

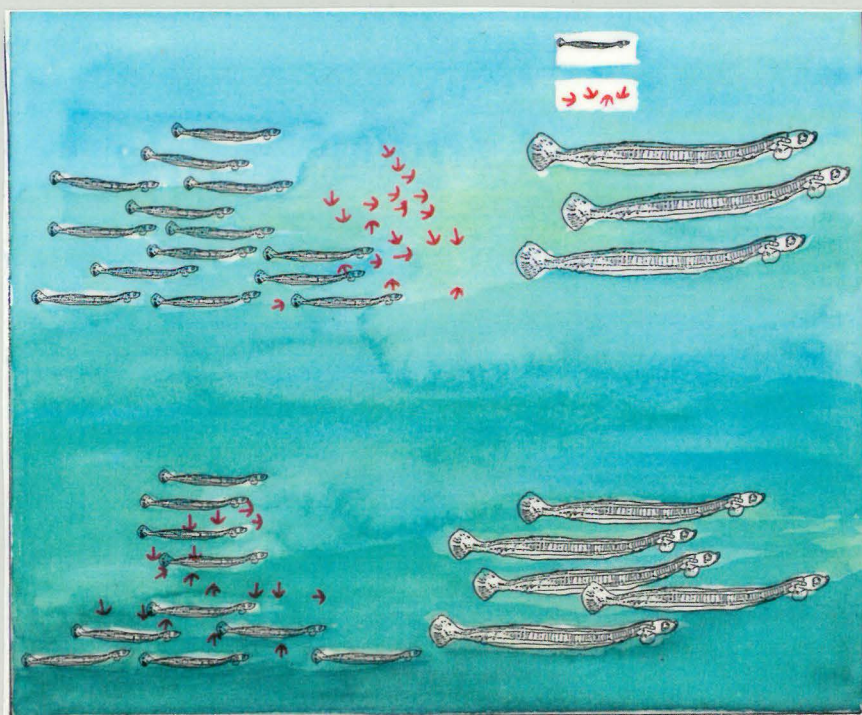
Aspects of recruitment with examples from commercially important fish stocks in Norwegian waters

by

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Preface

My research on fish larvae started in 1981 when I joined "The Cod Larvae Group" under the leadership of Mr. Per Solemdal. First of all, I wish to thank him for all help and support over the years. I also wish to thank the other members of the group at that time, Snorre Tilseth, Bjørnar Ellertsen and Svein Sundby, for their support.

Following this period, I worked on herring and capelin larvae in the Egg and Larval Program of the Institute of Marine Research. I want to thank the head of this program, Mr. Roald Sætre, for giving rise to this thesis. However, most of all I want to thank my friend and colleague Dr. Erlend Moksness who really set me "on fire" and never let this fire die out during the years we worked together on microstructure of herring larvae otoliths. I also thank Dr. Jarl Giske, Dr. Olav S. Kjesbu, and Dr. Victor Øiestad for valuable suggestions and corrections during the writing of this thesis.

I am very grateful to my technical assistants, Ellen Sophie Thobro, Laura Rey, Kjell Bakkeplass, and Per Bratland, with whom I have been working on various research topics.

I want to thank Rolf Mällberg who helped me to gain the self-confidence to carry on with the project.

The thesis is dedicated to my beloved wife Aase and our wonderful children, Marianne, Linn, and Kristian.

Bergen, March 24, 1994

Petter Fossum

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Introduction

Fish recruitment is a complex and fascinating process, where in most cases eggs and larvae are members of pelagical ecosystems during a considerable amount of time. The number of negative feedback mechanisms in a pelagic ecosystem is high, especially in biologically controlled marine ecosystems at lower latitudes. With respect to fish recruitment in different types of ecosystems there are more differences than similarities. The evolution and strong selective forces have shaped the genetic material so that fish

populations consist of individuals capable of high reproductive rates, and with refined adaptations to the environment in which they live (Skjoldal *et al.* 1993). The degree to which different species are able to use distinct life strategies to adjust their biomass to changes in the size of their ecological niches is important for the species' survival (Kawasaki 1983). Thus, several reproductive strategies have evolved in different types of ecosystems, from systems with large variability and few but numerous species at higher latitudes, to more stable systems with many species but few in numbers at lower latitudes. In marine ecosystems in the tropics, the most important negative feedback system influencing recruitment seems to be predation (Hunter 1981; Bailey and Houde 1989). This favours strategies with lengthened spawning season, perhaps including the whole year, to find "windows" in space and time with little overlap between the egg and larval stages and predators. In other ecosystems, such as shelf areas in higher latitudes, and upwelling and estuarine areas, fish typically adjust reproduction to the temporal variability of the system.

The reason for the high but variable fish production in the arcto-boreal marine ecosystems on the eastern side of the Atlantic Ocean is that these are productive systems with large recruitment variability. Recruitment seems to be controlled by the supply of warm Atlantic water masses. A positive temperature anomaly has been outlined as a necessary but not sufficient factor for good recruitment of cod, *Gadus morhua*, herring, *Clupea harengus* and haddock, *Melanogrammus aeglefinus* (Sætersdal and Loeng 1987; Ellertsen *et al.* 1989), but the underlying mechanisms are not fully understood. The variability in the inflow of Atlantic water masses to the Nordic Seas (Fig. 1) is governed by the large-scale circulation pattern of the north Atlantic Ocean, and the variation in this system sets the conditions within which recruitment can vary. The northward transport of heat by the supply of warm Atlantic water is known to play an important role in the climate of the northern hemisphere and to the entire globe (Broecker and Denton 1990). The circulation of this warm, nutritious Atlantic water within the Nordic Seas,

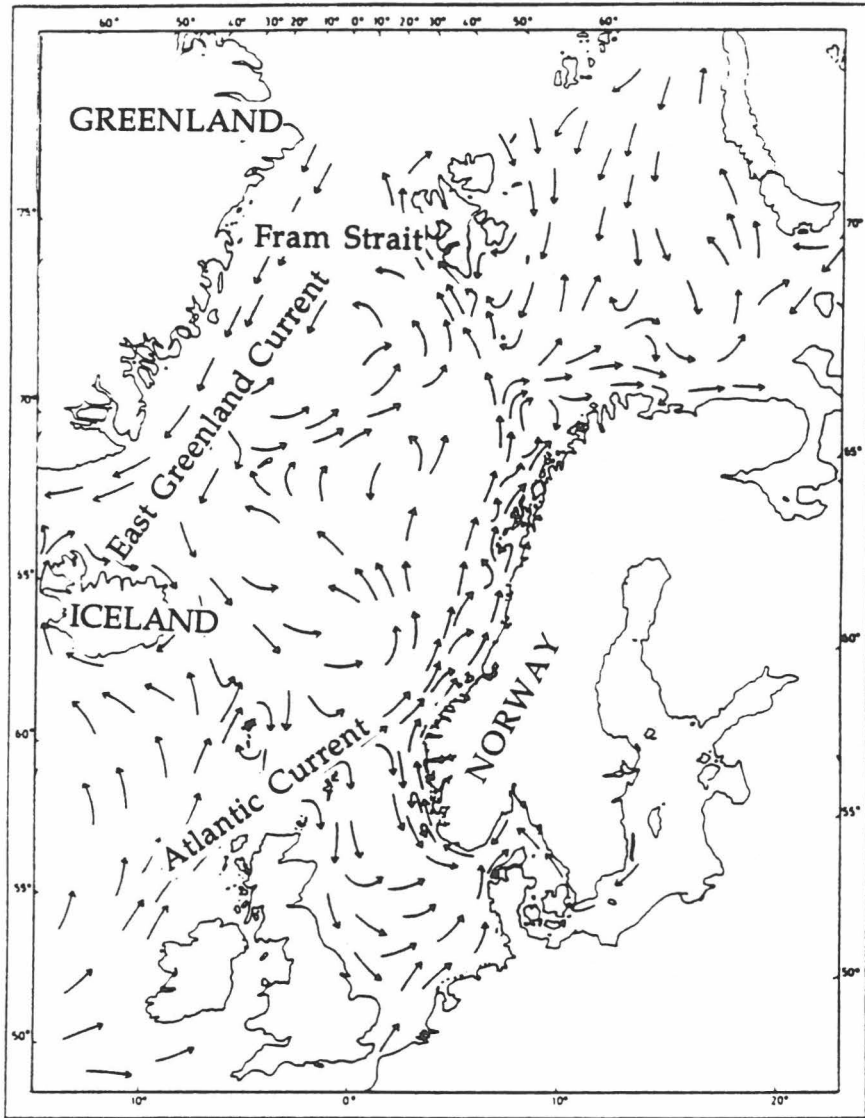


Fig. 1. Surface currents in the Nordic Seas (from Skjoldal *et. al* 1993).

also influences the advection and entrainment of zooplankton into the Coastal and the Barents Sea ecosystems, in this manner being an important mechanism for production of food for larvae and juveniles (Skjoldal and Rey 1989; Helle 1994).

Another and less direct way in which variations in the large-scale circulation pattern of the Nordic Seas influence recruitment is through concurrent changes in the biomass of the Norwegian spring-spawning herring stock. The stock size of this subspecies is influenced by the variability in size and production of the feeding areas in the Nordic Seas (Cushing and Dickson 1976). A collapse in the zooplankton production in this area was observed in 1876-77 (Sars 1878) and again in the 1960s (Malmberg 1969; Blindheim 1989). In the 1960s, the supply of polar water to the East Greenland Current increased considerably, giving rise to climatic anomalies that strongly altered the ecosystems within and surrounding the Nordic Seas. This may be looked upon as a sort of pseudoglacial event, where a change in the wind regime brought lots of ice from the Polar Basin through the Fram Strait, and in which the salinity in the upper layer was reduced due to the increased input of fresh water from ice-melting (Dickson *et al.* 1988). In addition to the observed change in the ecosystems this input of fresh water may have reduced the deep convection and formation of bottom water and thereby the northward transport of heat (Skjoldal *et al.* 1993).

In the 1950s, the biomass of the spawning stock of Norwegian spring-spawning herring was on the order of 10 million metric tons (Dragesund *et al.* 1980). This spawning stock size had considerable implications for the coastal ecosystems, introducing up to 2-3 million metric tons of biomass to these systems per year, directly as prey for demersal stocks and indirectly as spawning products. In 1950 and 1959, strong year-classes of Norwegian spring spawning herring were produced. Later on no strong year-classes were produced before the stock collapsed, but there was no complete recruitment failure throughout the 1960s (Dragesund 1970). However, during this period,

when the zooplankton production in the Nordic Seas failed, the feeding condition for the whole herring stock deteriorated. Disregarding this situation, the fishing pressure on all year-classes rose to a high level, almost wiping out the stock over a relatively short period (Dragesund *et al.* 1980).

The implication of the collapse of the herring stock for two other commercial important stocks, Arcto-Norwegian cod and Barents Sea capelin (*Mallotus villosus*), was significant. The cod stock dependent on herring as prey was only partly able to substitute capelin for herring in the diet, and could not resist the large fishing pressure put on during the 1970s and 80s. Hence the spawning stock size steadily declined during this period (Øiestad 1994; Nakken 1994). Capelin, however, the opportunist in the system, increased and became numerous in the 1970s (Hamre 1991). There is a strong working hypothesis of an inverse relationship between capelin recruitment and presence of one and two-year-old herring in the Barents Sea ecosystem, owing to predation by herring on late larval and juvenile stages of capelin.

Large-scale variability in physical conditions thus sets the frame within which different recruitment mechanisms can operate (Koslow 1984; Shepherd *et al.* 1984). In a plot of year-class size versus spawning stock size, the data points will have a large spread. This spread is caused by variations in the different mechanisms influencing recruitment, including the influence of the ocean's and atmospheric climate on the match/mismatch between the production cycles of fish larvae, their prey, and predators (Hjort 1914; Cushing 1975), the drift pattern of larvae (Hjort 1926; Bakun 1985; Sinclair 1988), the encounter rates between prey and predator (Rothschild and Osborn 1988), the larval growth rate (Thomas 1986; Campana and Hurley 1989) and the condition of the spawning stock (Nikolskii 1962; Monteleone and Houde 1990; Buckley *et al.* 1991; Kjesbu *et al.* 1991). All these mechanisms may have strong effects on recruitment. An important task is to single out the most important ones.

Works on recruitment mechanisms, and the present is no exception, have

often been concerned with dramatic events during the first-feeding period, however, one should keep in mind that such effects can be outweighed by small persistent changes in growth or mortality rate during the on-growing period, when the larvae are members of the pelagic food web (Houde 1987). In addition, as concluded by Beyer (1989): "The variability in recruitment is much smaller than would be expected if the different recruitment mechanism should work at random; density-dependent feedback mechanisms during the egg and larval stage have the potential to stabilize the number of survivors over a wide range of initial egg abundances". The total effect on egg and larvae of density-dependent and density-independent mechanisms, will sum up to the number of recruits to the fishable stock or the spawning stock or, as stated more generally by Heath (1992), "The outcome of the complex development of a year-class to a particular stage of development."

The present thesis scrutinizes three potential recruitment mechanisms, set forward as hypotheses, and it investigates their importance for recruitment. The three mechanisms examined are:

- 1) The importance of the match/ mismatch phenomenon for the survival through the first-feeding stage (Papers I-IV).
- 2) The influence of small-scale hydrokinetics (small scale turbulence) on interactions between first-feeding larvae and their prey (Papers V-VII).
- 3) The importance of predation for recruitment (Paper VIII).

The reason to study these mechanisms are their basic importance for recruitment. These mechanisms are examined with examples from three species with significantly different life histories; the Norwegian spring-spawning herring, the Arcto-Norwegian cod, and the Barents Sea capelin.

The larval material is sampled on more than twenty cruises with research vessels of the Institute of Marine Research in Bergen.

First mechanism: Match/mismatch elaborated through otolith microstructure examinations of the survivors

The match/mismatch hypothesis, or the Critical period concept, is an old and well-known theory first put forward by Hjort (1914) and later reformulated by Cushing (1972; 1975; 1990). This hypothesis was tested by May (1974) and Dahlberg (1979) with an expanded set of data, but little evidence for any critical period during the larval stage was unveiled. Most of the survival curves examined showed a quite stable mortality rate throughout the egg, yolk-sac, and first-feeding stages. The same was shown for Arcto-Norwegian cod in the Lofoten area where a mean instantaneous mortality rate of 0.12 per day was estimated during the egg, yolk-sac and first-feeding period, and a paradox is that only 1-2% of the eggs originally spawned were alive at the end of the yolk-sac stage (Fossum 1988). The reason for the observed mortality rates may be that critical periods do not exist or that large surveys tend to camouflage small-scale temporal and spatial effects. Some of these data might also have been sampled in systems where food was less important for survival than other factors. Thus a broad ecological understanding of the ecosystem under investigation is needed.

In addition to this, starvation of larvae in the sea has proved to be difficult to show by morphometric methods (Ellertsen *et al.* 1990; Heath 1992). However, previous investigations where histological methods are used, have shown that starvation most likely can occur during the first-feeding period (Theilacker 1986). It is clear from model studies that the period from endogenic to exogenic feeding is a special challenge for fish larvae, as they require higher food densities than later on in their ontogenetic development (Laurence 1977; Vlymen 1977).

Various field investigations have found a negative response in growth rate or gut content of fish larvae exposed to low food concentrations (Bakun and Nelson 1977; Neilson *et al.* 1977; Parrish and MacCall 1978; Walsh *et al.* 1980;

Frank and Leggett 1982; Crecco and Savoy 1983; Yoder 1983; Papers V-VII), and several investigations indicate that survival of fish larvae seems to be size dependant (Ware 1975; Shepherd and Cushing 1980; Anderson 1988). Thus there appears to be a relationship between growth rate and survival rate. In this way, the critical period concept can be looked at in a somewhat different manner, where a reduced growth rate and thereby a prolonged vulnerability to predation is the main reason for mortality, and not the starvation itself.

Field investigations have been carried out to examine the abundance of cod larvae and their prey organisms in the Lofoten area (Ellertsen *et al.* 1990), but without being able to establish any critical period. Another way to evaluate this topic is to sample the survivors, those larvae or juveniles that managed to grow through the supposed "critical period" and to see if the "winners" have any special characteristics. The application of this method demands an accurate age estimate, which might be provided by otolith microstructure. The original findings of Pannella (1971) described the otolith microstructure of hake (*Merluccius bilinearis*) and cod and counted 360 daily rings between successive annual rings of adult fish. The one-to-one relationship between increments and age in days has been confirmed for other species (Brothers *et al.* 1976). Evidence of departures from this periodicity also has been reported, especially at very low growth rates (Methot and Kramer 1979; Campana 1984).

A daily pattern in increment formation has been validated for larvae of spring-spawning herring (Moksness 1992), the species examined in the present context. Samples of the surviving "winners" were taken on the Norwegian shelf when the larvae were 1-2 months old. The otoliths were removed from the herring larvae and their microstructure examined. The number of increments, their width, and pattern were analyzed to determine birth dates, growth rates, and geographical origins (Papers I-IV). The back-calculated hatching curves were compared with the hatching of herring larvae and the concentration of microzooplankton found over the spawning grounds during the first-feeding period of the larvae. Variation in survival rates of different

cohorts, estimated from the age distribution of older larvae and juveniles, has previously been looked at for anchovy, *Engraulis mordax*, and pollack, *Theragra chalcogramma* (Methot 1983; Butler 1989; Yoklavich and Bailey 1990), but in more diverse and less controlled systems.

In the years 1985 and 1991 (Paper II; Paper IV; Fig. 2.) no differences were found between the measured and the back-calculated hatching curves, indicating a match between the hatching of the first-feeding herring larvae and the occurrence of their main prey organisms, copepod eggs and nauplii. In 1985 there was no sampling of microzooplankton. However, investigations in 1991 supported the idea that there was a positive effect on survival of improved prey concentrations during the first-feeding period of the larvae. In the years 1989 and 1990, the back-calculated and the measured hatching curves were not in phase with each other. In 1989 the "survivors" came from the earliest part of the hatching period, in 1990 from the latest part of the hatching period (Papers II-III, Fig. 2.). This was in good agreement with the results from investigations on microzooplankton, with the highest abundances early in the hatching period in 1989 (H. Bjørke, Institute of Marine Research, Bergen, Pers. comm.) and late in the hatching period in 1990 (Paper III). However, another interpretation of this data can be that the increased abundance of nauplii is positive correlated to a general increase in zooplankton abundance. Thus, the predation pressure put on herring larvae will decrease and a larger number of herring larvae will survive through the first-feeding period. In 1991 the total number of *Calanus finmarchicus* per m² were registered on one station during the first-feeding period of herring, but based on this limited set of data no such correlation were found (T. Knutsen, Institute of Marine Research, Bergen, Pers. comm.).

However, as outlined by Campana and Jones (1992), the back-calculation of age from juveniles using otoliths can show relative survival among cohorts, but this method can be biased due to differential cumulative mortality and gear

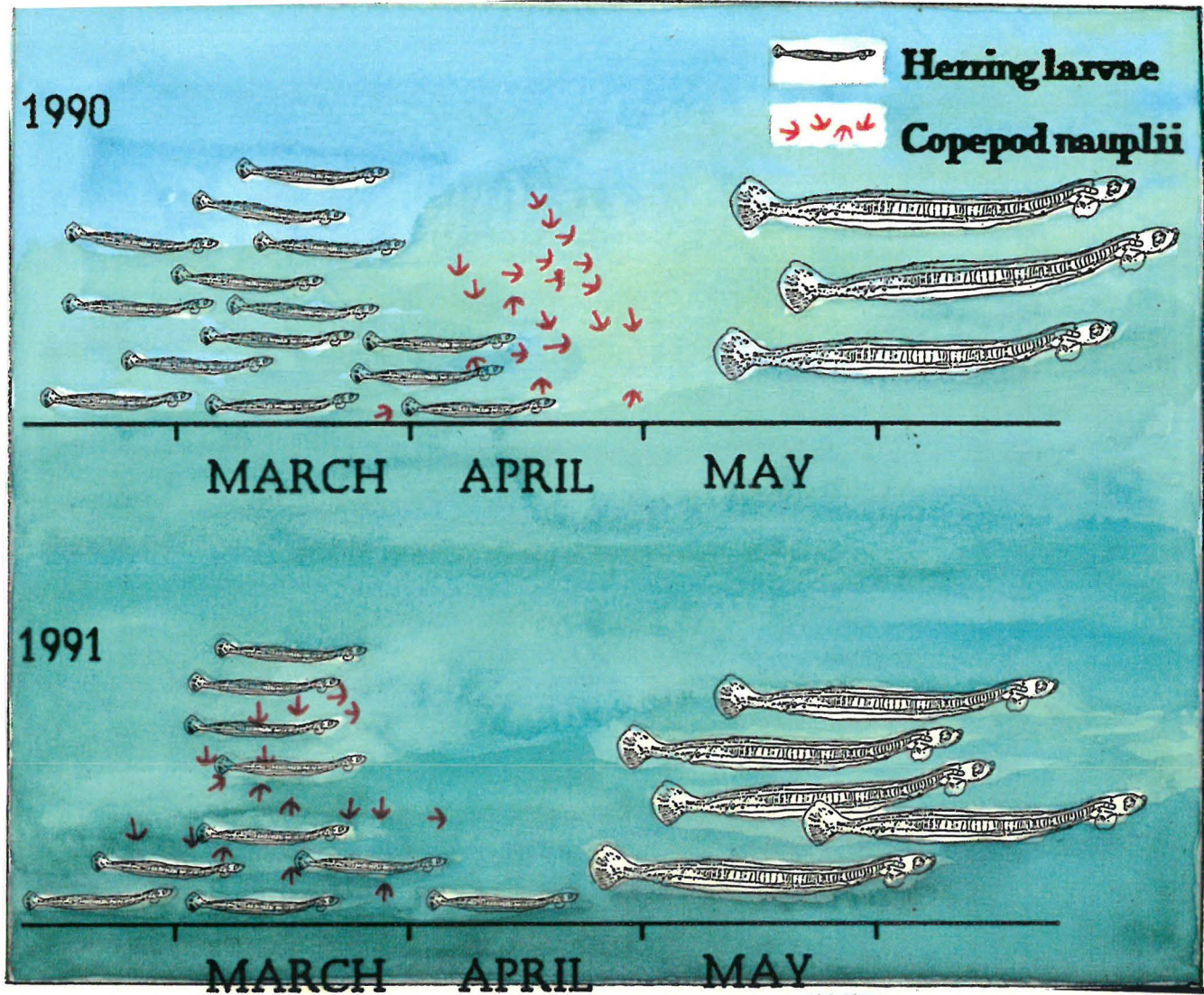


Fig. 2. Examples of match in 1991 and mismatch in 1990, between first-feeding herring larvae and their main prey organisms; nauplii of *Calanus finmarchicus*.

bias. The effect of including cumulative mortality on larvae from different parts of hatching period was investigated in Paper III, leading to only one days change in the estimate of the mean hatching date. The reason for this relative limited change in the estimate may have been that the sampling period occurred considerably later than the period with dramatic decline in mortality, found by Bailey and Houde (1989) to occur when the herring larvae were from 10 to 20 mm long. The potential gear bias calls for more concern. The threadlike herring larvae cling to the meshes of the Harstadtrål, a standard pelagic sampling trawl for gadoid juveniles described by Godø *et al.* (1993), and used in the present investigations. However, the normal length distribution obtained for the material sampled in May shows no sign of selection. Results (own unpublished) from a comparison between MIK (Methot Isaac Kidd Midwater Trawl; Munk 1988) and the Harstadtrål showed no significant length differences, although there seemed to be somewhat fewer larvae with a standard length below 20 mm in the Harstadtrål. In addition, the same age structure was found in the larval material sampled in late June as one month earlier, indicating that the May sample was representative (Paper IV). To conclude, the presented herring larvae material seems to give a reliable qualitative estimate of the true herring larvae distribution in the sea.

One of the main results from Papers II-IV is that the mean increment width seems to be relatively constant among years. This was also found by Butler (1989) when he compared the increment widths in otoliths from anchovy sampled in years with good and bad recruitment. Both these results indicates further that above normal recruitment might be recognized as years with high abundance of older stages of larvae and not, necessarily, as increased growth rate within the larval cohort.

A change in the spawning period from the end of March to the middle of March is described in the Papers II-IV. Such changes have previously been reported by Dragesund (1970) and Devold (1963), and may be explained by changes in the composition of the spawning stock, their maturation cycle or

the physical conditions in the overwintering and spawning areas.

From the present investigation it is not possible to single out the specific cause of larval mortality: whether the larvae hatched during the periods with low prey concentration, died from starvation, were eaten due to their reduced growth rate and condition or that concurrent changes in predator pressure during the season can be an explanation for the observed mortality. Predation and starvation can also be closely linked another way, since the most hungry larvae might take the largest risks to get food and thus become most vulnerable to predation (Giske and Aksnes 1992; Aksnes and Giske 1993). Fish larvae are, according to the same authors, "not old" before they are able to adjust their vertical position in the water column to optimize the probability of survival and dispersal into optimal areas.

However, the hypothesis; H_0 : "There is no relation between the number of herring larvae surviving through the first-feeding period and the prey concentrations in the same period" can be rejected based on the data presented in Papers II-IV. Match in the first-feeding period, however, is only one requirement towards establishing a large year-class. To gain more insight into the actual recruitment mechanisms which cause the greatest differences, a larger part of the ecosystem must be followed throughout the entire larval period (Campana and Jones 1992). In addition, the drift and predation patterns play an important role during the long period from the metamorphosis to the period when the adolescent herring are well established in the nursery areas in the Barents Sea and the size of the year-class is fixed, perhaps as late as 1-2 years after hatching.

Second mechanism: Hydrokinetics and larval feeding

The genetic selection pressure on fish stocks acts both on the timing and distribution elements of the spawning process. Most fish species spawn in

gyres, eddies or in connection with frontal zones with increased abundance of prey organisms, thus optimizing the progeny's probability of survival. The special character of each first-feeding area may be imprinted in the otoliths of each individual fish larva, and can later be used to identify their geographical origin (Paper I, III and IV). The larvae of species with demersal eggs hatch directly in the high concentration areas, while larvae from species with pelagic eggs are exposed to the dispersal processes during the incubation period. Various authors have described how larvae in gyres with patches of microzooplankton, in plume fronts, or in other productive frontal zones have been found to be better fed and in better condition than larvae in the surrounding water masses (Lasker 1975; Methot and Kramer 1979; O'Connell 1981; Kiørboe *et al.* 1988; Skreslet 1989; Grimes and Finucane 1991; Munk 1993). The degree to which the fish larvae are "members" of the high food concentration and high food production areas, is to a large extent determined by the year-to-year variations in the physical settings (Sinclair 1988).

Shepherd *et al.* (1984) looked at the impact of physical conditions on the recruitment and concluded that "there almost certainly are climatic effects on recruitment to fish stocks, and it is worthwhile attempting to quantify short-term effects in order to clarify possible stock-recruitment relationships, and long-term effects in order to acquire predictive ability in its own right." They also concluded that one should look at the effects of climate on recruitment at the border of ranges of fish stocks, where the impact from climate is presumed to be largest. However, they found little evidence for a general climatic effect on the fish stocks in the North East Atlantic. In the North Sea, (Shepherd *et al. op. cit.*) found that recruitment in five out of nine stocks was correlated with temperature, and as previously mentioned Sætersdal and Loeng (1987) and Ellertsen *et al.* (1989) found the same correlation between temperature and recruitment of cod, herring and haddock. A multiple linear regression analysis performed by Svendsen *et al.* (1994) showed that about 70% of the year-to-year recruitment variability of several of the fish stocks in the North Sea may be explained by variations in the ocean climate prior to and during

the period of larval stages.

Looking at temperature as a recruitment factor for Arcto-Norwegian cod, Cushing (1972) proposed that the changes in temperature are largely caused by changes in wind stress and direction, and that this has implications for the match/mismatch between primary production, subsequent secondary production, and cod larvae. Sund (1924) linked recruitment to the freshwater outflow and dispersal of larvae, and Skreslet (1981) proposed a connection between freshwater outflow and condition of the overwintering zooplankton as the most important recruitment mechanism. Kislyakov (1960) points to larval drift and development time versus temperature to explain variability in recruitment. Jointly, all these mechanisms may explain some of the variability in cod recruitment.

As previously stated, Ellertsen *et al.* (1989) were not able to verify Hjort's (1914) "critical period" concept in field investigations on cod larvae in Lofoten. Ellertsen *et al.* (*op. cit.*) found, however, a relationship between temperature and recruitment: that is, temperature above mean value was necessary, but not sufficient to produce a strong year-class. Investigations also showed that cod larvae, like some other species, start their exogenous food uptake before yolk depletion (Houde 1974; Ellertsen *et al.* 1980; Yin and Blaxter 1987; van der Meeren 1991; Paper V). At the initiation of feeding the cod larvae are opportunistic feeders, capable of ingesting a variety of prey such as ciliates, bivalves, rotifers, copepod eggs, copepod nauplii in addition to copepod faecal pellets, algae and different forms of "marine snow" (Wiborg 1948; Marak 1960; Bainbridge and McKay 1968; van der Meeren 1991; van der Meeren and Næss 1993; Paper V; Paper VII; Fig. 3.). Within a few days, however, the cod larvae become specialized feeders on copepod nauplii if such prey items are present in the water column, if not they continue to be opportunistic feeders (Wiborg 1948; van der Meeren and Næss 1993; Paper V; Fig. 3.), and later on the cod larvae shift to copepodite feeding (Paper V). During the period 1979-1986 in Lofoten, the diet of the cod larvae was totally dominated by nauplii of *Calanus*

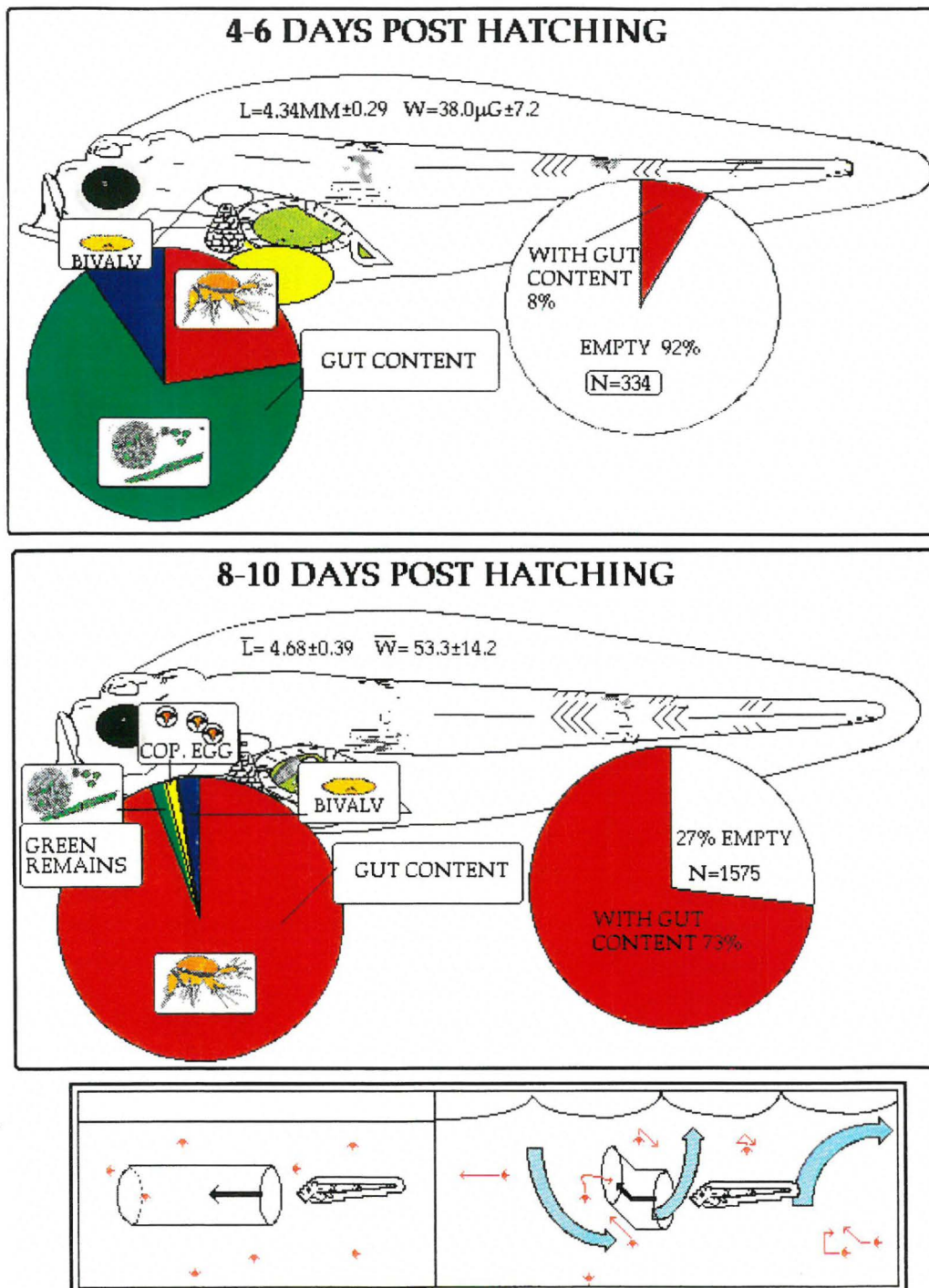


Fig. 3. The gut content of first-feeding cod larvae caught in the Lofoten area during the period 1979-1986, and an illustration of how increased turbulence affect the cod larvae.

finmarchicus (Paper V; Fig. 3.).

The investigations of Ellertsen *et al.* (1989) also indicated a positive relationship between the densities of copepod nauplii and the number of nauplii per cod larval gut. However, this data set showed large variations around the regression line. The data were therefore re-analyzed to see if some of this variation could be explained by small-scale turbulence inducing variations in contact rates between cod larvae and their prey and thus number of nauplii per cod larval gut (Paper VI). This re-analysis, made according to a model suggested by Rothschild and Osborn (1988), showed that the impact on contact rates from the variability in small-scale turbulence was able to explain most of the variation in the data set. Moderate wind stress increased contact rates 2-3 fold (Fig. 3). A recent investigation has confirmed this result (Paper VII). According to Sundby (1994), the increased contact rate from small-scale turbulence is probably important not only during first-feeding, but during the first two months of life of the cod. He also proposed that poor recruitment occasionally found in years with high temperatures may be related to low wind speed. Increased contact rate between fish larvae and their prey from small-scale turbulence may also play an important role for first-feeding of other species like herring and capelin. However, the tube formed gut of such larvae, and the emptying of the gut content during sampling and fixation makes it difficult to perform field studies with these species.

As demonstrated year-to-year variations in ocean climate are important for the recruitment of different boreal and arcto-boreal fish stocks. Correlations between temperature and recruitment are often found. However, results from such investigations can be questionable, since temperature may often not be the direct cause of changes in recruitment, but rather an indirect measure of the important processes involved. The problem is to identify the forcing parameter or parameters that are critical for recruitment. Understanding the implications of wind-induced small-scale turbulence on contact rates between fish larvae and their prey is a step towards a better understanding of such

processes.

Third mechanism: Predation, the bottleneck for fish recruitment

Fish eggs and larvae are prey for a wide range of invertebrates and vertebrates, ranging from the dinoflagellate *Noctiluca scintillans* (Hattori 1962) to sea birds (Barrett *et al.* 1987) and sea mammals. Predation in the form of cannibalism may also be important since it reflects a density-dependent recruitment mechanism (Ricker 1954; MacCall 1980; Rothschild 1986).

Greene (1985) developed a rational framework to classify predators. He first distinguished between invertebrates and vertebrates and then between ambush, raptorial, and cruising predators. Invertebrates select mostly for small prey due to their small size and modest capturing abilities, while vertebrates often select for a wider range of prey, using vision to detect them. Important invertebrate predators on fish eggs and larvae are: gelatinous zooplankton (Fraser 1969; Møller 1980; 1984; Bailey and Batty 1984; Purcell 1985), euphausiids (Theilacker and Lasker 1974; Bailey 1984; Theilacker 1988), amphipods (Shedder and Evans 1975), copepods (Greene 1986) and chaetognaths (Lebour 1923; Brewer *et al.* 1984). The most important vertebrate predators on fish eggs and larvae are fish themselves. Highly effective cruising and filter-feeding fish are mainly found among engraulids and clupeids (Hunter and Kimbrell 1980; Alheit 1987). Melle (1985) showed that predation from herring could have a significant impact on Arcto-Norwegian cod eggs. Perhaps the most effective predators on fish eggs and larvae are facultative feeders that switch from filter feeding to raptorial feeding depending on prey abundance and light conditions (Batty *et al.* 1986), like Atlantic herring (Paper VIII), northern anchovy, and Pacific mackerel (*Scomber japonicus*) (Bailey and Houde 1989).

Fish have various adaptations to avoid predation. They spawn at night

(Ferraro 1980), thus maximizing the dispersal of the spawning products before visual predators can recognize the egg patches. There also seems to be a tendency towards spawning and hatching before the blooms of gelatinous plankton (van der Veer 1985; Bailey and Houde 1989). However, this is probably not an adaptive reproductive strategy, but rather an indication that other planktonic zooplankton organisms occurring later in the season are the main prey organisms of gelatinous predators. Spatial separation of fish eggs and larvae and their predators also seems to be important (Bailey and Yen 1983; Frank and Leggett 1985; van der Veer 1985). Mass hatching in capelin was studied by Frank and Leggett (1982) and they concluded that this could be another strategy and have a positive effect due to "swamping" and satiation of predators.

Starvation has been shown to increase vulnerability to predation (Ivlev 1961; Laurence 1972; Rothschild *et al.* 1982; Booman *et al.* 1991). However, starvation seems to be most important for larval behaviour in the first-feeding period, and thus increases vulnerability to predation during this period. Eggs and inactive newly hatched larvae are often less vulnerable to predation because of less encounters with ambush predators than active swimming yolk-sac larvae with poorly developed sensory organs (Bailey and Yen 1983; Folkvord and Hunter 1986).

Later on, predation is part of a size-selective process and the vulnerability of fish larvae to a certain predator changes dramatically through successive changes in larval development (Anderson 1988). Large size is advantageous during the younger stages, which have less swimming capacity, greater vulnerability to starvation, less feeding success, lower burst speed, and less developed sensory and locomotory organs than later in the ontogeny (Yin and Blaxter 1987). However, as stated by Houde (1989): "One predator has to consume more than 80% of the year-class' spawning product before it alone would be likely to have an effect on recruitment. On the other hand the continual size-selective predation pressure exerted by a range of species over

the entire larval phase would be expected to exert considerable influence over recruitment.”

To look at the size-selective processes within a population, Tsukamoto *et al.* (1989) marked and released red sea bream, *Pagrus major*, larvae into a bay system. They found that mortality was inversely related to length of larvae at release. Post and Prankevicus (1987) found, with help of back-calculation from otolith microstructure, that the smallest juveniles in a cohort of freshwater perch had disappeared. Rosenberg and Haugen (1982) came to the same conclusion in a mesocosm study with turbot, *Scophthalmus maximus*.

Predators do feed on the older larval and juvenile stages. Even though the startling and escape responses of the larvae and juveniles are improving (Folkvord and Hunter 1986; Blaxter and Fuiman 1990), there will be highly effective predators present among sea birds and facultative filter-and-raptorial feeding fishes, which are only gape-size limited, and often select for the largest prey among larvae and juveniles. Trends of larvae and juveniles becoming more vulnerable as their size increases have been shown by Kozlow (1981), Zaret (1980) and Pepin *et al.* (1987). Brownell (1985) reported that cape anchovy would cannibalize the largest juvenile specimens. Puffins (*Fratercula arctica*) are positively size-selective on herring juveniles (Anker-Nilssen and Lorentsen 1990).

Norwegian spring-spawning herring, already described as effective facultative feeders that switch from filter feeding to raptorial feeding dependent on prey density and light conditions, spawn on the Norwegian shelf and use the Norwegian Coastal Current as a transport route. The nurcery areas of small and medium year-classes of this stock are fjords and inlet systems in mid and northern Norway and to lesser extent the Barents Sea (Dragesund 1970). However, large year-classes have the Barents Sea as main nurcery area for juvenile and adolescent herring which are leaving this ecosystem after 3-4 years. After such herring periods like the early 1950's and the early 1960's the

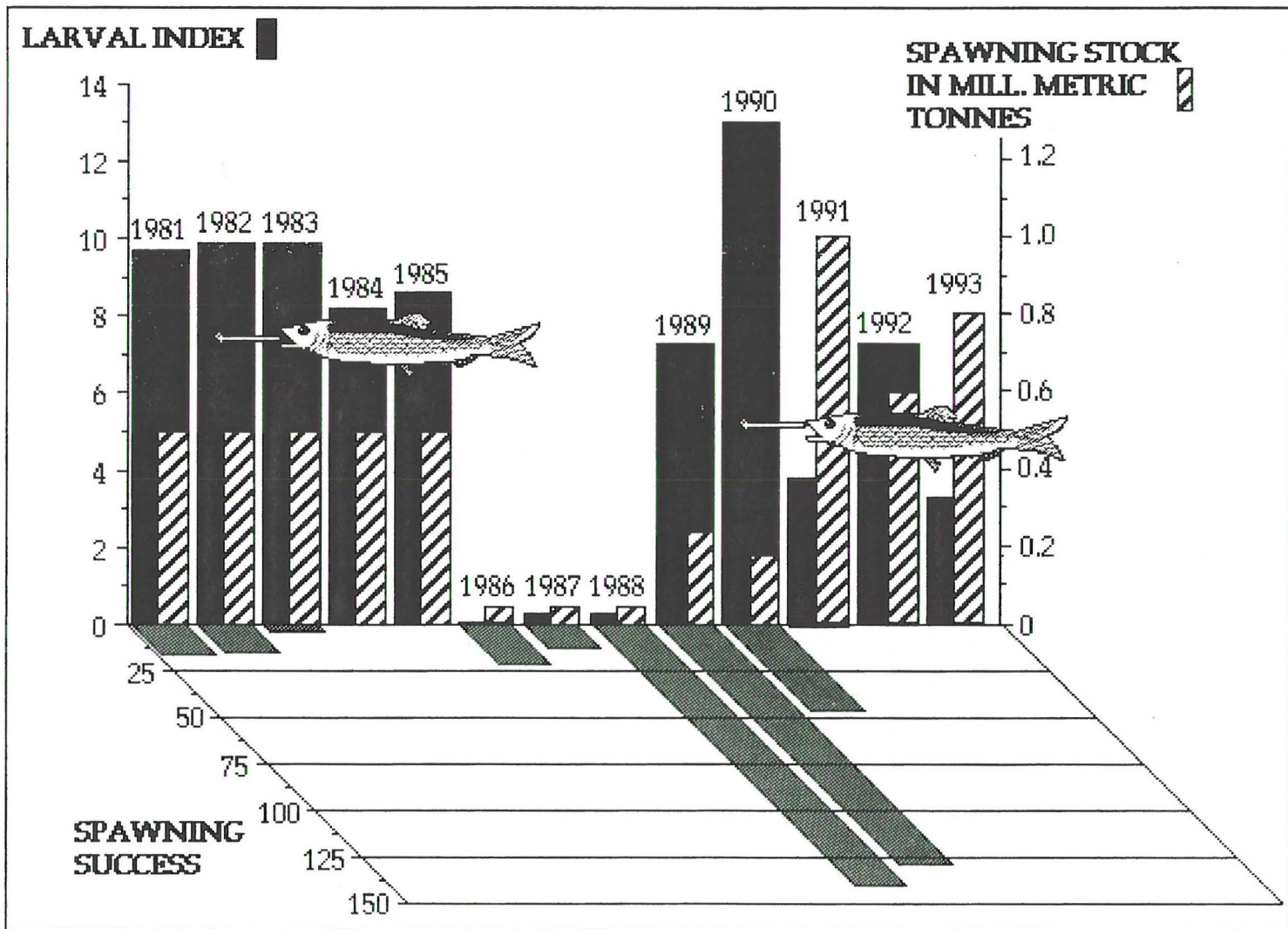


Fig. 4. Larval index ($N \cdot 10^{-12}$) and spawning stock biomass versus spawning success of the Barents Sea capelin during the period 1981-1993 (spawning success as number of two-year-olds per female spawner two years earlier).

capelin have disappeared. This is reported by Olsen (1965) and discussed by Hamre (1991). The same observation was done during the period 1983-1986 and again since 1991, where the one and two-year-old herring present in high number in the ecosystem, seemed to wipe out the capelin larvae (Paper VIII; Fig. 4.). Cruises during the summer 1993 found few areas with overlapping distribution of herring and capelin larvae, so the hypothesis of herring predating on capelin larvae could neither be rejected nor accepted. However, the few capelin larvae found in the herring guts were significantly larger than the mean sized capelin larvae in the ocean (B. Ellertsen, Inst. of Marine Research, Bergen, Norway, Pers. comm.). Implications of this is that the whole larval period must be covered to find areas with overlapping distributions of herring and capelin larvae, and that herring seems to select positively for prey-size. Thus, "it is not always best to be largest", also suggested by Pepin and Myers (1991).

During the period 1970-1983, there seems to have been a remarkably stable recruitment of the capelin stock in the Barents Sea (10-20 two-years-old offspring per female spawner, Paper VIII; Fig. 4; Anon. 1993) and thus a strong relationship between spawning stock and recruitment (Hamre 1991). The reason for this may have been a strong density-dependent regulating mechanism from the cod stock and perhaps the capelin stock itself, feeding on juvenile capelin according to their abundance. With herring present in the drift route of capelin larvae, recruitment was almost wiped out. A study of larval mortality rate in the first-feeding period (Paper VIII), showed no relation between mortality rate in the early stages and year-class size. Thus predation from herring on the older larval and juvenile stages could not be rejected as the main reason for high mortality and recruitment failure on basis of this study. However, after the crisis in the middle of the 1980s there were few density-dependent regulating mechanisms left and recruitment success rose to a very high level (more than 100 two-year-old offspring per female spawner, Fig. 4; Paper VIII). Consequently this seems to be a system where the predation including cannibalism is the bottleneck for recruitment of the

capelin stock.

Three species with different life history strategies

The genetic material of a fish species is constantly influenced by the selective processes in the sea, and fish species respond to this pressure by evolving different life history strategies. Kawasaki (1983) distinguishes between two different types of life history strategies with respect to recruitment (Fig. 5.). Type I is unstable and unpredictable, with two subtypes: Ia: irregular and short-spaced, Ib: large scale and cyclical. Type II is stable and predictable. Type I is characterized by relatively small bodied animals that are able to convert much of their weight to spawning products. In this way they are able to adjust to short periodic changes in their niches. Type II are adapted to an environment with smaller changes in their niches. They have large larval and juvenile mortality and severe interspecific competition, as a consequence of this recruitment give little reward so energy is mostly used for individual growth and maintainance. These types are only theoretical extremes; actual species usually can be classified somewhere between these achetypes. Of the three species presented here, capelin can be classified as type Ia, herring, as type Ib, and cod somewhere between type Ib and II. Typically, these species' recruitment varies within one order of magnitude (cod), two orders of magnitude (herring), and three orders of magnitude (capelin). They are all migratory species with large but variable stock sizes. According to Roff (1988), migratory species will be better exploiters and discoverers of resources than stationary ones, and able to exploit resources far away like the Nordic Seas and the most productive areas in the Barents Sea. Both herring and capelin (as secondary consumers) utilize the zooplankton reserves, while cod are a top predator in the system. The capelin have a sort of "big bang" recruitment, putting all reserves into spawning products as an answer to short-term changes in its niche. Thus, when the niche is expanding large year-classes can be produced immediately. Herring, however, have to build up larger

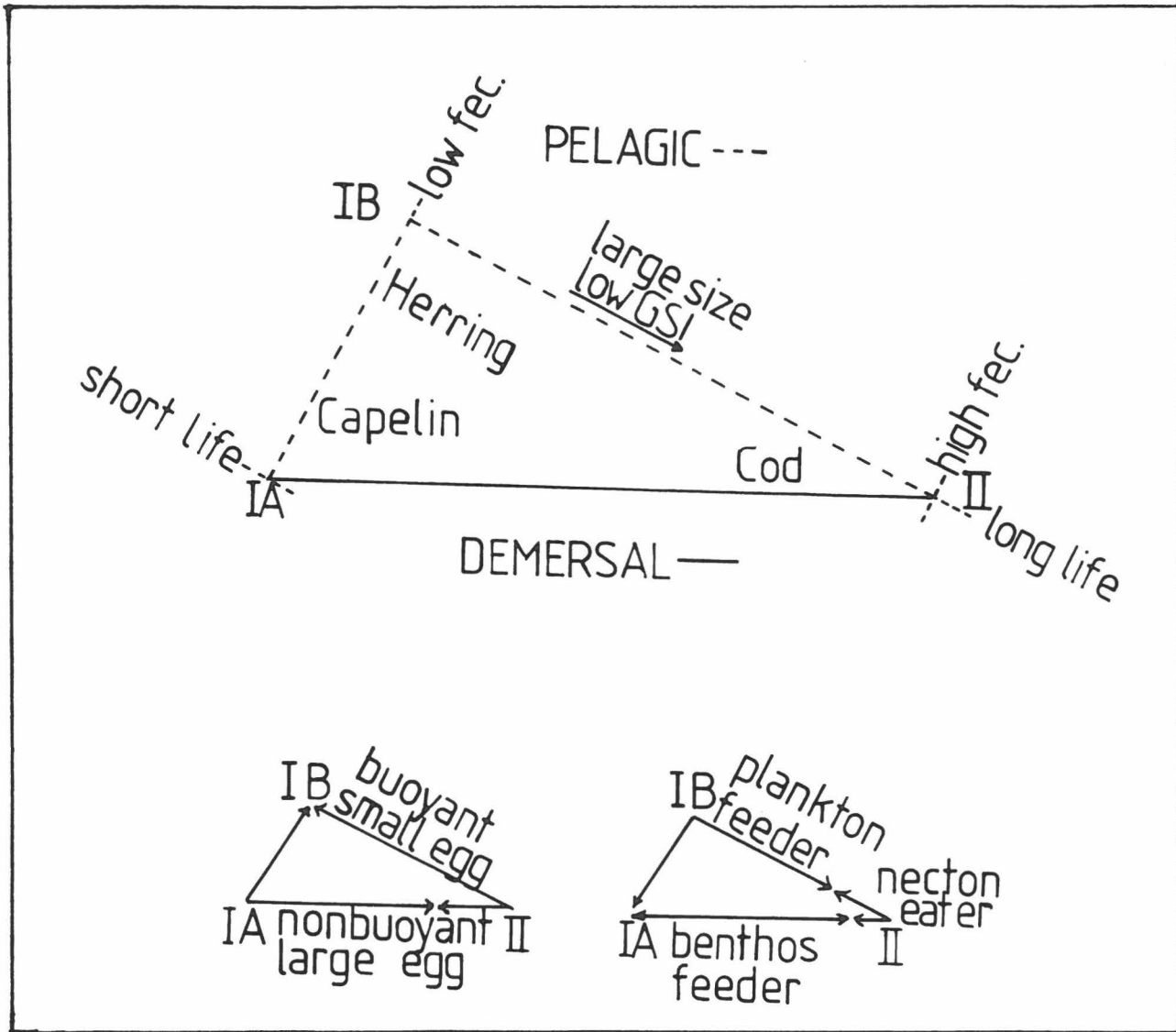


Fig. 5. Life historical triangles of the marine teleost (after Kawasaki 1983).

spawning stocks as an answer to long-term changes. Herring invest more energy into growth because of their extreme migratory pattern. Finally, cod are less dependent on short- and long-term changes in the environment, their niche is more stable as prey other than herring and capelin can be utilized. The implication is that the large cod invest more energy in growth and maintenance and less on spawning products than the other two species. Cod eggs, yolk-sac larvae and post larvae are found in the wind mixed layer, where the spawning products are exposed to density-dependent mortality during the embryonic, larval, and juvenile phases. Later on the cannibalistic cod may be exposed to density-dependent mortality as one and two-year-old fish. Hence the recruitment per female is relative small and constant compared to capelin and herring.

The different life history strategies of the three species have large implications for the exploitation of the three stocks. The utilization of the capelin stock must be dynamic and able to respond in coordination to the large changes in the stock size. The utilization of the herring and especially the cod stock must be more conservative. At present, great concern has been given in rebuilding large spawning stocks of herring and cod.

Summary

Recruitment is indeed a complex process, studied by scientists for more than a century without attaining the complete understanding of the phenomenon. What makes it so complex is that the process varies greatly among species and within different kinds of ecosystems. In addition, the tiny fish larvae grow as a part of the planktonic community, through different food webs in the sea and through various trophic levels. The ontogeny of the fish makes it first a primary consumer, then a secondary consumer, and later up to in some instances a top predator. The recruitment process is well adjusted to variations in the sizes of the niches through the different life history strategies of each

species. Without this adjustment, the species will lose in the “cruel” game of genetic selection and evolution.

This thesis focuses on the recruitment mechanisms of fish species in Norwegian waters: primarily Norwegian spring-spawning herring, Arcto-Norwegian cod and Barents Sea capelin. Hence, this thesis focuses on three different recruitment mechanisms: 1) the match/ mismatch phenomenon, 2) the influence of small-scale microturbulence on feeding and 3) predation, and the three mechanisms are exemplified with herring, cod, and capelin. This thesis show how useful the otolith microstructure tool can be in investigating aspects of recruitment of fish stocks. Although the present three species have different life history strategies the impact from the investigated recruitment mechanisms can be significant for the recruitment of all three species. The most important results from the present thesis are that:

1. Good larval feeding conditions; dependent of match in time and space of larvae and prey and increased contact rates between prey and larvae due to wind induced turbulence and
2. Low rate of predation on the older stages of larvae and juvenils are both necessary conditions for creating strong yearclasses.

Thus, the survival of first-feeding larvae seems to be related to the zooplankton production, and a match between the production cycles of larvae and their prey is an important first step towards establishing a strong year-class. Later on the predation pressure on later larval stages and juveniles, linked to the growth rate of the larvae, combined with the drift pattern will determine the final number of recruits.

This thesis does not attempt to explain the whole recruitment problem. Rather, it attempts to elucidate three important mechanisms to get a better understanding of this important and interesting process. To explain the “whole recruitment problem” more effort must in the future be put into

quantitative investigations to evaluate the relative importance of the different mechanisms involved. In addition to this the impact from ocean climate and zooplankton on recruitment must be further studied and effort must also be put on recruitment models and process related studies.

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