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**Baltic Cod: Resolving processes determining spatial and temporal  
windows of survival.**

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**Abstract:**

The linking of environmental processes to variations in recruitment success of fish stocks, the holy grail of fisheries oceanographers, has proved difficult. Typically research has followed two approaches. First is the linking of enhanced condition, growth or feeding success of a specific stage relative to a specific environmental condition. Secondly, a correlative approach has been employed relating the duration or intensity of a process to recruitment success. The former approach gives little information about the survival success of individuals to later stages, while the latter does not identify processes influencing the survival of the recruits, which are invariably a small component of the potential survivors. What is required is the identification of specific processes occurring during the early life history stages leading to increased survival success. Hence, we have chosen to look at the characteristics of settled juveniles to elucidate the processes occurring during the

viability and with a varying growth potential are injected into an environment where a series of stochastic processes manifested through starvation and predation act to determine their survival. Under this light there is little wonder that the either/or approach to food vs predation as the mechanisms driving variability in larval survival is viewed as flawed (Leggett and Deblois, 1994).

Clearly mortality in the larval stage can act both gradually, removing a percentage daily and episodically removing a large proportion of a population of fish larvae (e.g. Houde 1989). Recruitment to the population of surviving juveniles should therefore be reflected in the age distribution of the survivors dependent upon the mode by which mortality acts on the population. For example, age specific mortality rates removing a percentage of the population daily over a long spawning period should result in an age structured population dominated by individuals with a birthdate representing by that of peak spawning. Conversely, episodic mortality/survival should result in survivor age distributions biased by windows of variable survival success or mortality. Co-occurrence of environmental processes with these windows allows us to identify environmental processes acting to modify survival success.

An approach, termed "characteristics of survivors" (Fritz et al., 1990; Taggart and Frank 1990) is based on the examination of phenotypic and genotypic characteristics of individuals before and after experiencing an event allows the resolution of traits and processes modulating survival success. For example, if, after exposure to a specific process, a random subset of survivors exists from the initial population no phenotypic or genotypic selective advantage exists with respect to this process. However, if a particular characteristic or process results in an increased survival success this characteristic or event can be described as increasing the fitness of individuals. To date, the characteristics of survivors approach as primarily been used to identify survivors in terms of growth rates (e.g. Rosenberg & Haugen 1982; Meekan and Fortier, 1996; Miller 1997). Here we will through the examination of otolith characteristics (hatch check, daily increment number) in surviving late pelagic and demersal juvenile Baltic cod and the overlap with stochastic processes such as transport processes identify key mechanisms influencing recruitment variability of Baltic cod. Thereby this approach will provide a holistic examination of the regulatory

Arkona Basin into the Bornholm Basin (e.g. Stigebrandt 1987), convective winter mixing down to the halocline and vertical turbulent mixing caused by wind forcing also result in fluxes of oxygen to the deep layer (e.g. Stigebrandt & Wulff, 1987; Matthaus, 1995; St. John et al., 1996)

### **Potential Processes Influencing Survival in Baltic Cod.**

As in other stocks, a number of processes, including feeding success and predation potentially influence the probability of larval survival. However, unlike many stocks, Baltic cod, due to the prolonged spawning period (Wieland and Horbowa 1996, Wieland & Jarre-Teichmann 1997), and age and size dependent timing of spawning (Tomkiewicz et al., 1998). Hence, the potential exists for eggs and larvae of differing quality to be exposed to varying environmental and predation scenarios due to;

- a) intra-annual variation in oxygen conditions at the depth of egg development (MacKenzie et al., 1996; Wieland & Jarre-Teichmann 1997; Mackenzie et al., 2000)
- b) variations in predation on developing eggs by sprat and herring (e.g. Köster and Schnack 1994; Mollman and Köster )
- c) temporally varying food environment ( i.e. from the onset of the spring bloom to the fall bloom; St. John et al., In prep),
- d) a spatially varying food environment (e.g. St. John et al., 1995; Grønkjær et al., 1997)
- e) varying larval transport (e.g. Hinrichsen et al., 1997)

These processes all have the potential to influence the survival success of the egg larval and early pelagic juvenile stages. In order to resolve the importance of these processes on recruitment success we will utilise survivor characteristics (age of survivors, otolith hatch check size) coupled with environmental data and model simulations to identify;

- a) environmentally influenced windows of survival as well as,

spawning. Egg buoyancy varies with egg size and lipid content both of which are related to the size of female and batch number with large females typically produce larger more buoyant eggs (e.g. Kjesbu et al., 1992; Nissling & Vallin 1996; Nissling & Westin 1997) of higher lipid content (Grauman, 1965) hence increasing the probability that their offspring will survive in marginal oxygen conditions. The utilisation of the oxygen minimum in conjunction with the salinity of neutral buoyancy has resulted in the development of an index of “reproductive volume”. Hence, variations in the volume of water suitable for the development of cod eggs can be compared between years (e.g. Plikshs et al., 1993; Sparholt 1996; MacKenzie et al., 2000).

Late stage and hatching eggs as well as early larvae are found in the halocline and deep saline waters of the Bornholm Basin (e.g. Grønkjær & Weiland 1997). The highest abundances of young egg sack larvae are typically found in and below the halocline (Grønkjær & Weiland 1997).

#### **Bottlenecks on survival: Egg and Pre Feeding Larvae.**

The basis of most fisheries management strategies is the existence of a relationship between the spawning stock biomass (as a proxy for egg production) and recruitment. However, historically a lack of correlation between SSB and recruitment success has been identified making the utilization of this measure of recruitment potential questionable (e.g. Gilbert 1997; Marshall et al., 1998). Increasingly the importance of the reproductive outputs of different year classes (e.g. Marteinsdottir & Thorarinsson, 1998) and the condition of the spawning females (Marshall et al., 1999) is being recognised as key to reducing the uncertainty in estimating recruitment success. In the Baltic sea, due to the unique hydrographic conditions, the effects of stock age structure and female condition have been postulated to be a key to understanding the dynamics of this stock (Mackenzie et al., 1996; Nissling and Vallin 1996). A number of selective processes have been identified in the laboratory and field studies to potentially influence egg survival. The first of these is the selective pressure of oxygen on the egg stages. In cod, large repeat spawning females typically produce a number of batches containing larger eggs than smaller or first spawning

The basis of this argument being that larvae are neutrally buoyant at the depth of hatch thus requiring the expenditure of energy to maintain themselves in the lower density surface waters (Grønkjær & Wieland 1997). Laval quality varies with the size and nutritional condition of the female and batch number with a reduction in egg size and dry weight leading to a reduction in larval size (Kjesbu, 1989; Kjesbu et al., 1991). These characteristics as well as intrinsic factors such as metabolic rate and competitiveness (Mosegaard 1990, Titus & Mosegaard 1991, Metcalfe et al. 1992) will be reflected in the relative size of the hatch check. Comparison of the otolith check size distribution in pre migrating larvae and those in the surface layer will resolve the importance of egg quality and female contribution to the survival success of Baltic cod larvae.

#### **Characteristics of survivors: Egg and Pre Feeding Larvae.**

Evidence for selective processes influencing the survival of eggs and egg sack larvae of Baltic cod in the Bornholm Basin comes from research on vertical distribution and condition of larvae (Grønkjær & Weiland, 1997; Grønkjær et al, 1997; Grønkjær & Schytte, 1999). These results were based on cod larvae sampled during four investigations of the vertical distribution of cod larvae in the Bornholm Basin. Sampling took place during May, June and July 1994 and May 1995 in order to examine the periods of peak larval abundance. For details of sampling protocols see Grønkjær and Weiland (1997).

Our hypothesis that poor oxygen conditions would favour larvae from large eggs was examined by comparing otolith hatch-check sizes of larvae caught in the surface from May 94, July 94 and May 95 with those captured at depth. Water column characteristics during the sampling periods are presented in figure 2. Larval hatch checks in the surface layer were significantly larger than those found at depth supporting the hypothesis that larvae from smaller eggs suffered higher mortality rates. (**Fig. 3**). Furthermore, examination of the hatch check of larvae surviving after day 10 post hatch revealed that a higher percentage of larvae with large hatch-checks ( $>250 \mu\text{m}^2$ ) to later stages (**Fig. 4**). These observations suggest that the combination of low oxygen conditions and smaller egg size act as a selectively to remove larvae

the sea surface results in Ekman transport of the surface mixed layer with coastal jets in the direction of the wind produced along both coasts of the basin. These are compensated for by a weak return flow in the central interior of the basin (Kraus and Brügge, 1991). Results based on the analysis of the vertical distribution of cod larvae suggest that larval transport occurs in the depth range of the compensating return flow below the Ekman layer (Hinrichsen et al., 1997; Grønkjaer and Wieland, 1997).

### **Bottlenecks on Survival: Feeding Larvae and Pelagic Juveniles.**

A number of processes driven by variations in feeding success and predation have the potential to influence the survival success of post egg sack larvae and juveniles. First is the temporal match between cod larvae and the abundance of their prey. Cod spawning occurs over an extended period in Eastern Baltic stock (e.g. Mackenzie et al., 1996) with larvae and juveniles experiencing feeding conditions occurring from the onset of the spring bloom to the fall bloom (HELCOM 1990; St. John et al., In prep). Larval and juvenile prey abundances vary dramatically within a season as well as horizontally with peak abundances observed in late summer as well as in relation to oceanographic features (HELCOM 1990; St. John et al., 1995; Grønkjær & Weiland 1997). This prolonged period of larval production potentially creates a situation whereby certain temporal components of larval production are exposed to high levels of prey abundances whereas others experience a temporal mismatch with the occurrence of their prey (e.g. Cushing, 1990). Consequently, these variations in match and mismatch will create temporal variations in growth and potentially survival success. These variations in survival success can potentially be identified through comparison with egg and larval production and the age distribution of surviving demersal juveniles through otolith ageing of surviving individuals.

As well as varying temporally, the distribution of potential prey items of cod early life stages varies spatially due to the effects of intermediate scale oceanographic processes such as coastal upwelling (Haapala, 1994), pycnocline bottom interactions (e.g. Kahru 1986; St. John et al., 1995; Josefson & Conley, 1997) as well as in coastal regions where increased primary production is the result of anthropogenic processes (e.g. Witek et al., 1997). The occurrence of increased primary and secondary

smaller later settling conspecifics to reduced food availability and higher predation pressure due to the inability to obtain optimal habitats defended by older and larger conspecifics. This has led to the hypothesis that recruitment success at this stage is regulated primarily by density-dependent processes (Myers and Cadigan 1993) mediated through competition for a limiting resource and predation (e.g. Tupper & Boutilier 1995; Hüsey et al., 1997). Otolith estimates of age and growth will resolve the importance of horizontal distribution and birth date on growth and survival.

### **Characteristics of Survivors: Feeding Larvae and Juveniles**

In order to examine the potential impact of hatch timing, transport and demersal distribution on survival success of Baltic cod larvae and juveniles we will examine the characteristics of surviving 0-group cod obtained during a multidisciplinary cruise performed in November-December 1995. The cruise primary goal of this cruise was to obtain an estimate of the horizontal and vertical distribution of 0-group cod using trawl and hydroacoustic techniques (for details on sampling protocols see Nielsen & Lehmann, 1996). Analyses of individual juvenile cod included measurement of total length (mm), weight (mg), age determination (daily otolith increments, Stevenson & Campana, 1992) increment widths. In order to obtain survivor characteristics from individual fish, otoliths were examined under a transmitted light microscope with polarised light at a magnification of 150x and 300x. The microscope was connected with camera and computer (software used: *Global Lab Image*, ver. 3.1). All measurements were taken along an axis from the nucleus to the anterior edge of the otolith. Settling checks, visible as abrupt and distinct changes in the otolith structure and coloration, were identified. Both distance from nucleus to the anterior edge, the otolith width over the nucleus and the distance from the nucleus to the settling checks were measured. The number of increments was counted from the edge as far towards the nucleus as possible. The number of increments contained in the uncountable area around the nucleus was then estimated using the age-otolith size relations from larval fish spawned at approximately the same time as the fish investigated in this study [otolith size (in  $\mu\text{m}$ )= $\exp(0.045*\text{age}+2.18)$ ].

These results suggest that the peak abundance of surviving juveniles came from a temporal window approximately 3 weeks after the period of peak larval abundance. Figure 6 illustrates the timing of hatch of larval survivors relative to the abundance of larvae as estimated from egg surveys.

### *Larval Transport Hypothesis*

A temporal coherence between occurrence of larvae and processes influencing the transport to or retention of individuals in optimal environments has also been identified as a processes potentially influencing survival probabilities. In order to examine the potential for variations in larval drift periods and final destinations we have employed the Baltic Sea model, a three-dimensional eddy resolving model in this study (Lehmann, 1995; Hinrichsen et al., 1997). Calculation of larval drift routes was performed following a Lagrangian particle tracking technique (Hinrichsen et al., 1997). Three-dimensional fields of temperature and salinity were employed for initialising the model. These fields were created, utilising a data set representing the three dimensional distribution of temperature and salinity for the entire Baltic Sea for spring conditions (April). Model simulations commenced on 1 April, 1995 and continued until December 10th 1995. For time  $t=0$  (1-April-1995) the velocity components were set to zero and the surface elevation was taken from the initial fields. Atmospheric forcing was switched on and the model allowed to equilibrate to the prescribed mass field over a period of a few days. Data assimilation techniques (Bretherton et al., 1976) using data from monthly hydrographic surveys carried out in the Arkona Basin, Bornholm Basin and Stolpe Trench during May and July 1995 were performed. Vertical temperature and salinity distributions were created by interpolating these fields observations onto the three-dimensional model grid employing objective analysis (Bretherton et al., 1976). Atmospheric forcing for the simulation was obtained from the EUROPA Model of the German Weather Service (Deutscher Wetterdienst in Offenbach). Data included two-dimensional wind fields, dew point temperature (2 m height), air temperature (2 m) and precipitation. The EUROPA model data were available at 3 hours intervals. The heat budget was calculated from incoming short and long wave radiation, outgoing long wave radiation



be expected due to the differences of circulation patterns caused by variability of the meteorological forcing during their hatching period. In order to illustrate differences in the advection of larvae hatched between late July and September 1995, release locations and final destinations of larval drifters are presented in **Fig. 7 b,c,d**. Each larval drifter was given an identifying code stipulating time of release (hatch) and assessed with a daily vertical migration pattern (Voss et al., 1999).

### ***Transport North***

In contrast, relatively late spawned cod larvae (Julian day 242) caught as juvenile fish in the northern shallow water area of the Bornholm Basin show a different drift behavior (**Fig. 7b**). Results of the numerical simulation suggest that these larvae might have spawned at different locations within the central deep water region of the Bornholm Basin (depth > 80 m). At the beginning of the drift period, due to strong easterly and northerly winds the larval drifters were advected rapidly towards the east. After 5 days of drift, the drifters were embedded in a basin wide cyclonic circulation cell yielding a drift towards the north along the 60 m isobath. Finally, the larval drifters turned towards the west reaching their catch location at ages between 30 and 57 days. In generally, 0-group cod found close to the Swedish coastal environment (**Fig. 7b**) hatched within the northern and central part of the deep Bornholm Basin. Due to a cyclonic circulation pattern the larval drifters arrived in their nursery areas at ages between 25 and 60 days. Although, cod larvae have the potential to be transported towards areas (Gdansk Deep; **Fig. 8b**) which finally can not be identified as their nursery areas.

### ***Transport East***

The origin of larvae finally settling within the Stolpe Trench (**Fig. 7c**) was also identified to be located within the northern deep-water region of the Bornholm Basin. During the first part of their 60 days drift periods the larval drifters experienced a weak eastward orientated flow component (southern edge of the cyclonic circulation cell). Due to the onset of the above mentioned strong storm event of northern and eastern direction at the beginning of September the larvae were rapidly transported

processes potentially acting to influence the survival and growth potential. First it is clear from the characteristics of the hatch check distributions of surviving larvae that the majority of survivors in marginal oxygen conditions are the result of the reproductive efforts of large females. Oxygen acts to modify the population of survivors by exerting selective pressure on both eggs and larvae.

In the case of cod eggs, oxygen influences survival through selection pressure via egg buoyancy and metabolism. The survival success of cod eggs has previously been observed to decrease from 8.0 to 2.4 ml. l<sup>-1</sup> after which no survival occurs (e.g. Weiland et al., 1994). The buoyancy of cod eggs vary with egg size (e.g. Nissling & Vallin, 1996) with larger eggs produced by large females being more buoyant and existing higher in the water column. Smaller eggs from small females or females in poor reproductive condition reach neutral buoyancy at greater depths where, due to degradation of organic material by bacteria, oxygen levels are lower. Thus the reproductive output of younger smaller females or females of poor reproductive condition have a lower survival thus reduced survival success occurs with depth and egg. Secondly, reduced metabolic rates and development of eggs occurs in low oxygen conditions (e.g. Nissling & Vallin 1996; Weiland et al., 1994) thereby causing a prolongation of the period of development. This extends the period when egg stages are available for predation by herring and sprat (Köster & Schnack 1994) thus increasing mortality rates due to predation.

Campana, (1996) predicted year class strength through the examination of otolith growth histories of newly settled juveniles. This approach when coupled with hatch date identification utilised here this technique can also be used to resolve temporal windows of survival thereby identifying stochastic processes contributing to recruitment success. In this study, drift modelling coupled with otolith age determinations of surviving juveniles identified that enhanced survivor success occurred to those larvae experiencing a rapid transport to coastal shallow water habitats. Hence, identifying the potential importance of larval transport variations for recruitment modelling exercises.

In order to predict the potential effects of climate change on fish recruitment success we must be able to identify the key processes which influencing survival

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### Figure captions:

Figure 1: Location of spawning areas of Baltic cod (from Bagge 1994).

Figure 2: Hydrographic regimes in the Bornholm Basin during the sampling programs for larval cod during May 94 and July 94, 95. (Temp: Full line; Salinity (psu):

Fig 1

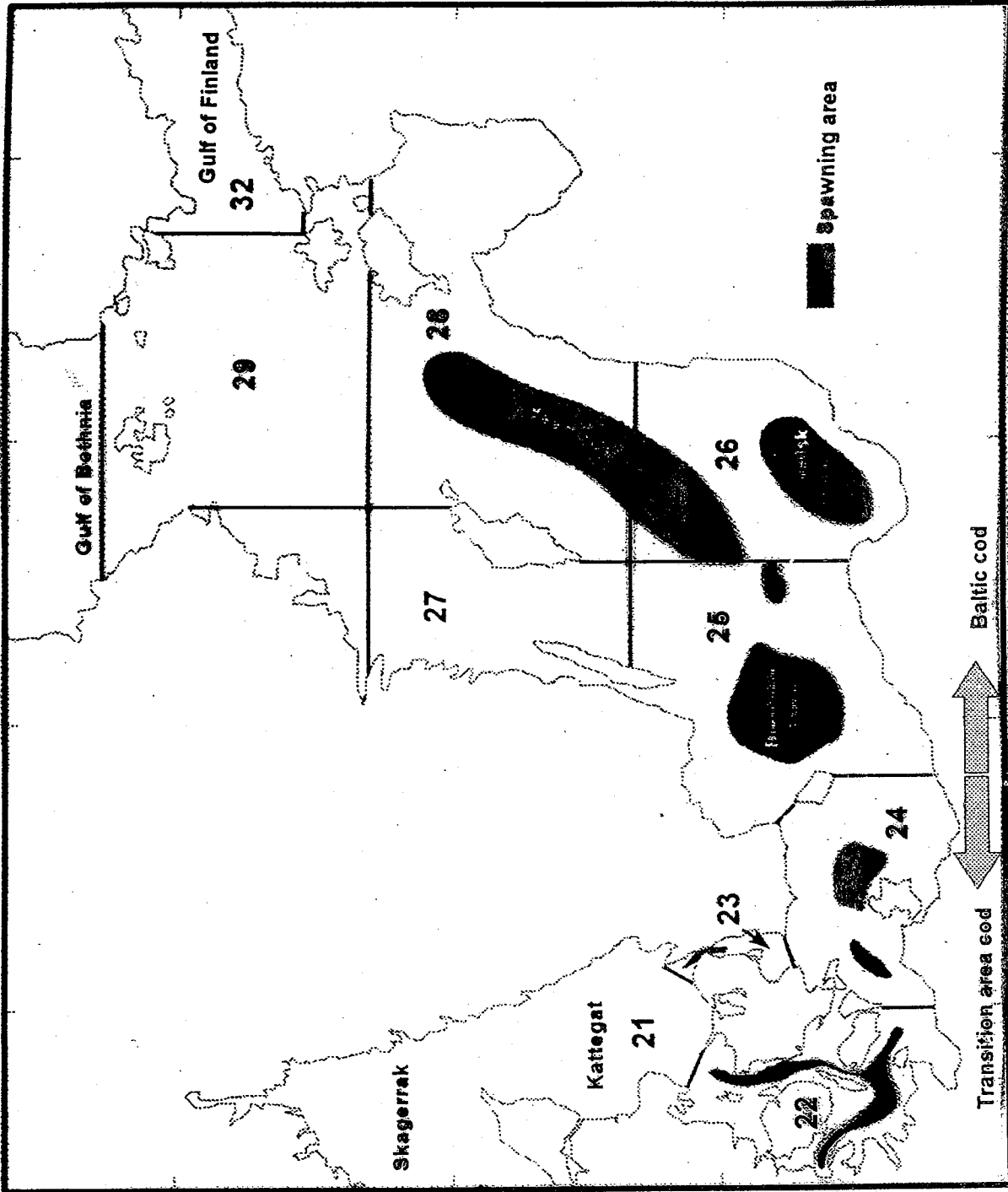
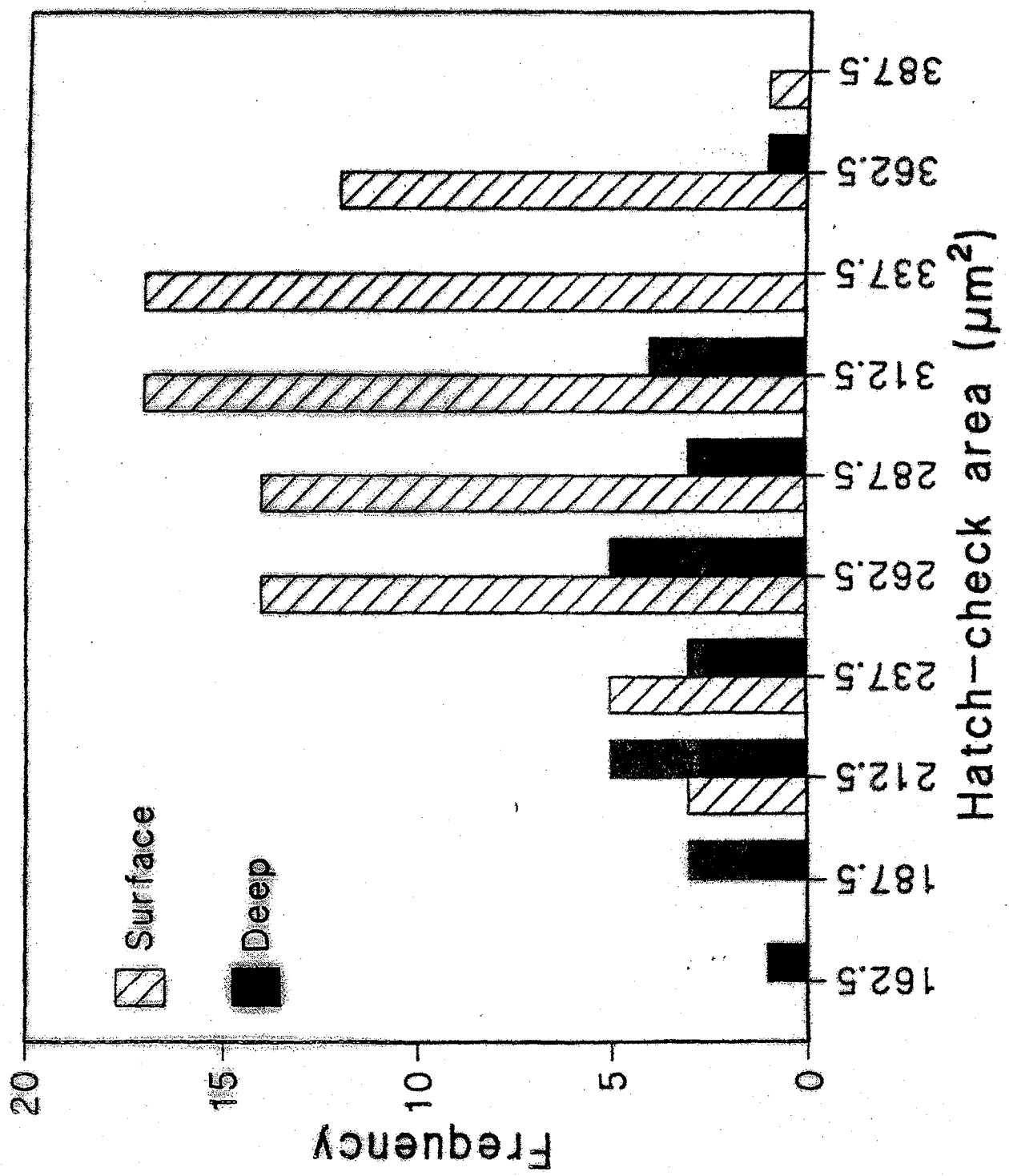


Fig 3.



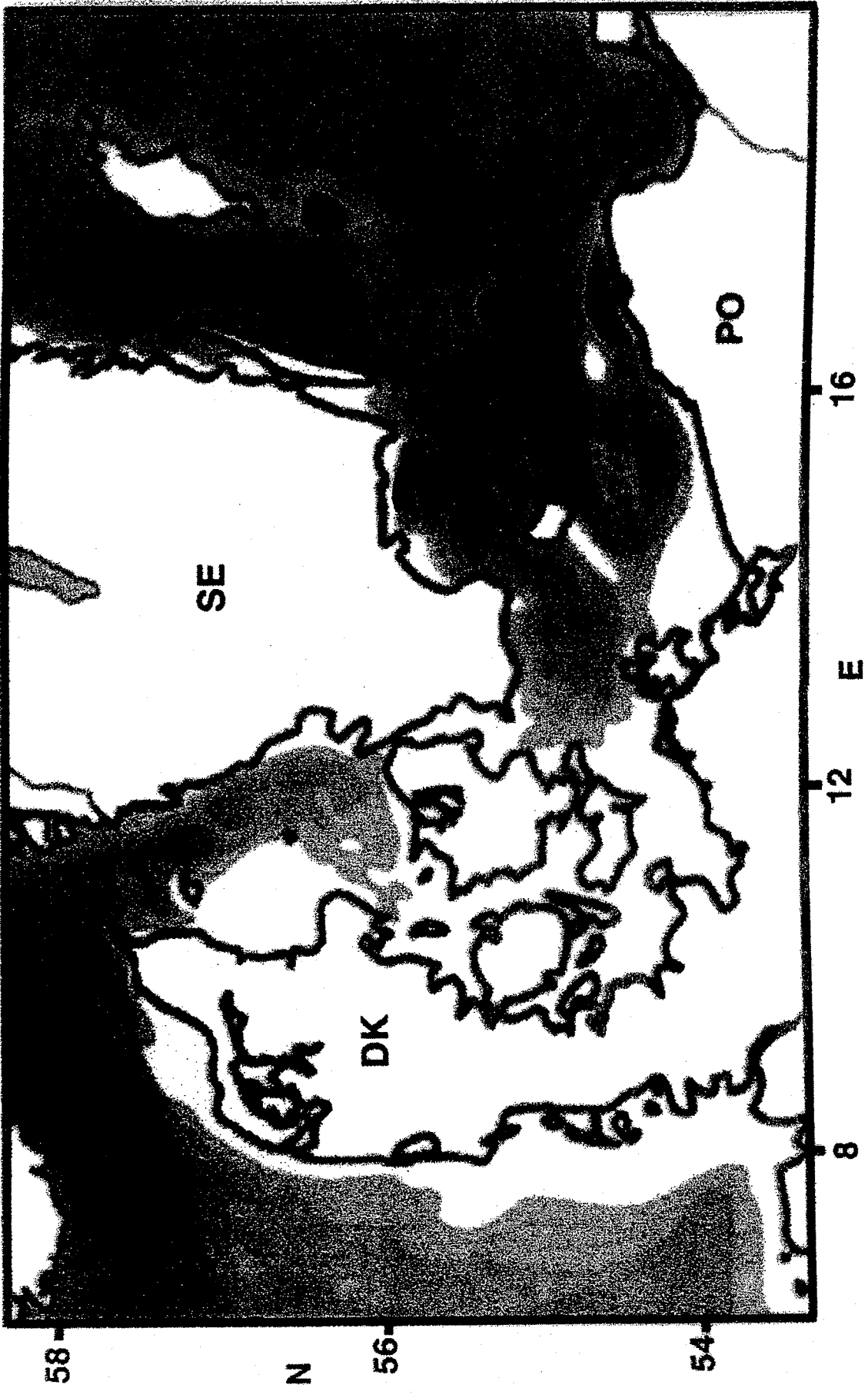


Fig 5



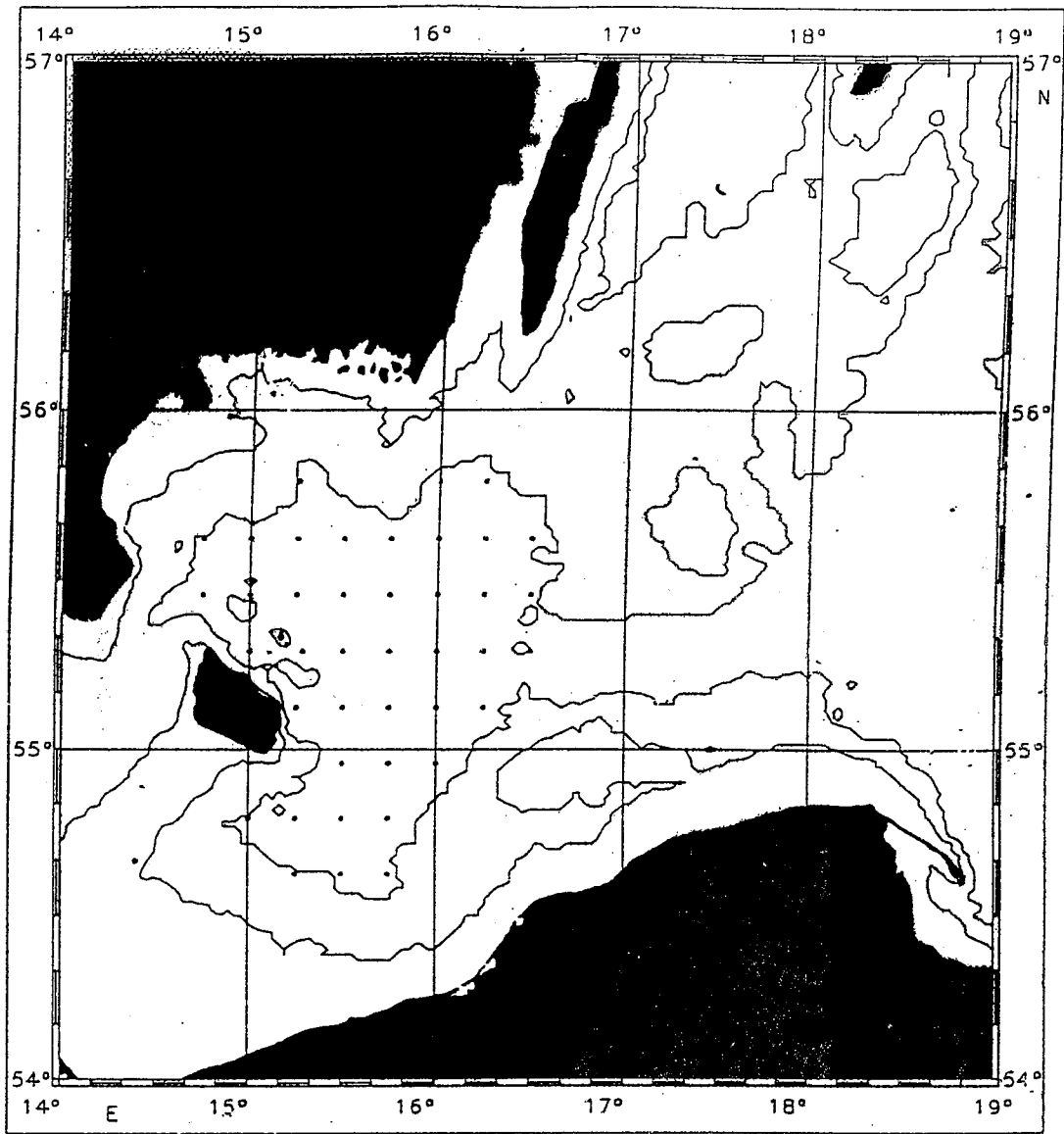


Fig 7a

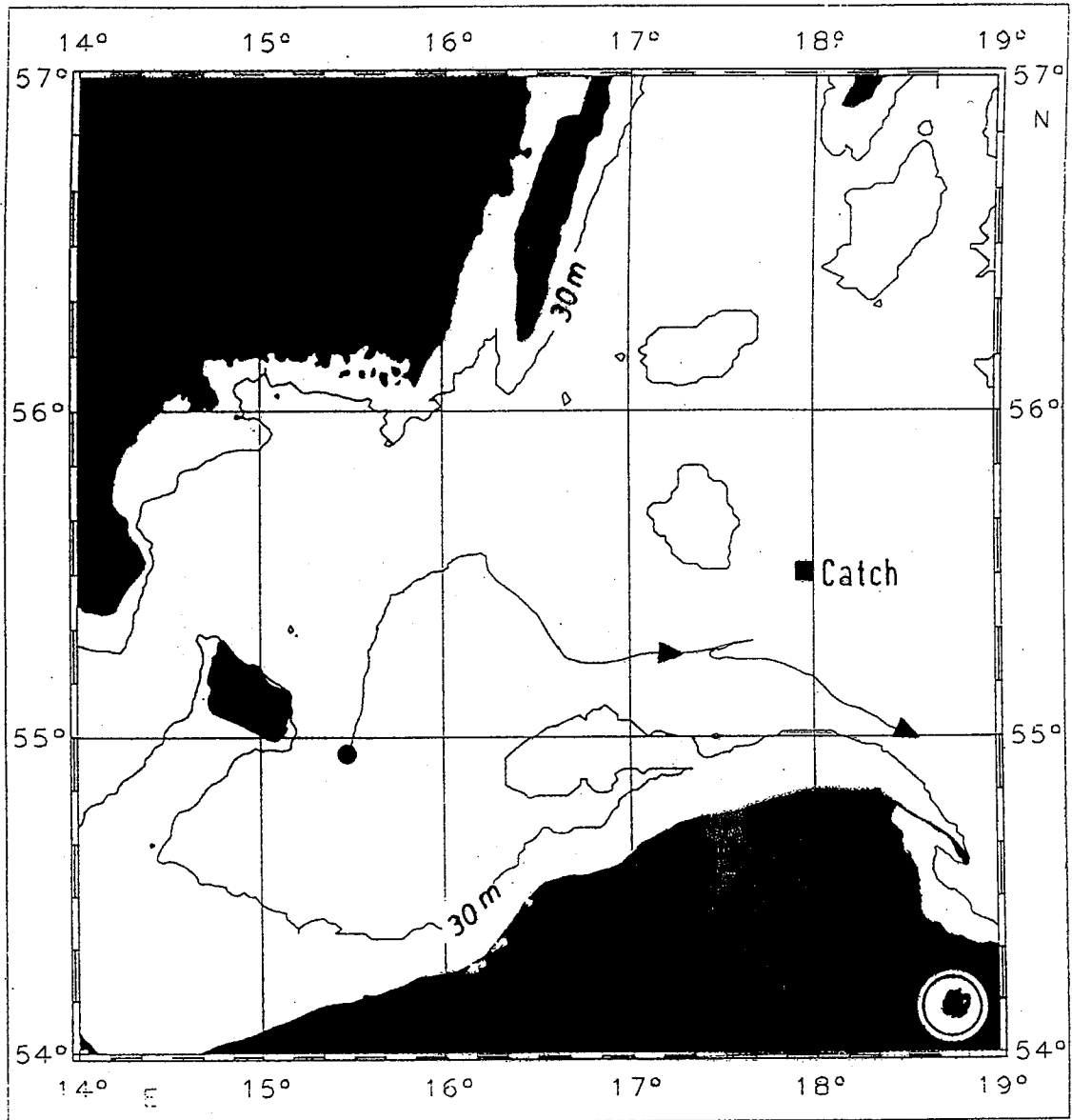


Fig 7c

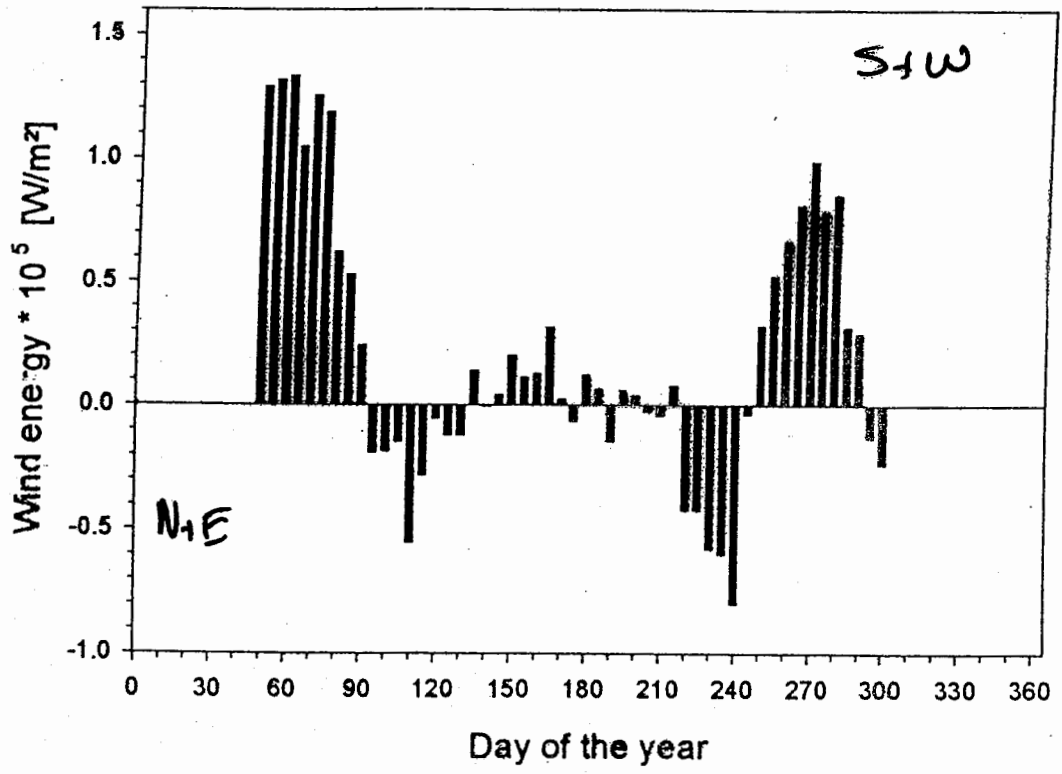


Fig 8

