consisted of two parts: first, that fish in temperate waters spawned at a fixed time and, secondly, the larvae were released during the spring or autumn peaks in plankton production.

The variation in production of larval food (e.g. copepod nauplii and copepodites for many fish; the appendicularian *Oikopleura* for the plaice, *Pleuronectes platessa* L. in the southern North Sea) then depended on the variation in the time of onset and the duration of primary production (Cushing, 1974, 1975). The hypothesis assumed that during the spring peak, plankton production followed Sverdrup's (1953) model, and that during the autumn peak the same principles applied, but in reverse – spring and autumn are the periods of mixing or weak stratification.

The hypothesis was based on two observations. First, the spring and autumn spawning herring stocks (*Clupea harengus* L.) in the northeast Atlantic did in fact release their larvae at a time when they would grow in the spring and autumn peaks in plankton production (Cushing, 1967). The seasonal estimates of "greenness" for each spawning area were averaged over a number of years using the Continuous Plankton Recorder Network (Cushing, 1967). The plankton recorder has a coarse mesh through which the smaller algal cells are able to escape when present in small quantities; however, when present in large quantities, they are retained on the mesh. During peaks of phytoplankton, the production of all algae is governed by the critical depth and the production ratio (i.e. compensation depth depth of mixing). The estimate of "greenness" as a relative index of the quantity of phytoplankton was validated by Gieskes and Kraay (1977). I also reported each stock's peak time for spawning, the spread in time over which spawning took place and the number of days to the point of no return (i.e. the time at which the larvae must have food in order to survive).

The autumn spawners hatch in the western North Sea and the larvae then drift and migrate as young juveniles to the nursery grounds in the east (Cushing, 1962). On this eastward movement, they feed on zooplankton which grows in a pronounced autumn outburst of "greenness" (Cushing, 1967). The areas from which these "greenness" data were taken, together with the spawning grounds of the herring (Harden Jones, 1968), are shown in Fig. 1. Bückmann (1942) was able to present some evidence for this drift across the North Sea by larvae from the Downs and Dogger spawning groups. Hainbücher *et al.* (1986) have provided average trajectories of water particles (in "Sverdrups") under wind stress between 1969 and 1982, starting from different points. The relevant courses from the Thames and Rhine (the Downs spawning group), the Humber (the Dogger spawning group) and an

area off the Moray Firth (the Buchan spawning group, which includes the West of Scotland) are plotted in Fig. 1 (Saville and Bailey, 1979). Note that the term "spawning group" has been used to avoid confusion with the present unit of management, i.e. the North Sea stock.

Bartsch and Backhaus (1987) have calculated similar trajectories with different forms of vertical migration made by herring larvae. They suggest that year-to-year differences in advection may contribute to the annual variability of recruitment. Subsequently, Bartsch *et al.* (1989) presented evidence to show that herring larvae cross the North Sea from their spawning grounds in the west to their nursery grounds in the east – and that this passage is wind-influenced.

The second observation (Cushing, 1969) was that four temperate species – herring, plaice, sockeye salmon (*Oncorhynchus nerka* Walbaum) and cod (*Gadus morhua* L.) – spawn at a fixed season, the peak date of which has a standard deviation of about 1 week, although the fish may spawn for a period of 2–3 months. Two standard deviations amount to about 2 weeks, but the standard error of the mean date is only 1–2 days; Rothschild (1986) has noted that the first statistic shows the spread as the average of evolutionary processes, and that the second indicates the most important time for spawning. Subsequent analysis suggested that the spawning of the Arcto-Norwegian cod did, in fact, occur 1 week or so later over an extended period between 1891 and 1931 (Cushing and Dickson, 1976). The material was based on the weekly distribution of catches in the Vestfjord for many decades. Using evidence of maturation, (Pedersen, 1984) found that the peak date for spawning is somewhat later than the date of peak catch. Ellertsen *et al.* (1987), taking the dates of 50% spawning at Lofoten between 1976 and 1983, have shown that the real date of peak spawning is 14 days later than that of peak catch. The main conclusion was that the aforementioned four species spawned at about the same time each year in temperate or high latitudes.

The time of onset of the spring peak in plankton production in the North Sea and north east Atlantic can vary from year to year by as much as 6 weeks, as shown by the Continuous Plankton Recorder (CPR) data (Colebrook, 1965; Colebrook and Robinson, 1965; Robinson, 1970). Colebrook (1979) has extended the analysis of the CPR observations and has illustrated spatial and temporal differences. Dickson *et al.* (1988a) found that the time of onset of the spring peak in plankton production in the western North Sea shifted 4–6 weeks later between the 1950s and the 1970s, shifting back again in the 1980s. Colebrook (1982) also showed that the spring peak in the northeast Atlantic occurred before the water column was fully stabilized, i.e.

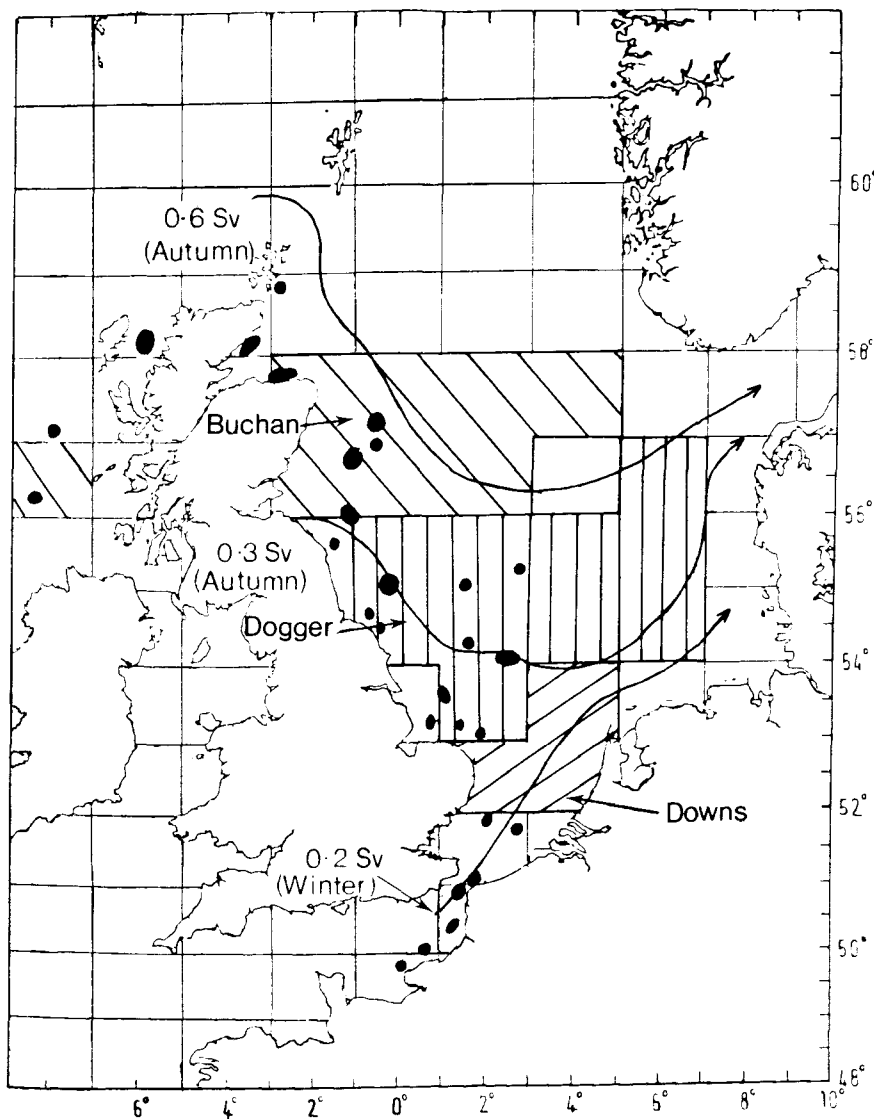


FIG. 1. The autumn spawning grounds of the North Sea herring (black areas: from Harden Jones, 1968) and the climatological mean transports (arrows: Hainbucher *et al.*, 1986) from the spawning grounds (Buchan and Dogger, autumn transport; Downs, winter transport) to the nursery grounds in the eastern North Sea. The hatched areas include the small squares used for sampling the "greenness" in each of the presumed larval drifts.

the period of weak stratification. There are two main ecosystems in the sea, fully stratified and weakly stratified water (Cushing, 1989). The original match mismatch hypothesis was based on the contrast between the relatively fixed time of spawning and the highly variable time of peak production. However, to this should be added the possibility of the start of production being brought forward or delayed.

The recognition of the extent of thermal fronts in tidal seas (Simpson and Hunter, 1974; Pingree *et al.*, 1975; Le Fèvre, 1986) has changed our view of the production cycle in two ways. First, in protected coastal waters shoreward of the fronts, there is a continuous production cycle which peaks in June or July, (Grall, quoted by Le Fèvre, 1986; Kremer and Nixon, 1978; Diwan, quoted in Rayment, 1980; Franz and Gieskes, 1984). In relatively shallow and protected water with the constant attenuation of irradiance, production starts when the critical depth exceeds the depth of water, and the subsequent course of production is governed by the production ratio. In other words, with a constant coefficient of attenuation, the time of onset of production and its subsequent development depends only on irradiance. Production commences in shallow water and develops later in deeper water (Cushing, 1972) to a depth, where stratification begins, i.e. where the fronts develop in summer. However, such areas are often susceptible to strong winds in spring and the coefficient of attenuation is decreased (Lee and Folkard, 1969; Dickson and Reid, 1983). The time of onset is then delayed as a function of strong winds, as is the rate of development of peak production. Thus, in enclosed tidal areas, the time of onset of production is controlled solely by irradiance, whereas in open tidal areas it is also controlled by attenuation which is governed by the presence or absence of strong winds. It is interesting to note that herring spawn in relatively shallow waters and that their larvae grow in mixed water regimes.

The second consequence of the recognition of thermal fronts is that phytoplankton production in temperate waters has been shown to be concentrated within the thermocline during the summer (Pingree *et al.*, 1977; Holligan and Harbour, 1977). Production continues above the thermocline (Holligan *et al.*, 1984). The result is spring and autumn peaks with production at the thermocline and in the euphotic layer in between. Because there is apparently no variation in the timing of the production in the summer in stratified waters, the match mismatch hypothesis will not apply in that season.

The match mismatch hypothesis is illustrated conceptually in Fig. 2. Because fish in temperate waters may spawn at a fixed season, production of fish larvae and that of their food may be matched or mismatched in time. Larval development is an inverse power function of temperature, and is extended in cold water. (Note that the error bars shown above the distri-

bution of production in time in Fig. 2 are asymmetrical. The variability in time of the production of larval food is represented by the much broader symmetrical error bands above the distribution of larval food.)

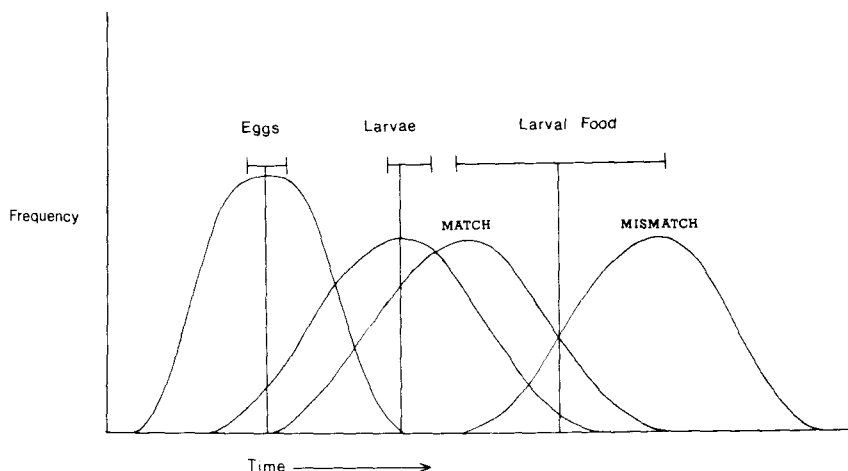


FIG. 2. The match mismatch hypothesis. The production of eggs, larvae and larval food are shown as distributions in time. The match or mismatch is represented by the overlap in time between the production of fish larvae and that of their food. In temperate waters, fish may spawn at a fixed season and the production of early stage eggs reflects this. The production of larvae, like all egg stages, is inversely related to temperature by a power law; this is expressed in the asymmetrical error bars, based on inter-annual differences. The production of larval food depends upon the timing of the production cycle and the long error bar expresses the annual variation. With a low stock, there is a greater chance of mismatch than with a high stock (recruitment is usually more variable with a low stock).

Full match and full mismatch are equally unlikely, but they may correspond to uncommonly rich and poor year-classes. The question arises as to why fish have not evolved a mechanism to match their larval production to that of their food. As will be shown below, such mechanisms exist where the interval between batch spawnings depends upon food (at least in waters equatorward of 40° latitude). In temperate waters, such a device may well exist but may not be effective. Fish that spawn before the spring peak in plankton production have to forecast its time of onset, which is difficult taking into account the highly variable stress caused by the weather. One way of overcoming this problem is to spread spawning activity over a period of time (as pointed out by Dr John Shepherd, pers. comm.).

The hypothesis of match mismatch is based on the belief that some of the

variability of recruitment to temperate fish stocks is affected by climatic change. Williamson (1961) analysed a change from a neritic to an oceanic planktonic regime in the northern North Sea by Principal Component Analysis and showed that half of the variance was correlated with a change in the degree of vertical mixing. This was not a response by a single population, but one by a community. Dickson *et al.* (1988a) have shown that the delay of about 1 month in the time of onset of the spring peak and the decline in number of *Pseudocalanus* by a factor of five in the western North Sea, was associated with the increase in northerly winds and gales between the 1950s and the 1970s; both delay and decline were reversed in the early 1980s. Thus, in addition to the variation in time of onset of the spring peak, there are secular trends based on climatic change.

Many correlations between recruitment and climatic factors, such as wind strength and temperature, have been published. Though their failure may have been due to improper statistical manipulation, it was more likely due to the highly non-linear properties of a system responding to climatic change (Rothschild, 1986). Cushing (1982) discussed the possible relations between recruitment and climatic change in some detail. Such relations may originate in the year-to-year differences in the time of onset of primary production, which is the simplest way in which climatic factors can affect recruitment. Shepherd *et al.* (1984) found a correlation between the first principal component of the recruitments of the stocks of nine fish species in the North Sea and the first principal component of temperature in that region. A similar conclusion emerged from Hollowed *et al.*'s (1987) analysis of recruitment in the Alaska gyral; they found that recruitments were correlated within, but not between, regions several hundred kilometres across, the same size as depressions and anticyclones. Also, within such a region, some prominent year-classes were common to a number of stocks. Such are the current bases of the belief that climatic factors or climatic change affect the generation of recruitment at an early stage in the life-history of fish.

III. The Member/Vagrant Hypothesis

In considering the member vagrant hypothesis here, I discuss only the bearing of this hypothesis on that of match mismatch and not its more general consequences. An essential part of the member vagrant hypothesis is the idea of a "larval retention area". For example, herring larvae are supposed to be retained by behavioural mechanisms close to thermal fronts for several months at places around the British Isles and on Georges' Bank off the east coast of the U.S.A. They are said to grow there at a constant rate irrespective of the different types of food available (Iles and Sinclair, 1982).

More precisely:

larvae of a discrete herring population develop within, and are thus adapted to the specific oceanographic conditions of their larval retention areas . . . larvae are not retained passively by the circulation features of the larval distributional area, but rather by an active behavioral response to the physical regime . . . populations are observed to maintain a discrete distribution in a relatively fixed location for several months" (Sinclair and Tremblay, 1984).

In the shelf waters around the British Isles, the fronts collapse during equinoctial gales and the larvae are not necessarily retained within the thermal fronts but, aided by winds, drift eastwards across the North Sea, as noted by Bückmann (1942; see also Cushing, 1986). More developed methods have confirmed this conclusion. The larvae and juveniles of capelin (*Mallotus villosus* L.), yellowtail flounder (*Limanda ferruginea* (Storer)) and American plaice (*Hippoglossoides platessoides* (Fabricius)) are retained on the southern Grand Bank (Frank *et al.*, 1989) and a proportion of young pelagic cod are retained within a swirl on their spawning grounds on Brown's Bank, the remainder drifting to the richer food grounds off southwest Nova Scotia (Suthers and Frank, 1989). Though retention areas do exist, like that off southwest Nova Scotia for herring larvae (originally proposed by Iles and Sinclair, 1982, and confirmed by Stephenson and Power, 1989), Campana *et al.* (1989) have found that during their passage from Brown's Bank to southwest Nova Scotia, cod larvae are retained along the course of the larval drift before being dispersed over Brown's Bank again. Furthermore, Heath and MacLachlan (1987), Heath *et al.* (1987), Kjørboe and Johansen (1986) and Kjørboe *et al.* (1988) have all shown that patches of early autumn-spawned herring larvae drift considerable distances off the Scottish coasts before the fronts collapse. There is thus a question as to whether herring larvae are retained in the fronts around the Scottish coasts; indeed, those from the West coast of Scotland move quickly eastward into the North Sea (Heath, 1989). I conclude that retention areas do exist (usually for short periods), and where they exist they form part of the larval drift between the spawning grounds and nursery grounds.

The crucial point is whether retention areas are necessary for growth and survival. Except off southwest Nova Scotia, they do not persist for very long. There are also places where retention areas do not exist at all, and one should beware of attributing properties of retention to hydrographic structures (see Sinclair, 1988, on the Southern Bight of the North Sea). A retention area may be described physically (as a swirl) or geographically (over a bank), and because it is really part of the larval drift or migration from the nursery ground to the spawning ground, one might imagine inter-annual differences arising in the course of that migration. Thus, different proportions of larvae might then reach a specified nursery ground (as

suggested by Bartsch *et al.*, 1989). Retention areas have stimulated a lot of research at sea, and if herring spawn in tidally mixed waters (to a depth of 100 m in the waters around the British Isles), their larvae must be found at the fronts or where the fronts had once been.

The second question concerns the effect of food, and whether fish larvae grow at a constant rate and whether they are distributed independently of their food. It has already been noted that the young pelagic cod on Brown's Bank drift towards richer feeding grounds. Frank (1988) showed that *Pseudocalanus*, the preferred food of the herring larvae off southwest Nova Scotia, was more abundant where the larvae lived. Munk *et al.* (1986), Kjørboe and Johansen (1986) and Kjørboe *et al.* (1988) have all shown that herring larvae growth is limited by food. From published observations at sea, Fortier and Gagné (in press) demonstrated that herring larvae grew at about half the maximal rate. They also found that spring-spawned larvae in mixed water in the St Lawrence hatched 2 weeks before the peak in plankton production, and that they had a good survival rate. In contrast, the autumn-spawned larvae suffered heavy mortality after the food stocks ran out. I conclude that the growth of fish is modified by the availability of food along the course of the larval drift.

Thirdly, Sinclair's member vagrant hypothesis states that the time of spawning and the time of onset of production should be decoupled (Sinclair and Tremblay, 1984). This is based on the idea that the time at which spawning takes place is governed by the need to metamorphose in summer, between April and October. Spring-spawning herring proceed to metamorphosis quickly, whereas autumn spawners do so slowly throughout the winter. Sinclair and Tremblay (1984) suggest (without evidence) that conditions in the spring retention areas are better than those in the autumn ones. Spring- and autumn-spawning herring do spawn before the spring and autumn peaks in plankton production (Cushing, 1967). The time at which seven species in the Southern Bight of the North Sea spawn is coupled to the time of onset of the spring peak in plankton production (see Fig. 5). The simplest explanation is that they do so in order to exploit the available food. It is possible that autumn-spawned herring larvae survive on the overwintering populations of *Pseudocalanus* and metamorphose in the following summer. The suggested decoupling of the time at which spawning takes place from the onset of production is not supported by the facts.

An anonymous reviewer suggests that the two hypotheses be reconciled. Sinclair and Tremblay (1984) state that each spawning group must be adapted to "the specific oceanographic conditions of their larval retention area". If and where there are retention areas along the passage of the larval drift, such conditions might include the availability of food. The spawning date of each population has evolved in response to the average timing of the onset of production of plankton that exists in a retention area. However,

such production cycles can exist independently of such areas, e.g. the seven species in the Southern Bight of the North Sea (see Fig. 5). Thus, the basis of the match/mismatch hypothesis holds for the variation of climatic factors, as expressed by the critical depth and the production ratio.

IV. Extension to Waters Equatorward of 40° Latitude

A. Background

In 1974, there was no direct evidence to show that recruitment was in fact linked to match or mismatch (Cushing, 1974). Later, it was noted that the Californian sardine (*Sardinops caerulea* (Girard)) spawned during many months of the year (Cushing, 1969). Similarly, in the oceans of the tropics and subtropics, it was shown that tuna and tuna-like species tended to spawn right across these waters for most seasons of the year. Hence, the form of mechanism displayed in Fig. 2 was not then considered to apply equatorward of 40° latitude. This conclusion is now reconsidered.

I have noted (Cushing, 1989) that there are two primary ecosystems in the open ocean: one based on very small grazers in the microbial food loop, and the other based on rather larger ones ($> 5 \mu\text{m}$). The first is found in the oligotrophic ocean and in the well-stratified summer waters of lakes and seas. (It will be recalled that the period of the summer thermocline in temperate seas was excluded from the match/mismatch hypothesis.) The second ecosystem is the traditional food chain – diatoms, copepods and fish – which is found where the water is weakly stratified, in the early and middle stages of a spring peak, in the later stages of an autumn peak and in an upwelling area or an oceanic divergence.

Let us now examine events in tropical and subtropical seas outside the oligotrophic ocean.

B. Events in Upwelling Areas

In the last decade or so, many links have been established between indices of upwelling and recruitment. Because the food for fish larvae is produced in upwelling areas, positive correlations between recruitment and upwelling are to be expected. In recent years, negative correlations have been associated with offshore drift, and hence with the advective loss of larvae. However, I pointed out that the greatest production would derive from moderate or slow upwelling (Cushing, 1971). Hence the simple distinction between positive and negative correlations for indicating the effect of food or offshore drift may be misleading.

Marr (1960) found a positive relationship between the recruitment of the Californian sardine and the inshore temperature at the Scripps pier, an inverse relation with upwelling (Marr did not attempt correlation because there was one "outlier" in the relationship, the 1939 year-class, for which he gave a reasonable explanation). Dickson *et al.* (1988a) also demonstrated an inverse relationship between upwelling (averaged over the 3 years preceding the catch) and the sardine (*Sardinia pilchardus* L.) catch off Portugal. There are also relationships between upwelling and sardine (Bakun and Parrish, 1981), mackerel (*Scomber japonicus* Houttuyn: Parrish and McCall, 1978), Dungeness crab (*Cancer magister* Dana: Peterson, 1973; Botsford and Wickham, 1975) and hake (*Merluccius productus*: Bailey, 1981) year-classes, some of which are direct, some inverse, some simple and others complex, some with catches lagged by 3 years and others with recruitment. Upwelling is a complex process and it has many forms, any of which may change its nature in the course of time.

A negative relation between recruitment and an index of upwelling might indicate, among other things, that a proportion of the eggs and larvae is swept offshore. Bailey (1981) showed that recruitment to the stock of Pacific hake was inversely related to Ekman transport. Indeed, that best year-classes were recorded in years of downwelling (which, incidentally, would have brought the larvae inshore to their nursery ground). Such losses must exist, because no inherently variable current system can deliver all survivors to the nursery grounds. Indeed, the gonad must include a proportion devoted to such loss. Losses may be considered to be a fraction of subsequent recruitment with a constant predatory mortality; alternatively, losses may be compensated for by subsequent processes. In this respect, the larger the initial loss, the greater the subsequent survival, either because more food becomes available or because predators lose interest. The first alternative explicitly denies any dependence of mortality on food during larval drift: indeed, the larvae should grow at a constant or even a maximal rate, and the effects of predation should be independent of density. In the second, the processes of growth and mortality continue during the larval drift, in a similar manner to that indicated earlier as an essential part of the match mismatch hypothesis.

I have suggested (Cushing, 1971) that the greatest production can only be achieved by a slow rate of upwelling because a fast rate will sweep eggs and larvae away before peak production is reached in the rising water and they become vulnerable to grazing. Bakun and Parrish (1981) and Husby and Nelson (1982) both suggest that pelagic fish tend to spawn where there is a relatively slow rate of upwelling. Cury and Roy (1989) distinguish upwellings linked to turbulence from those that are not. They suggest that recruitment depends directly on upwelling if turbulence is absent, as off the

Ivory Coast. In turbulent upwellings (Morocco, Peru, Senegal) with wind stress < 5 m/s, recruitment might become reduced. Hence, both direct and inverse relationships are expected as turbulence increases. Dickson *et al.* (1988a) found that the Pacific sardine, with its high growth rate, probably needs a relatively low but consistent rate of upwelling; the northern anchovy, which grows at half the rate of the sardine, tolerates a faster rate of upwelling (data from Ahlstrom, 1966). Thus positive and inverse links between recruitment and indices of upwelling can arise from turbulence and also from biological factors, such as differences in growth rates. Therefore, the dichotomy of positive/negative links between upwelling and recruitment do not indicate dependence upon food or the lack of it. A negative relationship between recruitment and upwelling can, of course, be the result of offshore drift, but there are also other explanations.

C. Lasker Events

Hunter (1972) reported that the larvae of the northern anchovy require food densities of 1 nauplius l or 30 *Gymnodinium splendens*/l. Lasker (1975) thought that such densities of food only existed in the chlorophyll layers of the thermocline off southern California. When a storm upset the stability of the water column off San Onofre, there was not enough food for the larvae (Lasker, 1978). Furthermore, when most production in 1975 was diverted into diatoms (which the anchovies did not eat) and a red tide, the ensuing year-class was the worst for 15 years (Lasker, 1981). The use of daily growth ring counts on larval otoliths (Brothers *et al.*, 1976) yields a distribution of birth dates (Lasker, 1981), thus allowing the train of survival to be ascertained. Such distributions vary in time from year to year, in contrast to the fixed spawning season in temperate and high-latitude waters. Peterman and Bradford (1987) have demonstrated an inverse relationship between larval death rate and the number of calm periods per month (i.e. 4 days of wind stress < 5 m/s, – a Lasker event). Peterman *et al.* (1988) showed that there was no relationship between the number of 19-day-old larvae and subsequent recruitment in the northern anchovy (perhaps the time-series of recruitment estimates was too short). Mendelsohn and Mendo (1987) reported that there were few Lasker events off Peru. Cury and Roy (1989), however, noted an inverse relationship between turbulence and the number of Lasker events off Peru, thereby confirming Lasker's hypothesis. Lasker's work suggested that the processes which determine the magnitude of recruitment begin during larval life, and that they may depend upon the larval food supply. Upwelling off southern California is intermittent and northern anchovy larvae may need Lasker events to survive the first feeding stage, but their slow growth rate also allows them to survive more upwelling.

D. *Spawning and Food*

Many marine species produce several batches of eggs in a year. The northern anchovy completes many cycles in a season, from primary oocyte to ovulation, each of which lasts about 1 month (Hunter and Leong, 1980). Hunter and Leong also suggested that the number of batches per spawning season in the northern anchovy varied with ration. The growth of oocytes is governed by factors that affect body growth, i.e. food and metabolic hormones. Wootton (1977) showed that egg production per spawning batch in the stickleback (*Gasterosteus aculeatus* L.) did not depend on ration, but that the number of spawnings did, so that the interspawning interval was inversely related to ration. Therefore, upwelling areas or divergences present the chance of spawning in a food-rich environment. As periods of upwelling last for several months, there is every chance that such an opportunity will arise. This reproductive strategy may be characteristic of waters equatorward of 40° latitude.

In the North Pacific subtropical anticyclone, Yamanaka (1978) established an association between year-class strength and temperature in four tuna stocks (Fig. 3). The direct effect of temperature on the metabolism of the fish or on the rate of development of the eggs and larvae (which must be very rapid in the warm water, i.e. 2–3 days at the most), is unlikely to be more than slight. The wind stress across the ocean tends to be greater in the peripheral regions of the subtropical anticyclone where the tuna live and where the divergences are common (Hidaka and Ogawa, 1958). Divergences bring cool water to the surface and hence there is local plankton production. The tuna spawn for 9 months of the year and distribute their larvae across the whole Pacific (Matsumoto, 1966; Nishikawa *et al.*, 1985) thereby spawning as they feed. High recruitment tends to occur when the wind stress is relatively great and presumably where the divergences are more extensive and perhaps more intense. But there may be an additional mechanism, in that the fish may be able to average the effects of their food supply during the interspawning interval merely because they are large, so that hormonal control responds to averaged changes in food concentration.

When the Peruvian anchoveta (*Engraulis ringens* Jenyn) feeds on phytoplankton, it obtains a maintenance ration only, which is inadequate for growth and reproduction (Cushing, 1978, using the data of de Mendiola, 1971). In other words, they eat algae, apparently to their disadvantage. They spawn towards the end of the strong upwelling period and their larvae grow during the following period of weak upwelling when copepods comprise most of their food (Walsh, 1978). In an evolutionary sense, anchovies may adopt the reproductive strategy of spawning at the end of the period of strong upwelling, with the result that their larvae have food in the form of

nauplii and copepodites during the period of weak upwelling. However, the period of weak upwelling may, in fact, produce more food than the period of strong upwelling.

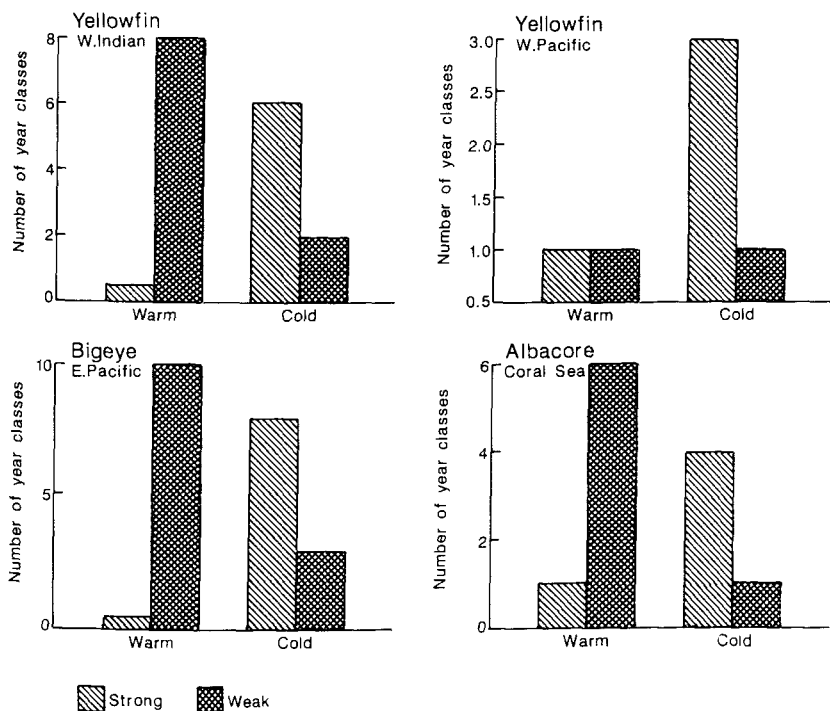


FIG. 3. Strong year-classes of tuna in cold water and poor year-classes in warm water in the Pacific - yellowfin in the West Pacific and West Indian Oceans, bigeye in the East Pacific and albacore in the Coral Sea (Yamanaka, 1978).

Thus, it appears that in these waters, fish - as exemplified by the anchovy, the sardine and the tuna - may well match their reproductive strategy and physiology to feeding. In other words, they spawn as they feed and their larvae grow in the food patches and the mismatch is minimized. Poleward of 40° latitude, the same objective is achieved by minimizing the spread in time of the onset of production by spawning at a fixed season. Thus, we apply the match-mismatch hypothesis in its original form to waters poleward of 40° latitude, and add to it the thesis that reproduction is more nearly matched to the production of larval food in upwelling areas and oceanic divergences equatorward of 40° latitude.

V. Testing the Hypothesis

Sinclair (1988) gives five tests of the match/mismatch hypothesis. The first contrasts the spring and autumn peaks in the Baie des Chaleurs in the Gulf of St Lawrence and the midsummer peak in the lower St Lawrence; the latter has a protected tidal production cycle. The spawning distributions in time of seven species are about the same in the two areas, but the larvae peak in May and June in the lower St Lawrence and in June and July in the Baie des Chaleurs. According to de la Fontaine *et al.* (1984a,b), there is a clear relationship between the number of larvae and the quantity of zooplankton in the Baie, but not in the lower St Lawrence, where the animals drift away from the sampling stations. This test does not deny the match/mismatch hypothesis, but it may well support it.

Methot (1983) provided the second test based on the survival of the larvae of the northern anchovy (data derived from the relative ratio of birth dates to that of the larval distribution by months). He found that survival was greater in a year of low upwelling than in one of normal upwelling, and concluded that low upwelling prevented loss of larvae in offshore flow. As noted above, this might be too simple an explanation and, indeed, there may have been more food available in the year of low upwelling.

For the third test, O'Boyle *et al.* (1984) found that eggs and larvae of four demersal fish species were present all year round on the Scotian shelf, so that there may have been no opportunity for match or mismatch. The material is presented as log *n* numbers on time so that we should look more closely at the peaks rather than the tails of the distributions. It can then be seen that they correspond reasonably well with the spring and autumn peaks in plankton production, as presented in Sinclair *et al.* (1984).

The fourth test, based on Koslow (1984) and Koslow *et al.* (1987), showed that the recruitments of stocks over broad areas were correlated within species. Sinclair believed that the timing of spawning events and plankton blooms could not coincide over such distances. As noted above, Shepherd *et al.* (1984) and Hollowed *et al.* (1987) show that recruitments are correlated within large regions but not between them.

The last test of the hypothesis is the link between the high survival rate of Pacific mackerel off Baja California and high sea level records from coastal tidal stations (Sinclair *et al.*, 1985); the survival rates were negatively correlated with a number of estimates of primary production and micro-zooplankton abundance between Point Conception and San Diego. The high sea level occurs in the El Niño years, and therefore the survival index is linked to northerly transport associated with the Kelvin wave possibly generated by El Niño. But Parrish and McCall (1978) found positive correlations between log *n* recruitment of Pacific mackerel and sea-surface

temperatures off La Jolla and in Marsden Square 102 (between Point Conception and San Diego) as a result of warm water flowing from the south. They also found positive correlations with upwelling and divergence. The water rising to the surface in the El Niño years would have been warm, with animals present not normally recorded from the region between Point Conception and San Diego. Hence the argument based on the negative correlation between survival index and food, further north, fails. Pacific mackerel depend on southerly transport, and therefore the argument for lack of advection for year-class success also fails. The match mismatch hypothesis has not been tested and the interpretations of data are not convincing.

If the match mismatch hypothesis were true, we would expect that:

- (1) Fish would release their larvae into peaks of plankton production or upwelling areas.
- (2) Because the essential processes depend upon food availability, larval growth rate would be expected to vary from year to year and to be nearly always less than the maximum, and that mortality due to constant predation should vary inversely with growth rate.
- (3) The earliest and crudest link between recruitment and food should be found during the larval stage.

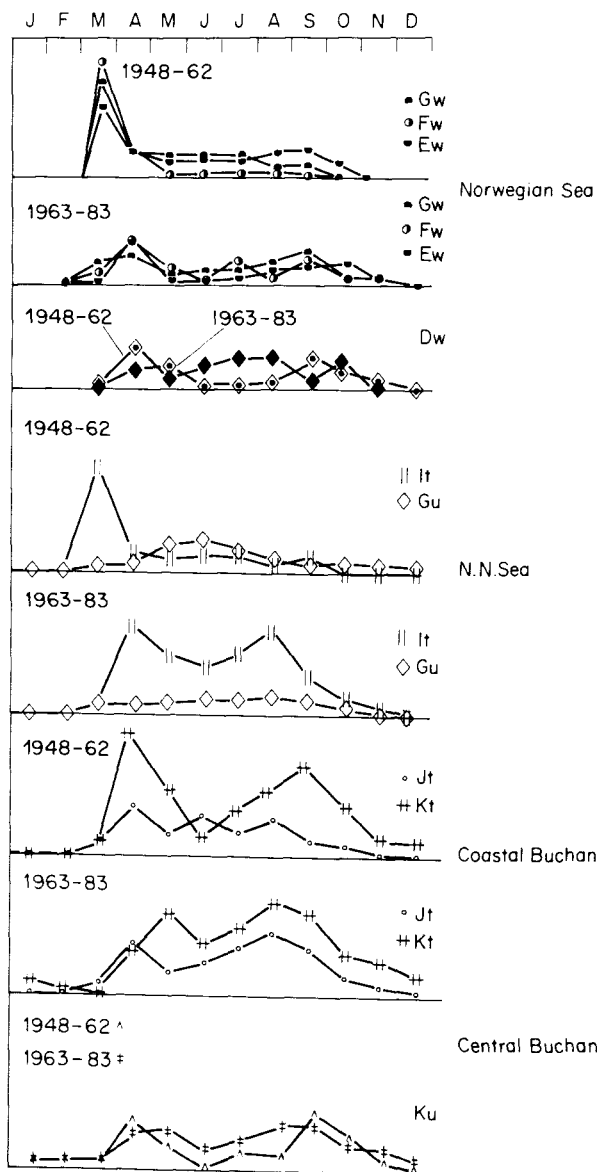
VI. Some Examples

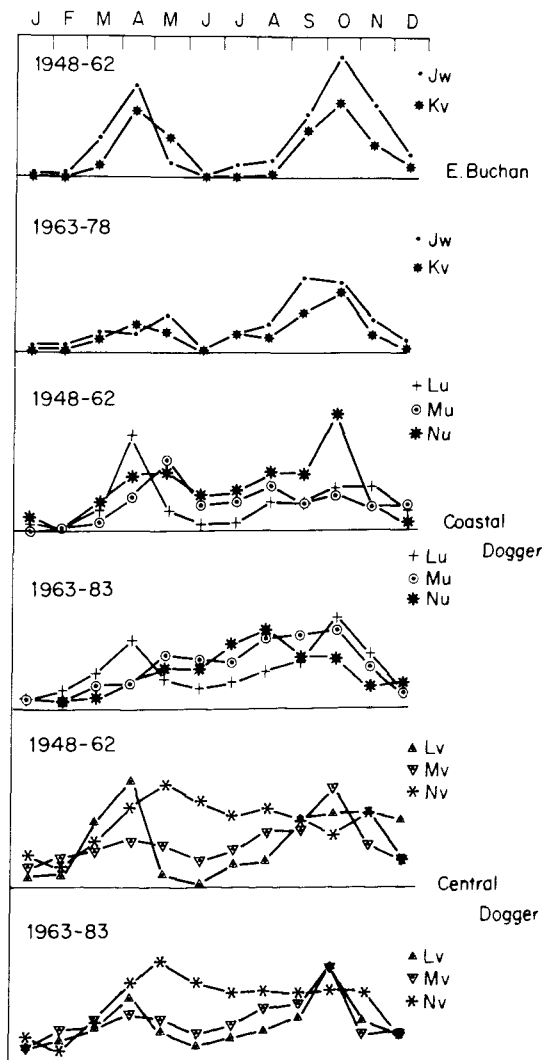
In addition to the original approach, a number of other events will be considered. These are the spawning distributions of demersal fish in the Southern Bight of the North Sea, the link between recruitment and larval abundance, the increase in cod and herring stocks in the Baltic, the "gadoid outburst" in the North Sea, the great salinity anomaly of the 1970s, the link between spiny lobster catches off Tasmania and New South Wales, and the time of onset of the spring peak in plankton production and the larval drift of the Arcto-Norwegian cod.

A. *The Original Approach*

Figure 4 shows the extension of the original seasonal distributions of "greenness" (1948–62) to more recent years (1963–83). The early 1980s, during which the decline in the zooplankton since the 1950s (Glover *et al.*, 1972) was reversed (Colebrook *et al.*, 1984), is not considered because it was so short a period of time compared with 1948–62 and 1963–83. In the future, it would be desirable to use in addition and separately the decade 1983–93

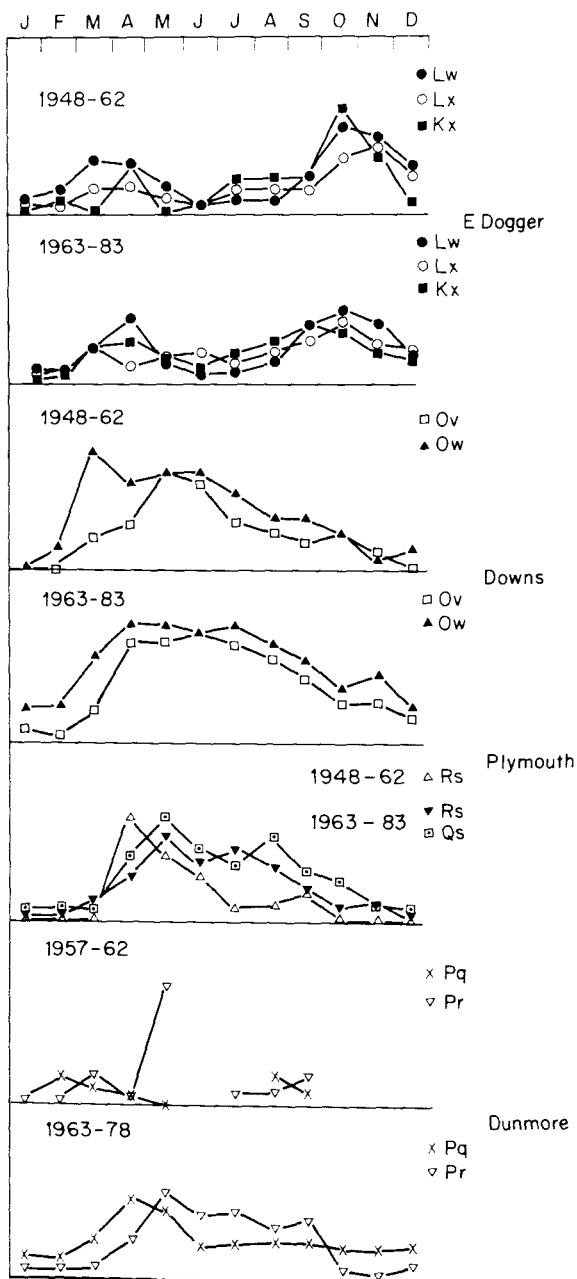
for the following reason. The recovery of the northeast Atlantic communities in the early 1980s was most marked in 1983, when the Atlanto-Scandian stock of herring started to recover as well as herring stocks in the northern North Sea.





(b)

FIG. 4. Seasonal cycles of production estimated by "greenness" in selected small squares of the Continuous Plankton Recorder Network, comparing 1948-62 with 1963-83 (a) Norwegian Sea to Central Buchan; (b) East Buchan to Central Dogger.



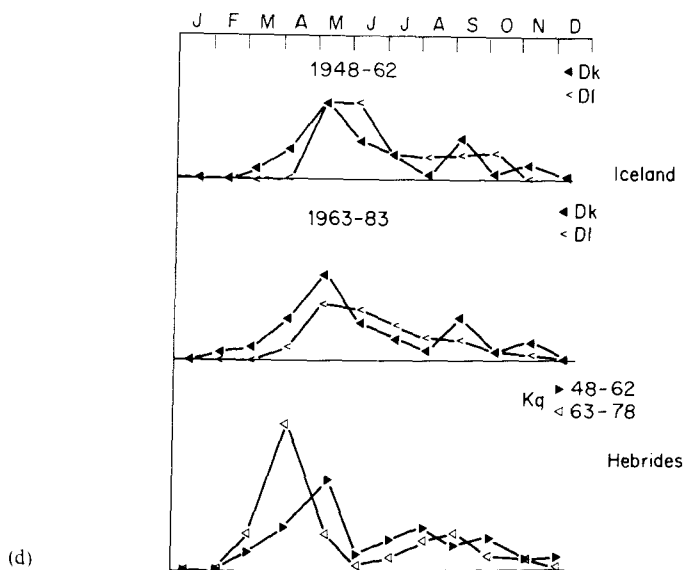


FIG. 4. (c) East Dogger, Downs and Plymouth; (d) Iceland and Hebrides. Such distributions were used in Cushing (1967) to show that the herring released their larvae at a favourable time in the production cycle.

In the western North Sea and in the southern Norwegian Sea, the spring peak in plankton production was delayed in 1963-83. In the eastern North Sea, there was no delay, although the magnitude of both the spring and autumn peaks was probably reduced. As noted above, Dickson *et al.* (1988a) showed that the delay in the western North Sea was due to an increase in northerly winds and gales during the spring. The Atlanto-Scandian stock of herring did not recover in the later period but did recover in 1983. However, the Continuous Plankton Recorder observations in the southern Norwegian Sea had been curtailed before that date. There was no change in the time of onset of the autumn peak in the North Sea, although it may have been reduced in magnitude. However, Reid (1978) showed that the abundance of diatoms was much reduced during the autumn peak in the central North Sea during the 1970s, which may have been caused by the diminished numbers of *Pseudocalanus*, such copepods depending on cells $> 5 \mu\text{m}$ in diameter. It is possible that the decline in North Sea herring recruitment in the 1970s was partly associated with this event.

B. The Spawning Distributions of Seven Species in the Southern Bight of the North Sea

Using egg distributions, Fig. 5 (adapted from Harding *et al.*, 1978) shows the spawning periods of seven species in the Southern Bight of the North Sea: plaice (*Pleuronectes platessa* L.), cod (*Gadus morhua* L.), sandeel (*Ammodytes* spp.), whiting (*Merlangius merlangus* L.), bib or pout (*Trisopterus luscus* L.), flounder (*Pleuronectes flesus* L.) and dab (*Limanda limanda* L.) (Cushing, 1990). Figure 5 also shows the increase in "greenness" averaged for the two periods 1948-62 and 1963-83, and for the two squares Ov and Ow of the Continuous Plankton Recorder Network, as an indication of the onset of the spring peak in plankton production. The seven species have timed their spawning periods so that their larvae grow during the spring peak in plankton production where their food develops. The plaice and sandeels feed on *Oikopleura*. The small cells taken by this appendicularian are produced under the same conditions as the larger phytoplankton sampled by the plankton recorder, i.e. production begins when the critical depth exceeds the depth of water; and the compensation depth as a fraction of the depth of water controls the rate of development of production.

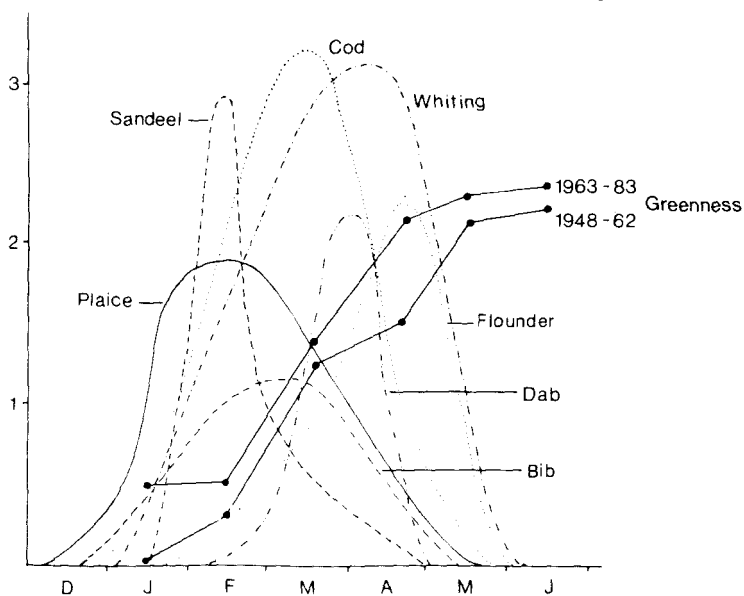


FIG. 5. The spawning distributions in time of seven fish species in the Southern Bight of the North Sea. Also, the development of "greenness" in the Southern Bight for the two periods 1948-62 and 1963-83, from the Continuous Plankton Recorder Network (this method was validated by Gieskes and Kraay, 1977).

C. *The Link Between Recruitment and Larval Abundance*

Brander and Thompson (1989) have shown that the night/day ratio of herring larval catches by high-speed nets (Gulf III, V or their derivatives) increases with the sizes of the larvae. The mean night/day ratio increases from about 1.5 when the larvae are 10 mm in length to 2.4 when they are 20 mm in length, as the proportion escaping increases with size. Hence the correlation between recruitment and numbers of larvae might be expected to decrease with size (although no such evidence appears from Table 1). An important general point to be made here is that unless the larvae are properly sampled at all ages, the measures of growth and mortality needed for understanding the processes will be difficult to establish. Moreover, the high-speed nets used in the North Sea are more efficient than many others that are in general use.

Burd and Parnell (1973), working with the Downs stock of herring, and MacCall (1979), working with the Californian sardine, have shown that in these two pelagic species at least, the magnitude of recruitment is linked in a rough way to the densities of their larvae. Van der Veer (1986) found that an index of recruitment to the southern North Sea plaice depends (only six observations) on the number of larval plaice in the flood waters of the Wadden Sea where the nursery ground lies.

Parmanne and Sjöblom (1984, 1987) have sampled herring larvae and their food at seven stations in four areas off the coast of Finland. Using a Gulf V net, samples were taken each week during May–August between 1974 and 1986. They established a link between the abundance of herring larvae and subsequent recruitment (as 0-groups from virtual population estimates), as shown in Table 1.

TABLE 1. CORRELATION BETWEEN NUMBERS OF HERRING LARVAE OFF FINLAND IN JUNE AND SUBSEQUENT RECRUITMENT, BY SIZE OF LARVAE AND BY AREA OF SAMPLING (After Parmanne and Sjöblom, 1984, 1987)^a

Size	Area		
	29	30	32
< 10 mm	0.714**	0.492*	0.209
10–15 mm	0.644*	0.480	0.798*
> 15 mm	0.632*	0.240	0.792**
> 10 mm	0.649*	0.464*	0.828**

^a Area 31 was excluded from the data in this table because the number of herring larvae caught there were so low.

* $P < 0.05$; ** $P < 0.02$.

Parmanne and Sjøblom also established correlations between recruitment (as 0-groups in the virtual population analysis) and zooplankton biomass per herring larva, particularly in July and August. The value of this work lies in the fact that such correlations can be established within a relatively short time, about 1–2 months after hatching.

Leggett and his colleagues have made a thorough study of the emergence of capelin larvae (from the seabed) and of their survival in the bays of eastern Newfoundland. The larvae emerge in relatively warm water during periods of onshore winds (Frank and Leggett, 1981, 1982). Offshore winds with local upwelling inhibit emergence because the upwelled water is cold and not turbulent. There was more zooplankton in the relatively warmer water. Finally, it was found that the continued emergence of larvae depended on the frequency of onshore winds, and that their subsequent growth depended on sustained temperatures, expressed as degree-days. Leggett *et al.* (1984) related year-class strength of capelin (as 0-groups from virtual population analysis) to the frequency of onshore winds and degree-days as follows:

$$\ln R = 16.10 - 0.19 \text{ Wind} + 0.19 \text{ Tempsum} (r^2 = 0.58)$$

where R is recruitment, Wind is the frequency of onshore winds and Tempsum is in degree-days.

The importance of this model is that it was derived step-by-step from detailed observations of (1) the development of the eggs with temperature, (2) the effects of the onshore winds and (3) the presence of food in the water. It is a realistic model of the structure of events that lead to the establishment of a year-class.

The survival of Arcto-Norwegian cod larvae will be discussed in more detail below. Figure 6 shows the dependence of numbers of 0-group cod on the post-larval index, or index of early juveniles, for 1979–85 (Sundby *et al.*, 1989). The juveniles, 2–3 months after hatching, still feed on *Calanus*. Recruitment indices at 3 years of age are correlated with the 0-group indices for 1966–81 ($r^2 = 0.67$; but the 1985 and 1986 year-classes were probably poorly estimated by the 0-group survey; Anon. 1988). Thus we have evidence from capelin, herring, plaice and cod that the magnitude of recruitment can be detected up to 2 months after hatching.

It has been believed that the magnitude of recruitment cannot be established until perhaps 9 months after hatching. There is now enough evidence to show that the processes by which recruitment is determined do begin during the larval stages. There is thus every reason to continue studies on the growth and mortality of fish larvae up to metamorphosis and perhaps just beyond.

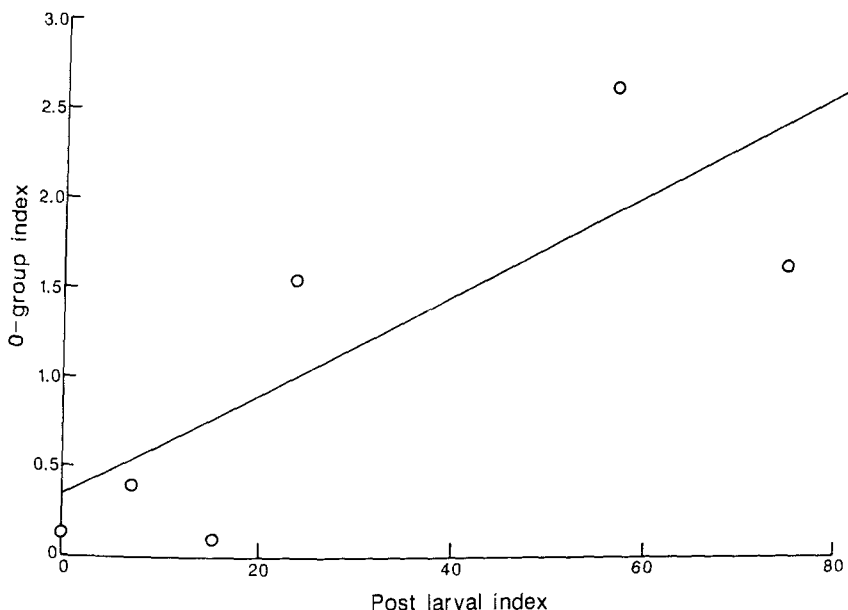


FIG. 6. Dependence of 0-group cod on the post-larval index of early juveniles (or post-larvae) for the Arcto-Norwegian cod stock (Sundby *et al.*, 1989). The 0-group index is used routinely for the prediction of recruitment in I.C.E.S. stock assessments.

D. The Baltic

In the 1920s and early 1930s, catches of the Baltic cod amounted to less than 10,000 tonnes. Meyer and Kalle (1950) noted that the catches increased during the late 1930s along the southern shore of the sea from Lübeck to Gdansk. Alander (1948) first associated this increase in catches with the recruitments of 1941–44 and 1947, and with the high salinity inflows into the Baltic which occurred then. The increase in salinity would cause the eggs to float, rather than sink, as they had done frequently when the salinity was low. Further, as the authors note, “a rise of 10 m or so in the halocline, where the fry hatch, gives better access to suitable food”.

Beverton and Holt (1964) presented tables in which the yield per recruit is given in terms of the estimated vital parameters:

$$R_0 = Y W_x Y'$$

where R_0 is the recruitment in the first year of life, Y is the catch in weight (kg. millions), W_x is the weight at infinite age and Y' is the yield per recruit

per unit of W_x . By periods of years (1925–28, 1935–39 and 1951–57) recruitment had increased by a factor of 17 between the 1920s and the mid-1950s (Cushing, 1982). In the 1950s and subsequently, catches remained high at an annual level of more than 200,000 tonnes. Figure 7 shows the increase in size of catches of the cod in the Baltic since the 1930s. Catches of herring and sprat also rose by the same order during the period.

Graumann (1966, 1974) showed that the larger and more buoyant eggs rose more quickly through the halocline to the region where the larvae fed and where the larval guts were full; below the halocline, the guts of the larvae were empty. Fonselius (1969) showed that between the 1930s and 1960s, the halocline rose from 80 to 60 m, which probably affected each year-class as it was generated, from the early 1940s onwards.

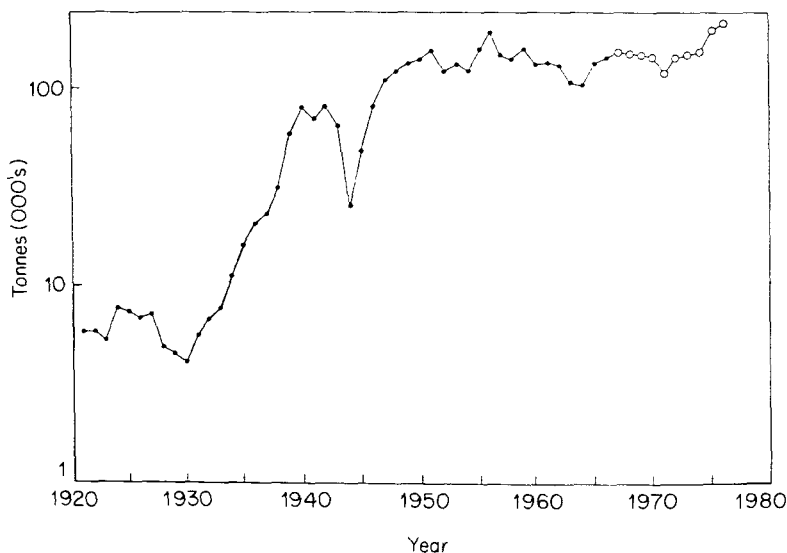


FIG. 7. Increase in annual cod catches (tonnes) in the Baltic between 1921 and 1976 (Cushing, 1982).

E. *The Gadoid Outburst*

From 1962 onwards, the catches and stocks of five gadoid species in the North Sea increased sharply and remained high: the event has been termed the "gadoid outburst" (Cushing, 1984). In the northeastern North Sea, to which most larval cod drift in spring, the monthly abundance of *Calanus* (the preferred food of the larval cod: Marak, 1974), was set back by 1 month if we compare 1949–61 and 1962–78 (Fig. 8). An annual index of delay was

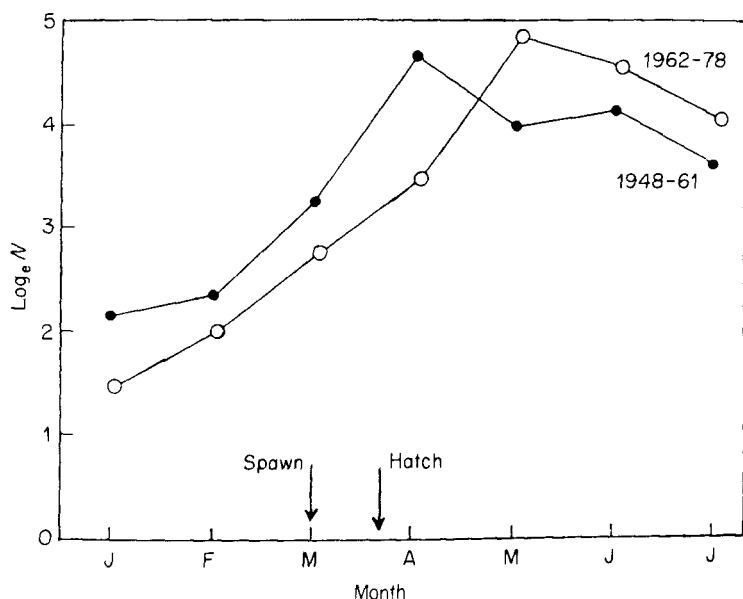


FIG. 8. The seasonal abundance of *Calanus* (as $\log_e N$) in the northeastern North Sea (area B1 of the Continuous Plankton Recorder Network) for 1948-61 and 1962-67 (Cushing, 1984).

prepared, showing the number of months between March and July at which the stock of *Calanus* peaked in any 1 year (after July, the little cod probably start to eat small fish: see Cushing, 1980). Cod recruitment was positively related to the index of delay between 1957 and 1977, i.e. before the increase in stock in the first year of the gadoid outburst and subsequently. There is thus a little evidence that cod recruitment tends to be greater when *Calanus* is produced later. Dickson *et al.* (1974) reported a spatial and temporal correlation between cod recruitment and temperature. A stepwise multiple regression of cod recruitment on the following factors was calculated ($r^2 = 0.75$):

<i>Calanus</i> abundance	-0.0013*
Delay in production	0.4537**
March temperature	0.1496**
<i>Calanus</i> abundance \times delay	0.0007*
Temperature \times delay	0.0854**

Where * $P < 0.05$ and ** $P < 0.01$.

Cod recruitment was correlated with the index of delay and it was modified by the abundance of *Calanus* and by temperature. The delay occurred during larval and post-larval life and it affected the magnitude of recruitment. Such might be expected if the match/mismatch hypothesis were true.

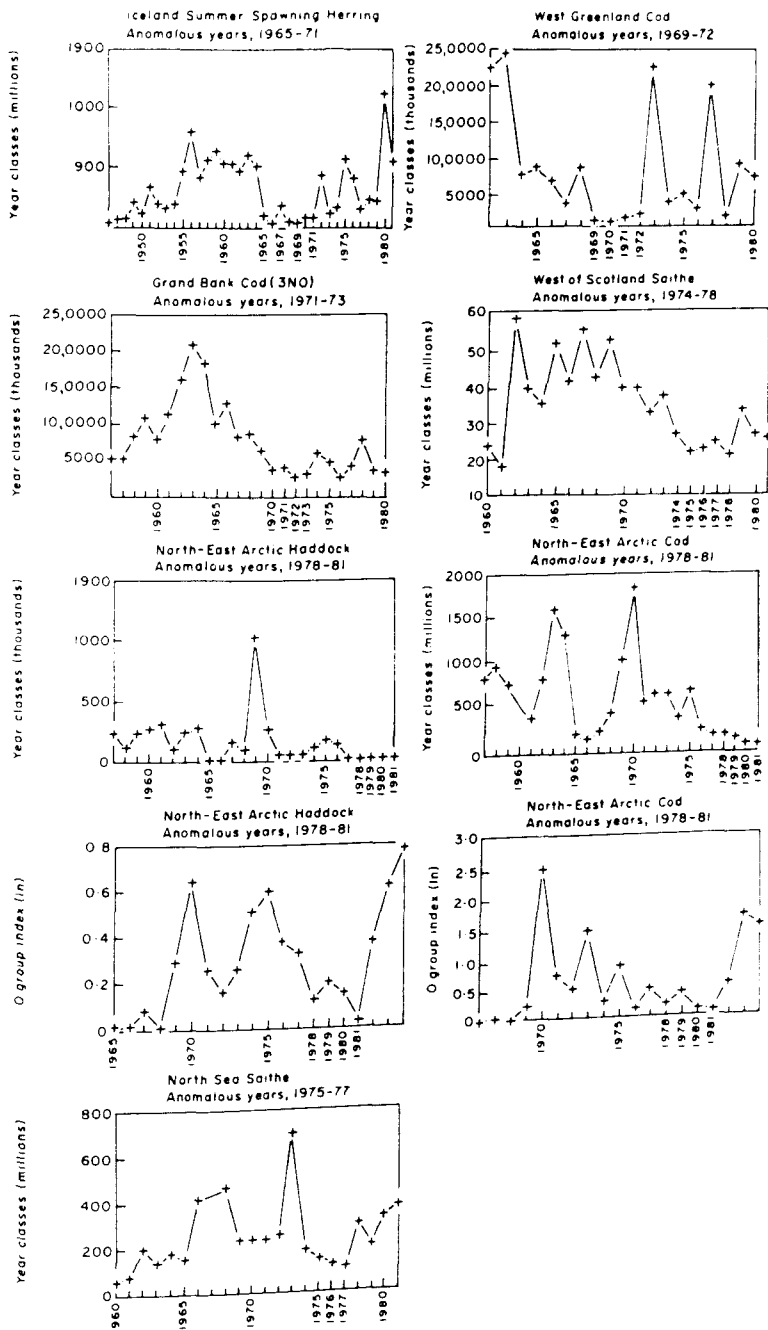
F. *The Great Salinity Anomaly of the 1970s*

Dickson *et al.* (1984), Dickson and Blindheim (1984) and Dickson *et al.* (1988b) have described the passage of the great salinity anomaly of the 1970s from the East Greenland Current to Iceland, West Greenland, the Grand Bank, across the Atlantic to the waters off the British Isles, the Norwegian Sea and the Barents Sea, in that order, between 1965 and 1982. The water mass, which was generated off east Greenland by cool northerly winds in winter in the early 1960s, was cooler and fresher than the surrounding sea; it was several hundred kilometres across and extended to a depth of 400 m, retaining its identity for a period of 17 years.

An example was made of the year-classes of 15 "deepwater" stocks that might have been affected by the passage of the anomalous water mass (Cushing, 1988). In waters such as the North Sea, mixed by tidal streams, the effect of the water mass upon recruitment might have been attenuated. Figure 9 shows some examples. Recruitment to the Iceland summer spawning herring was very low during the anomalous years 1965–71, and recruitments to a number of other stocks were low during other anomalous periods. Year-classes in the anomalous years were tested with a Wilcoxon rank test with respect to each stock series and, of the 15 stocks examined, 11 were significantly low.

North of Iceland, primary production was reduced by half (Thoradottir, 1977) and zooplankton by a factor of three (Astthorsson *et al.*, 1983) throughout the anomalous years 1965–71. Similarly, on the Grand Bank, zooplankton was reduced to the same degree for a period of 3 years (Robinson *et al.*, 1975). The reduced production of plankton in the cooler and fresher water is possibly linked to the low year-classes. Production must have been delayed because it takes longer to heat the cooler water, but the magnitude of the expected delay is as yet unknown. The cause is either a very reduced rate of development due to low food supplies, or a reduction in food

FIG. 9. Recruitment to the Icelandic summer spawning herring, West Greenland cod, Grand Bank cod, West Scotland saithe, northeast Arctic cod, northeast Arctic haddock (and the 0-groups of the two latter stocks), together with the years of the great salinity anomaly of the 1970s as it passed through the waters of the northeast Atlantic (Cushing, 1988). Significant relationships were established for 11 out of 15 "deepwater" stocks in the North Atlantic.



due to the delayed production during the period of transient thermoclines, before the seasonal thermocline becomes fully established. Whatever the proximate cause, the reduction in recruitment was possibly the consequence of the mismatch of the production of larvae to that of their food.

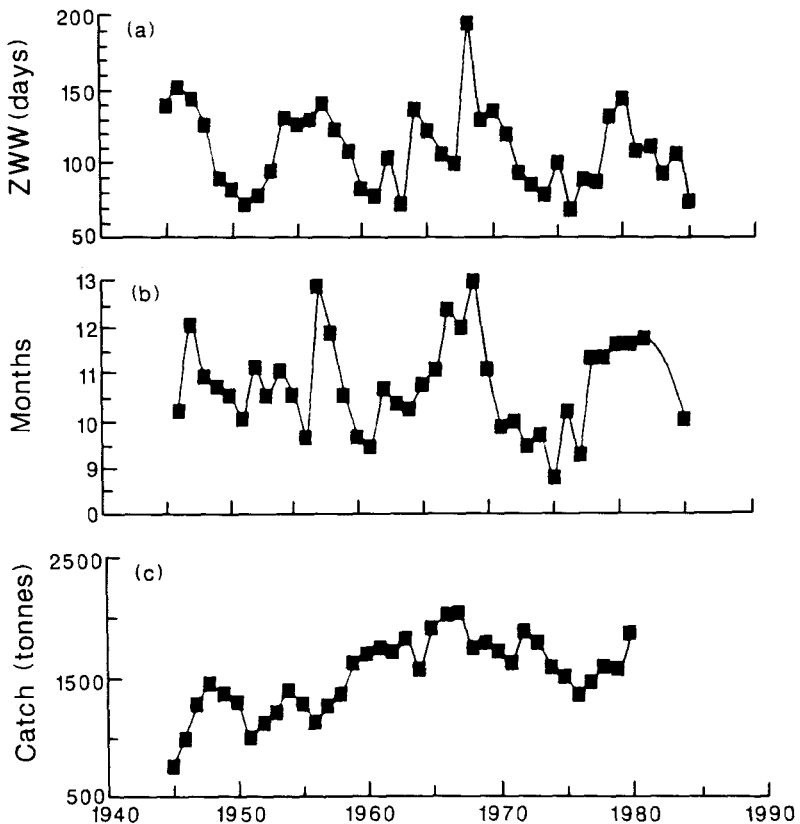


FIG. 10. The link between the west winds and catches of spiny lobsters off Tasmania. The changes in zonal westerly winds over Tasmania between 1945 and 1985. The date of onset of the spring bloom off Maria Island (off western Tasmania) is given in (b). Note the extraordinary variation in time of onset. (c) The time-series of catches of spiny lobsters off Tasmania, lagged by 7 years to indicate the timing of recruitment.

G. *Catches of Spiny Lobsters and the Time of Onset of the Spring Outburst off Tasmania*

Although fishes are my prime concern here, spiny lobsters share their habit of dispersing larvae into the pelagic environment and, as will be shown, their

recruitments may be matched or mismatched to the time of onset of the spring peak in plankton production. Figure 10a shows the time-series of zonal westerly winds over Tasmania between 1945 and 1985; the variation is determined by the position of the atmospheric high over Australia (which is linked to the El Niño/Southern Oscillation). As a consequence, the time of onset of the spring peak in plankton production varies by as much as $3\frac{1}{2}$ months between September and early January (Fig. 10b). Catches of spiny lobsters off Tasmania (lagged by 7 years to indicate the year of recruitment) were correlated with high sea temperatures off the east coast, i.e. with a late spring peak (in differenced observations in time series) as shown in Fig. 10c. Catches of spiny lobsters in New South Wales were correlated with an early spring peak (Harris *et al.*, 1988).

This study was successful partly because the time-series was a long one, but also because there was a wide variation in the time of onset of the spring peak in plankton production. The implication, which cannot be shown, is that the recruitment to the stocks of spiny lobsters depends on the match or mismatch of larval production to that of their food during the spring peak.

H. *Larvae of the Arcto-Norwegian Cod*

The survival of cod larvae in the Atlantic current north of the Vestfjord in northern Norway has been described by Ellertsen *et al.* (1987, 1989). They have shown that the number of *Calanus* nauplii per larval gut depends upon the numbers of nauplii per litre (in the manner of an Ivlev curve). Figure 11 shows the inverse relationship between temperature and the date at which the stock of *Calanus* copepodite stage 1 reaches a maximum off Skrova in the Lofoten Islands; if the water is cold, production is late, and vice versa. For a reduction in temperature of 2°C, there is a delay of about 6 weeks, very much more than the few days expected by an extended time of development. It may originate in a delayed production cycle, much as production may have been delayed during the passage of the salinity anomaly of the 1970s. Ellertsen and his colleagues also show that the length-weight relationship of the cod larvae varies from year to year. For 1982-85, the dry weights of larvae 6 mm long were estimated; they reach this length about 15 days after first-feeding (Yin and Blaxter, 1987). The dates of the peak stock of *Calanus* copepodite stage I for the 4 years were calculated from the dependence of the Julian date of peak stock on temperature. Table 2 shows that the cod larvae 6 mm long achieve a greater weight when their food is produced early.

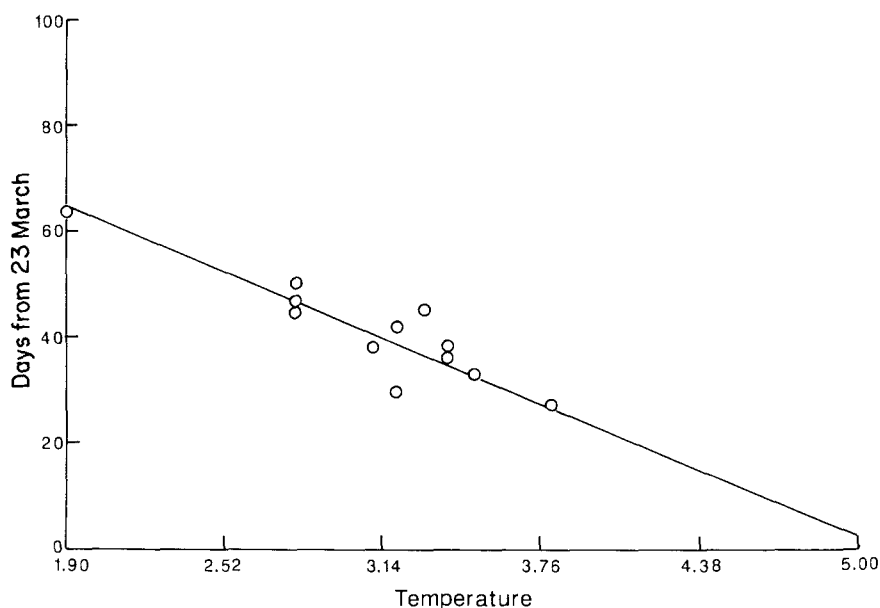


FIG. 11. The inverse relationship between the date of maximal production of *Calanus* and temperature in the Barents Sea (Ellertsen *et al.*, 1987). The range of 60 days cannot be accounted for by differences in the rate of development at the temperatures quoted.

TABLE 2. THE LINK BETWEEN THE WEIGHT OF COD LARVAE WHEN 6 mm IN LENGTH AND THE TIMING OF THE PEAK OF ABUNDANCE OF *CALANUS* COPEPODITE STAGE I (Based on Ellertsen *et al.*, 1987, 1989)

	Dry weight at 6 mm (μ g)	Temperature (°C)	Peak of abundance of <i>Calanus</i> (Julian days)
1982	98.75	2.10	149
1984	107.35	3.05	123
1985	120.00	3.50	114
1983	146.33	3.60	109

The earlier the production of *Calanus*, the greater the dry weight of larvae 6 mm long. Figure 12 (Ellertsen *et al.*, 1989) shows the match (1980, 1983, 1984, 1985) or mismatch (1960, 1981) of the production of cod larvae with their food (nauplii and copepodite stage 1), i.e. *Calanus finmarchicus*. Above a density of 5 nauplii l, the cod larvae are well fed. The 1983 year-class was a

strong one, yet from Figs 12 d, e and f (1983, 1984 and 1985), the matches appear to be the same. But the 1983 year-class individuals put on much more dry weight by the time they were 6 mm long and that year class was twice as strong as the other three year-classes (Anon., 1988). The two mismatched year-classes, (1960 and 1981) turned out to be poor ones (Rothschild, 1986; Anon., 1988); the 1980 year-class was well matched, but it probably suffered during the passage of the salinity anomaly. The production of larvae may be matched to that of their food, but the processes of growth and mortality during larval life must also be examined. A good match may initiate good growth, but it has to be sustained. Jones (1973) suggested that larval haddock grew with a cohort of *Calanus* on which they fed. The initial match or mismatch and the evolution of growth and mortality through the later stages of larval life are distinct but essential parts of the match/mismatch hypothesis. Though cod spawn at the same time each year, the onset of production of larval food varies from year to year by as much as 6 weeks.

Figure 6 shows how the numbers of post-larval cod (or early juveniles at about 60 days after hatching) are linked to the number of 0-groups and hence to recruitment. It remains to establish the relationship between the growing larvae at 15 days after first-feeding and the post-larvae (or early juveniles) which still feed on *Calanus*. Thus, recruitment depends upon the match of larval production to that of their food and probably upon growth and mortality during the larval stages.

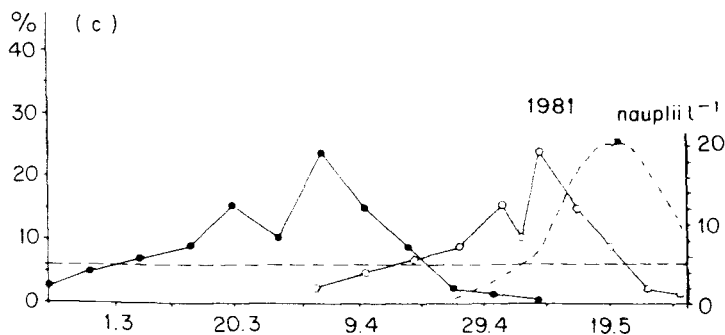
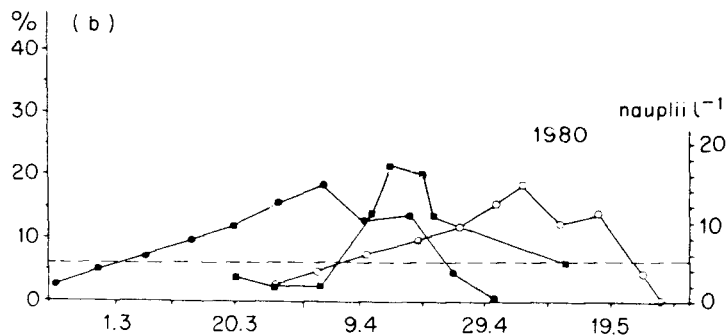
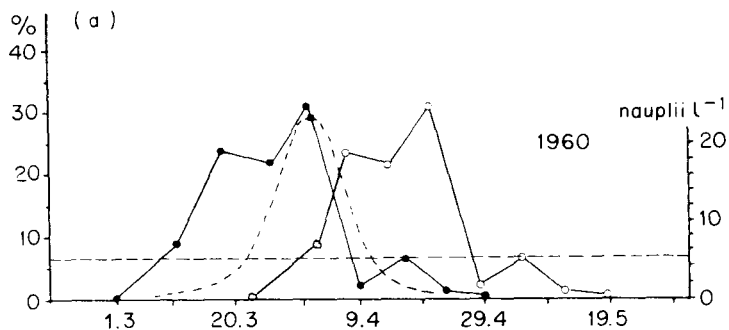
VII. Discussion

The match mismatch hypothesis has now been extended to the upwelling areas and oceanic divergences equatorward of 40° latitude on the basis that fish in these regions release batches of eggs more frequently when they are well fed and, more generally, that pelagic fish may modify their reproductive strategies so that they can feed and spawn at the same time.

However, the growth and mortality of fish larvae and post-larvae have not been covered, either by direct observation or by modelling. The main reason for this is that because the sampling of larvae has often been poor, the growth and mortality have not been well estimated. There are, however, exceptions, e.g. cod post-larvae or early juveniles (Sundby *et al.*, 1989).

However, Jones and Henderson (1988), using a simulation model with a fixed date for the spring peak in plankton production, showed that fish larvae should be hatched at the right place and at the right time, i.e. at the start of growth of their food cohort. Because the spring peak is short, the fish larvae need to grow fast, and there is an optimum period for start-

feeding. This is why spawning is spread over time. Such are the essential structures which provide match and mismatch when the date of the spring peak in plankton production varies. It also provides an explanation of why spawning is spread over time.



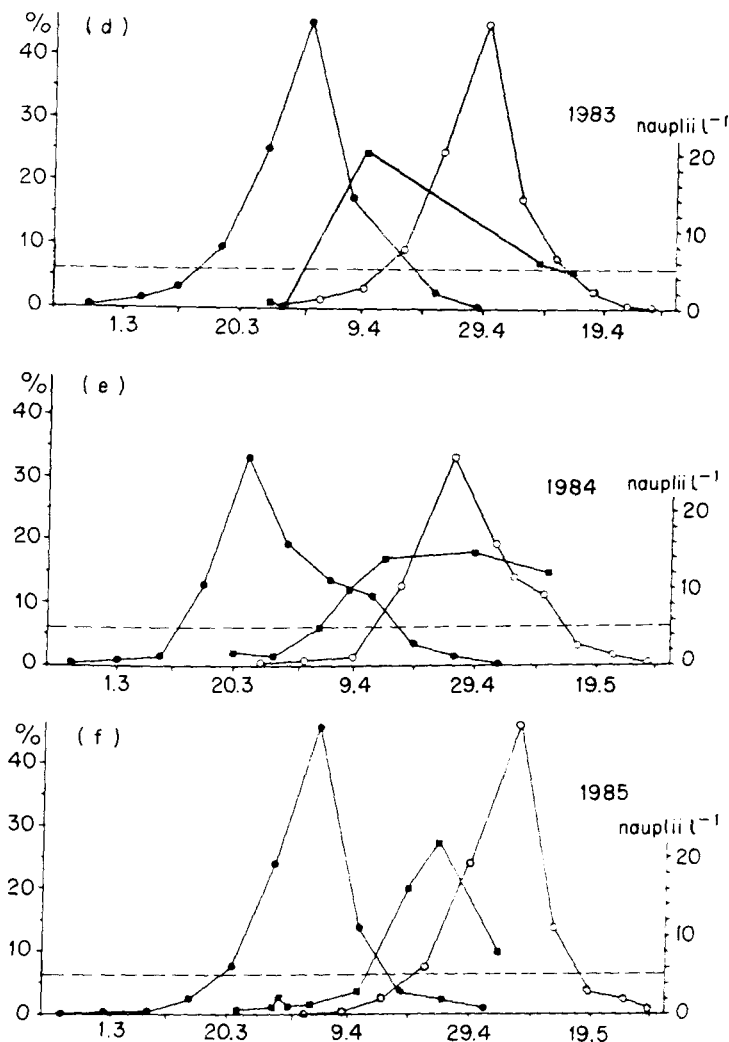


FIG. 12. The matches (1980, 1983, 1984 and 1985) and mismatches (1960 and 1981) of the production of cod larvae to that of their food (nauplii and copepodites stage 1 of *Calanus finmarchicus*; Ellertsen *et al.*, 1989). Above a density of 5 nauplii l, the cod larvae are well fed. Percentage distribution of newly spawned cod eggs (●) and first-feeding larvae (○); and the production of copepod nauplii (▲).

Nival *et al.* (1988) modelled the effect of food on the transfer rate from stage to stage of crustacean larvae. Starvation (representing a physical event such as mixing) produces the expected delay in transfer and such delays have

disproportionate effects under predation. Therefore, a delay in predation is of great importance, particularly when production peaks in early development. This model illustrates the difficulties that occur when growth and mortality are allowed to interact. One of the disappointments of the last decade has been the attention paid to either starvation or predation separately, although Ricker and Foerster (1948) noted that they were probably linked.

There are three consequences of the match/mismatch hypothesis. The first is that fish should release their larvae during the spring and autumn peaks in plankton production in temperate waters or into upwelling areas or divergences in low latitude seas. Spring and autumn spawning herring release their larvae during the spring or autumn peaks. In the southern North Sea, seven demersal species release their eggs during the spring peak. More generally, fish that spawn in spring or autumn temperate waters probably do so for the same reason.

In waters equatorward of 40° latitude, fish spawn in areas of upwelling and offshore divergence. By spawning more frequently where food is rich, and by adapting their reproductive strategies to feed and spawn at the same time, fish can match their spawning to the production of food for their larvae, as they try to do in temperate waters. This is an extended form of the match/mismatch hypothesis. The response of fishes to upwelling is more complex than has been thought, particularly in that more food may be produced where upwelling is moderate, which is where the pelagic fish tend to spawn. Furthermore, the effects of turbulence appear to be critical; without it, there is a simple direct response of recruitment to an index of upwelling, but if it is too strong recruitment is reduced.

The second consequence of the match/mismatch hypothesis is that correlations (if necessarily low) between larval numbers and recruitment are expected. Many such relationships have been established with indices of upwelling or divergence. This can probably only be effective during the larval stages, because the index of upwelling represents production, if in a somewhat complex manner, and hence the effects on larval food. Recruitment to the Baltic herring stock, the Newfoundland capelin stock and the Arcto-Norwegian cod stock can be roughly forecast 1–2 months after hatching.

By its nature, the hypothesis is hard to demonstrate. Yet there is evidence in the study of the gadoid outburst in the North Sea, the spiny lobster off Tasmania and New South Wales and the Arcto-Norwegian cod larvae that there are grounds to support it.

The reproductive strategy of some fishes begins the processes which tend to determine recruitment in larval life. The interleaved processes of growth and mortality from larval life onwards are then the prime agents in the gener-

ation of recruitment. They may be modified by other factors and there may be effects independent of them, such as advection. But the limited conclusion now and, as proposed by Rothschild (1986), is that investigations of fish larvae should continue to be a part of the study of population dynamics of fishes.

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IX. References

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