Rapport: FISKEN OG HAVET	NR. 4 - 1995

Tittel: SELECTIVE MECANISMS OF SIGNIFICANCE IN THE SURVIVAL OF FISH	Senter: Marint miljø
	Seksjon: Biologisk

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Sammendrag:

Dette er det oppgitte emnet til prøveforelesningene mine. Det tar for seg selektive mekanismer som har betydning for fisks overleving, og legger særlig vekt på de størrelsesselektive mekanismene som virker på egg og larvestadiet.

Emneord - norsk:
1.-Seleksjon størrelse
2-Egg/larver
3-Gytetidspunkt
4-Gytelokalitet

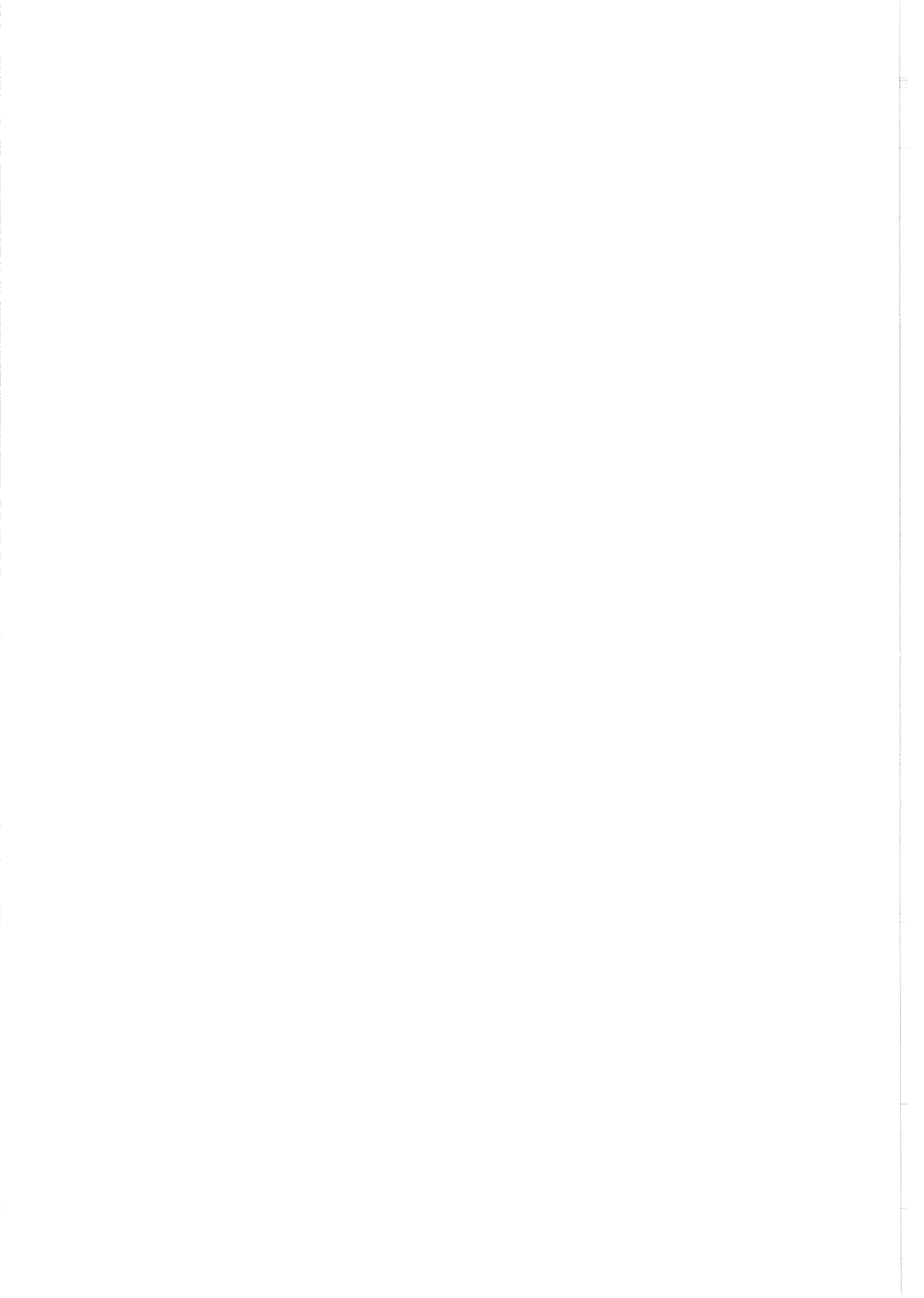Emneord - engelsk:
1. Size-selective mortality
2. Egg/larvae
3. Timing of spawning
4- Location of spawning

Prosjektleder

Seksjonsleder

ABSTRACT

The adult fish can during the reproductive process select for three different parameters; 1- time of spawning, 2- location of spawning, and 3- egg size. In this work all three parameters are discussed, but particular stress is laid upon the importance of size selective mortality in connection to size differences induced by different egg sizes. The two main conclusions are that 1-The fate of the tiny larvae is dependent on that the individual growth rate increase without an concurrent increase in the species-specific activity and thus mortality rate. 2- Selection for small eggs can be an adaptation to temporal pulses year in year out in the production of zooplankton. A good tactic can therefore be to wait for the good year and select for many small eggs, because even if the survival in years with low prey densities would have been better with large eggs this is more than compensated with the increased survival in years with high zooplankton production.

SAMMENDRAG

Fisk kan gjennom gyteprosessen selektere for tre forskjellige parametre; tidspunkt, sted og eggstørrelse. Disse tre parametrene vil bli behandlet i dette arbeidet, men det vil bli lagt størst vekt på størrelses-selektive mekanismer i forbindelse med størrelsesforskjeller indusert av forskjell i eggstørrelse. En konklusjon er at suksessen til en fiskelarve i stor grad er avhengig av at den kan øke veksthastigheten uten å øke aktivitetsnivået sitt slik at den blir sterkere utsatt for predasjon, at den har «flaks» med andre ord. En annen konklusjon er at seleksjon for mange små egg kan være en god tilpassning til et miljø med store årsvariasjoner i byttedyrtetthet. For selv om overlevingen i år med lave byttedyrtettheter er liten, blir dette mer enn kompensert i år med gode byttedyrforhold.

INTRODUCTION

The whole life of a fish is a struggle against the cruel game of selection and the winners in this game will be the individuals with the highest fitness to the ecosystem they inhabit.

The framework within which selective mechanisms have to work is that fish in all stages in order to have maximum fit will try to minimize mortality per unit of growth (Werner and Gilliam, 1984), on the other hand fish especially in higher latitudes have to grow at a significant speed in order to build up reserves to rely on in the coming winter season and the fish that succeed in both minimizing mortality and to grow and build up reserves is the winners in this cruel game.

In a Norwegian song we sing; «Why do you have to be big when you are lucky as a small one?» This can be true for people, but not for animals in the sea and fish eggs and larvae in particular.

Table 1. Relative importance of selective mechanisms of significance for survival in the different life history stages of fish.
(Relativ styrke av selektive mekanismer av betydning for overlevingen i de forskjellige livsstadiene hos fisk)

	Selection on size /growth	Selec. on vertical distri- bution	Selec. on horiz. distri- bution	Selec. on appear- ance	Selec. on behav- iour	Selec. on spawning time	Selec. on spawning place
Egg/ embryonic	++	+	+	+			
Larval	+++	++	+	+	+		
Juvenile	++	++	+	+	+		
Adult	+	+	+	+	+	+	+

Different selective mechanisms of importance for survival are put upon the

individuals during different life history stages as selection for size and growth, selection for camouflage, selection for a special pattern of behaviour as the way of swimming, schooling and overwintering. In addition a selection for an optimal vertical distribution and migration pattern are both of importance for the survival and I have tried to show this in the first table (Tab. 1).
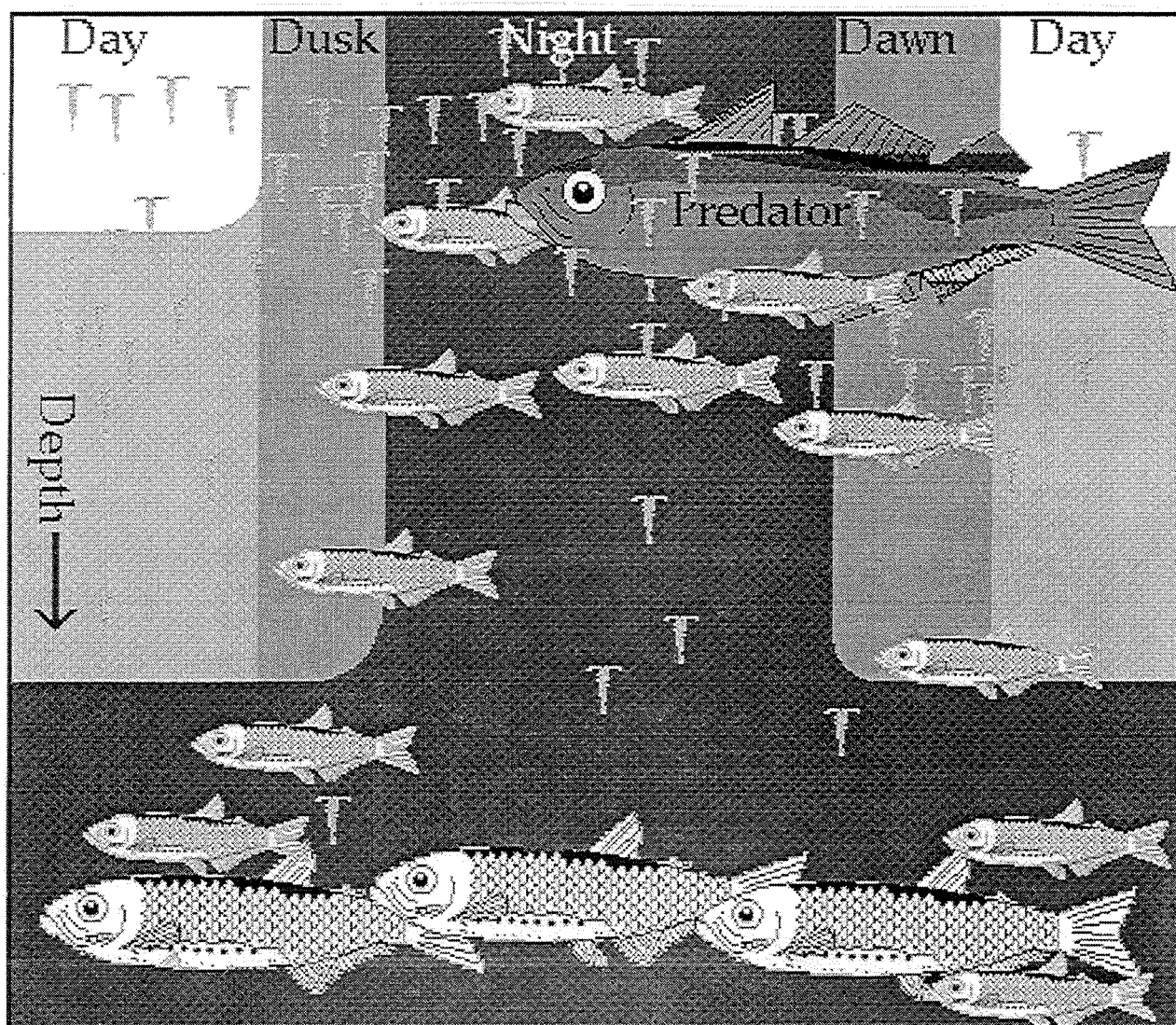

Fig. 1. Vertical distribution of Müllers pearlside (Maurolicus mülleri), in a fjord close to Bergen. Observed and modelled by Giske and Aksnes (1992)

(Vertikalfordelingen til laksesild, observert og modellert av Giske og Aksnes(1992) med data fra en fjord i nærheten av Bergen)

As an example of a selective mechanism I will show antipredatory behaviour expressed by the vertical distribution of Müllers pearlside (Maurolicus mülleri) investigated and modelled by Giske and Aksnes (1992) in a fjord close to Bergen. The pearlside is living after the following rule; «It is better to starve a little today than to be eaten, tomorrow I can perhaps do some compensatory growth. If I am too daring today I will be eaten and there will be no tomorrow» (Fig. 1).

However, the most important selective mechanisms for survival of fish are connected to the period of reproduction and recruitment, when the specialized multicellular organism is reduced by each act of reproduction into a large number of nonspecialized single cells, available for natural selection to act upon.

In this period only one out of approximately 10000 survive while later one perhaps 2 out of 10 are dying, and it is an open question if it is the most competent or the most lucky one that survive.

Pepin(1989) supported by results from Rosenberg and Haugen (1982) and Method (1983) showed that the size distribution of the surviving fish larvae is dependent on the overall survival of the cohort and that in years with high mortality only the individuals out on the extreme right limb of the normal distribution will survive resulting in a narrow size distribution with high mean growth rate. In years with high survival, the size distribution will be wider and the mean growth will be lower, an example of this is shown in the next figure (Fig. 2).

The duration of the most vulnerable stages are of significance for the survival and Houde (1987) shows the most important controlling mechanisms in a conceptualization of the recruitment process (Fig. 3). He also shows that it is necessarily not the dramatic episodes that is most important for the overall survival, but that small changes in mortality or growth over a long time period can have strong effect (Fig. 4).
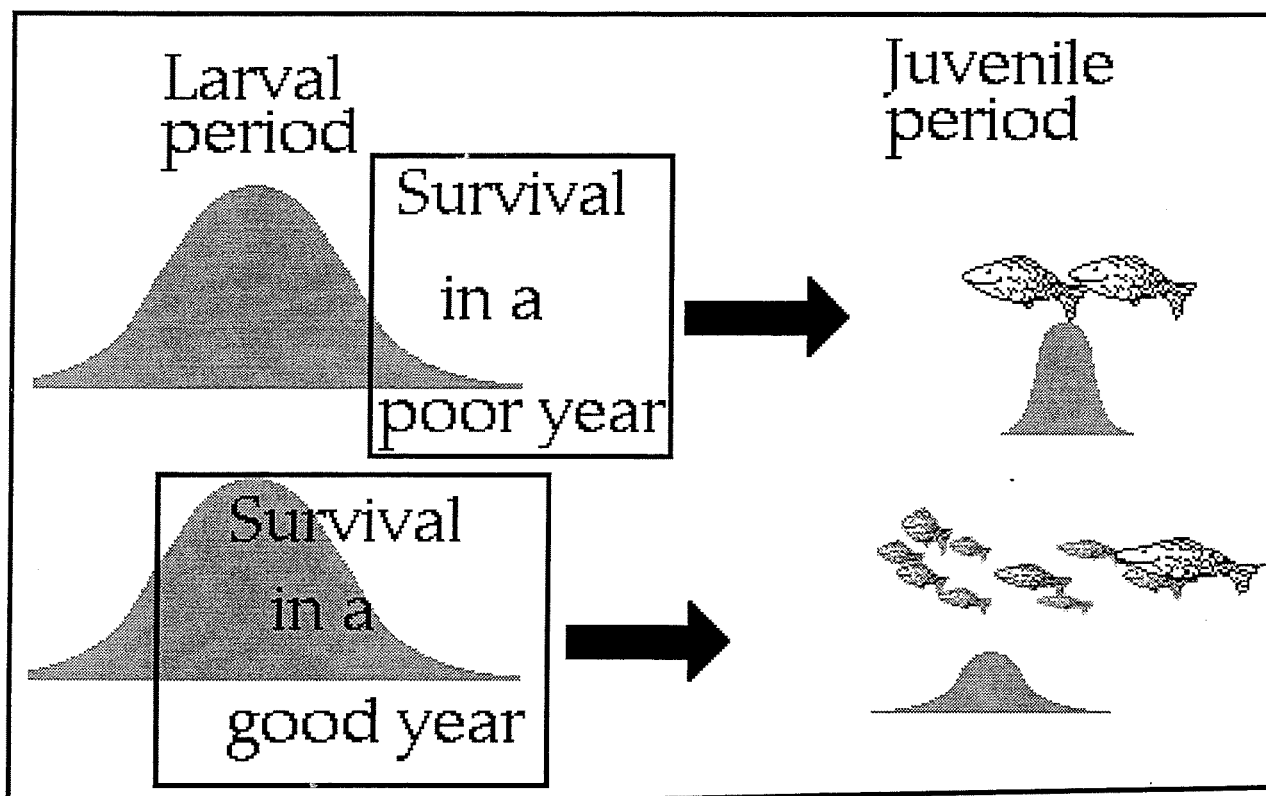
Fig. 2. Relation between overall survival during the larval period and the size distribution as juveniles. *(Sammenhengen mellom larveoverleving og størrelsesfordelingen av yngel)*
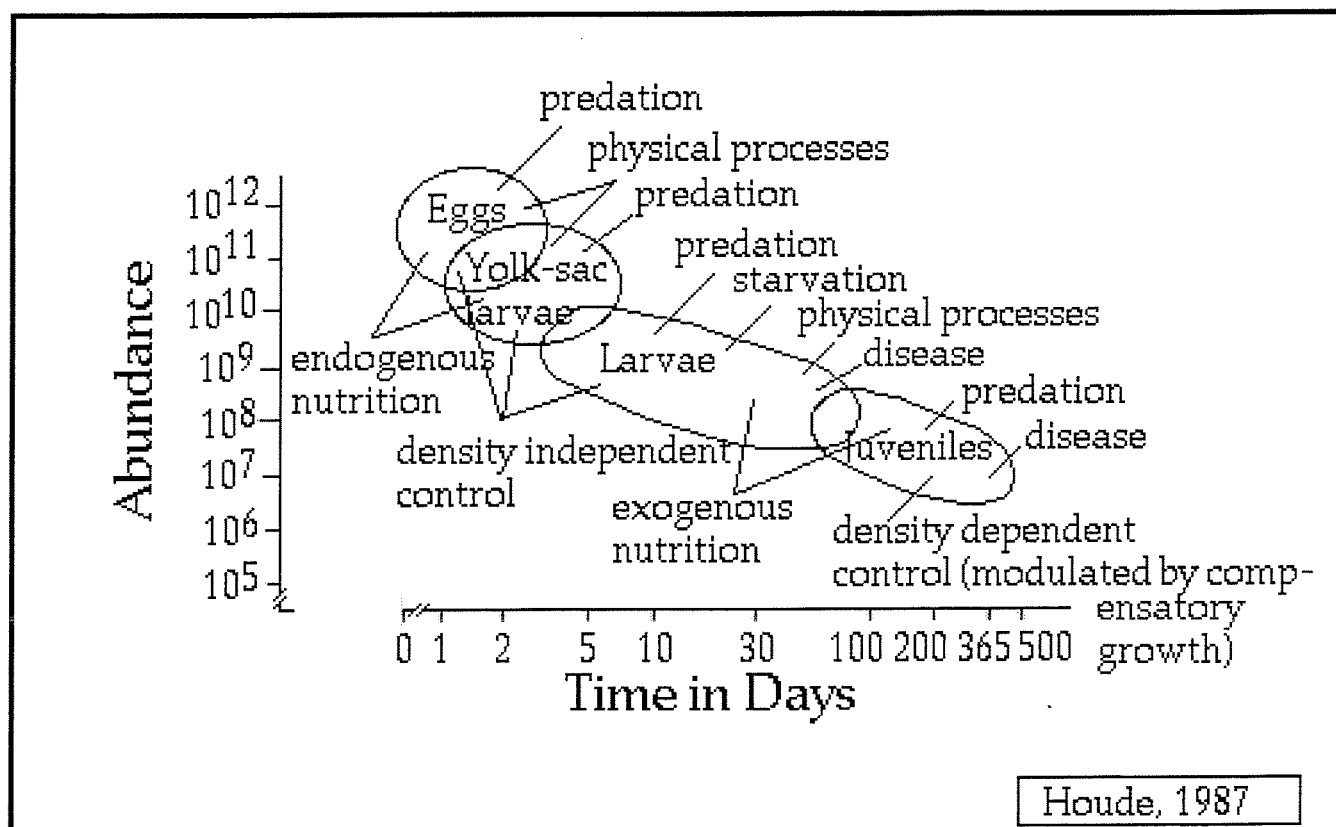

Fig. 3. A conceptualization of the recruitment process in fishes.

(En fremstilling av fisks rekrutteringsprosess)

Survival at metamorphosis

Specific growth rate (d)

0.1　　0.01　　0.001

0.20

0.0001
0.00001
0.15
0.000001
0.00000001
0.10
0.0000000001

0.15

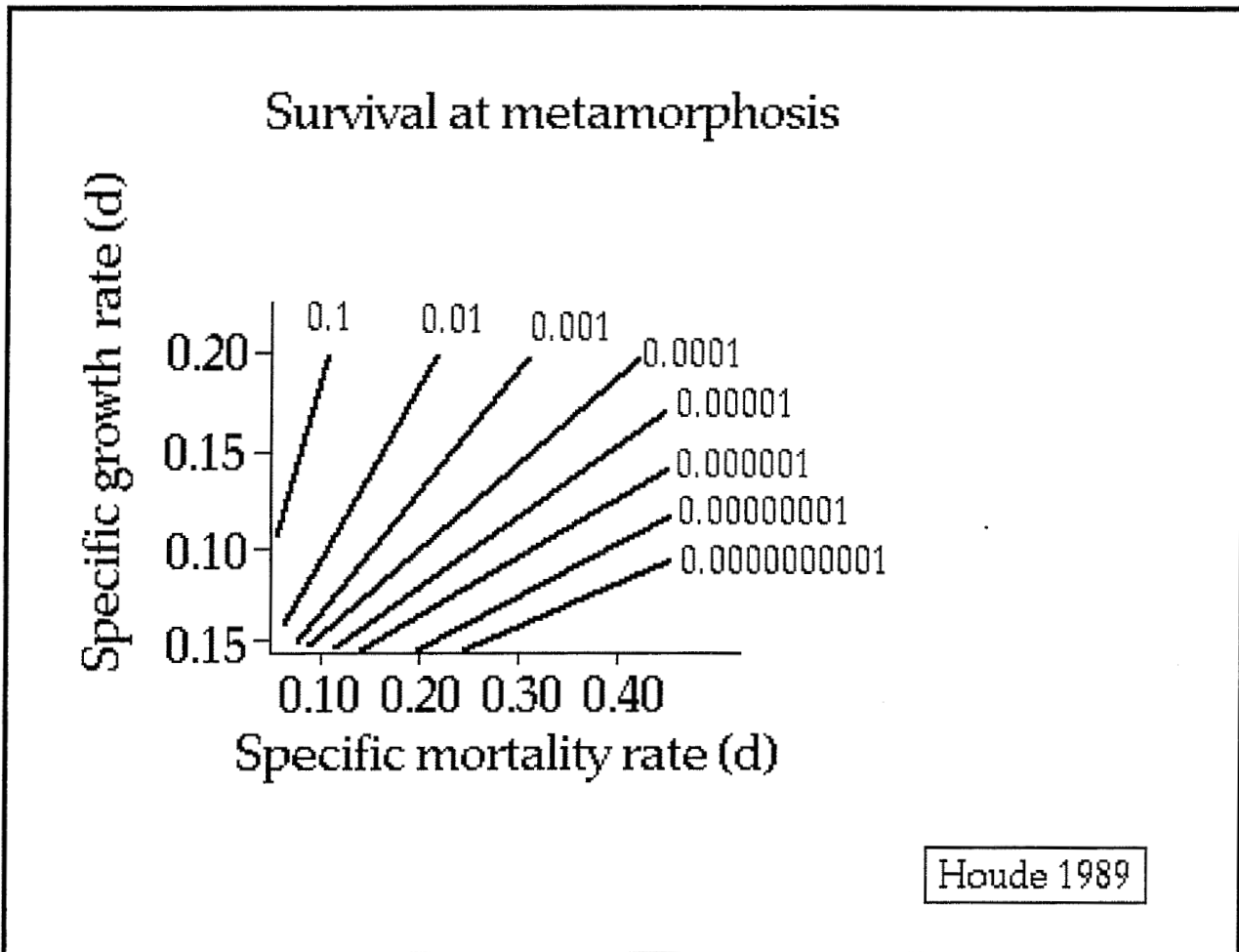0.10　0.20　0.30　0.40

Specific mortality rate (d)

Houde 1989

Fig. 4. An isoplet diagram of survival at metamorphosis at variable growth and mortality rates.(*Et isoplet diagram som viser overlevingen ved metamorfose ved varierende vekst og dødelighet*)

In this talk I will discuss the choices the adult fish can make in connection to the reproductive process in the marine pelagic ecosystem with significance for mortality of the progeny during their different early life stages.

The adult fish can during the reproductive process select for three different parameters; 1- time of spawning, 2- location of spawning, and 3- egg size. The resulting larvae have interspecific differences both with respect to type and function, like pattern of swimming and general level of activity. I will discuss these parameters, but I will lay particular stress on the importance of size selective mortality in connection to size differences induced by different egg sizes. At last I will try to put the three different species in my thesis, herring, cod and capelin with their different life-histories into this context.

TIMING OF SPAWNING

A few species reproduce at two or three years intervals while others spawn only once in their lifetime. However, the majority of fish species exhibit an annual cycle of reproductive development which is maintained for as long as the animal is reproductive competent (Bye, 1985).

Timing in fish reproduction is believed to have evolved as a mechanism to synchronize larval hatch and commencement of feeding at the season most favourable for their survival (Blaxter and Hunter, 1982), like spring blooms, monsoon periods or other periods with increased outflow of fresh water or periods when upwelling conditions are conductive to larval survival.

Many tropical fishes have extended spawning seasons all through the year, with intermittent periods of intense spawning, while most of fish species including many around equator have predictable, restricted spawning periods. For fish inhabiting an environment with pronounced seasonal climatic variability the breeding season is confined to a brief and specific period of the year (Fig. 5)(Cushing, 1970; Ellertsen et al. 1989).

There will be a strong selection pressure on accurate reproduction control, for should individuals breed at any other time of the year other than the ideal they will pass on few of their genes to the next generation. In order to be so precise the fish need an internal clock and external stimuli from temperature and photoperiod (Fig. 5).

In systems with more subtle seasonal differences other parameters like small pressure or salinity changes due to monsoons, flooding or upwelling events, the lunar cycle, nutrient deficiencies in the food web and vacant niches can be involved in the gametogenesis and timing of the breeding season.

The annual cycle in gametogenesis is much more extended than the breeding season. Gametogenesis need to start at least 4-5 months ahead of the breeding

season in a season with quite different conditions than in the breeding season. The cues which coordinate reproductive and environmental cycles are those which are most reliable as calendars such as day-length, temperature, and food availability. When endogenous rhythms have brought the fish to the final state of maturation, the spawning can be triggered by a sudden environmental stimuli like a drop in temperature or the neat bottom of a male in the neighbourhood.
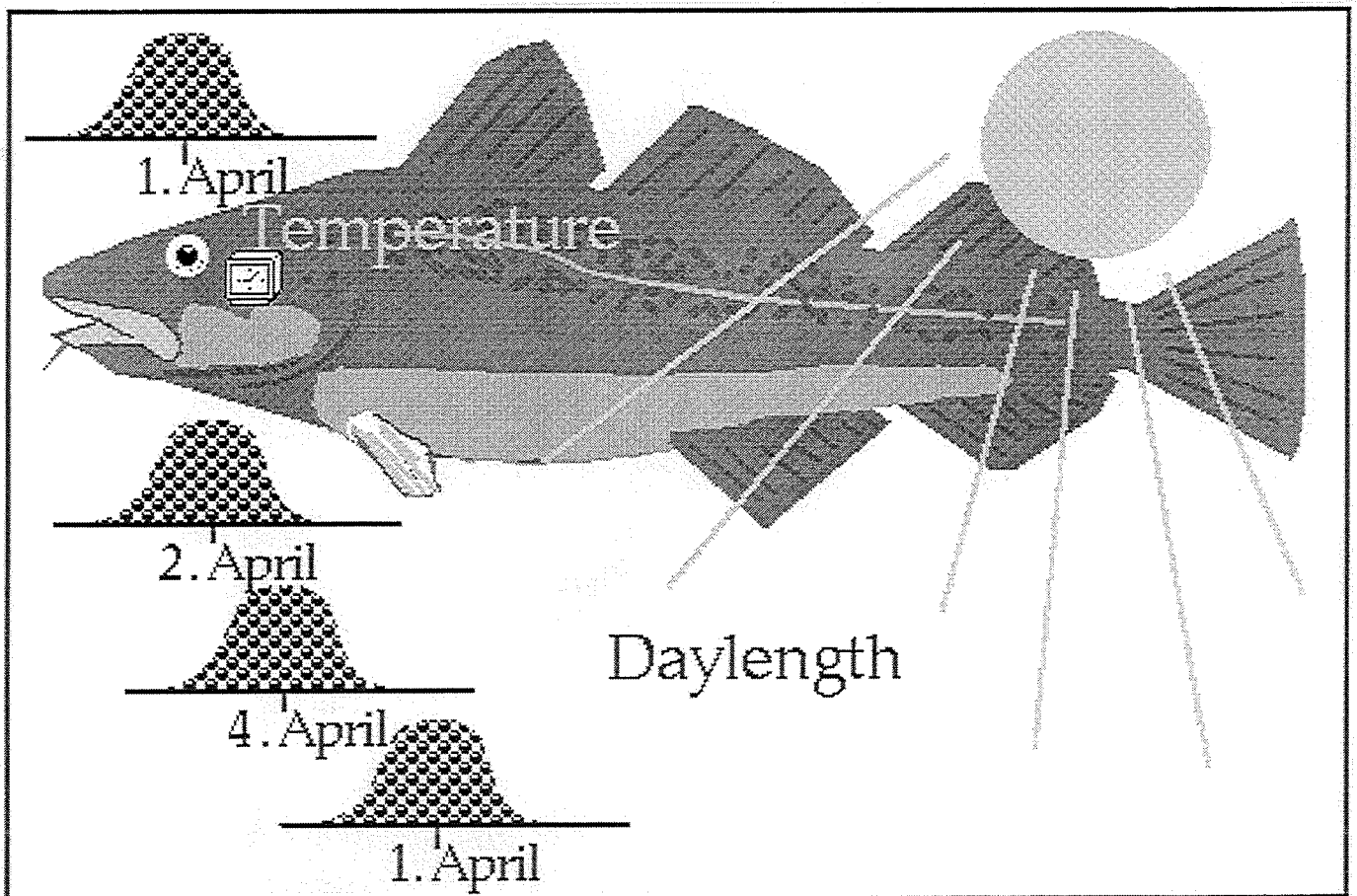

Fig. 5. The breeding season is often confined to a brief and specific period of the year, and in order to be so precise the fish need an internal clock and external stimuli from temperature and photoperiod.

(Gytesessongen er oftest svært stabil fra år til år, for å klare dette trenger fisken en indre klokke og utvendige stimuli fra lys og temperatur)

LOCATION OF SPAWNING

Fish spawn in fixed areas which gives the larvae optimal probabilities to be retained in areas suitable for growth and survival. Such areas can be coastal banks with gyres having high abundance of suitable prey organisms, it can be up against productive fronts or in areas with upwelling.

The other aspect is the dispersal of the larvae. They have to be spawned in an area that gives them maximum probability to continue to be members (Iles and Sinclair, 1982) of the stock. By retention in a specific area or drift into nursery areas suitable for growth and survival and later reunion with the rest of the stock (Fig. 6).
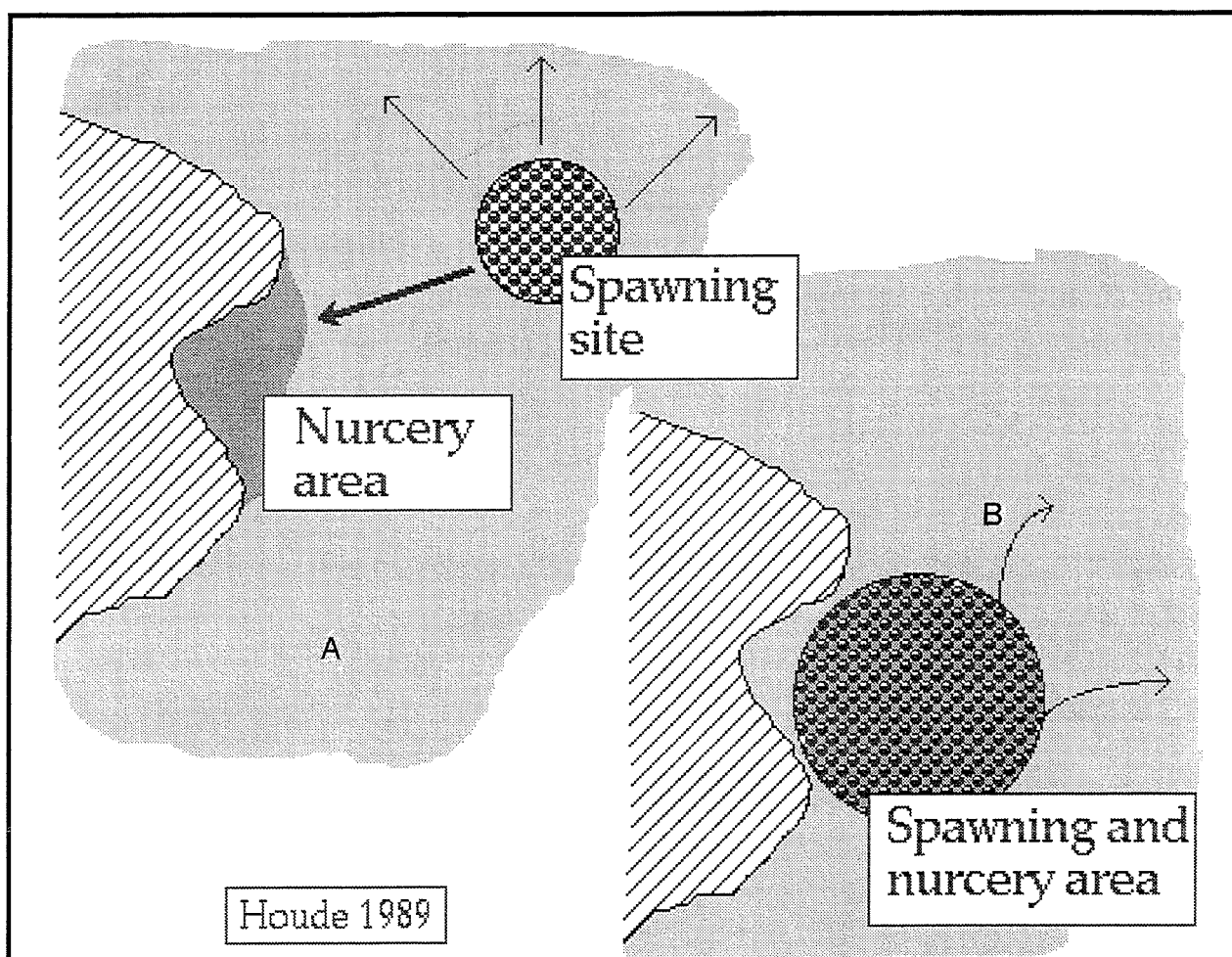

Fig. 6. Illustration of drift of a larval population into a nurcery area (a) or retention of a larval population in a spawning/ retention area (b).
(En skjematisk fremstilling av hvordan larvaer kan drive in i (a) eller bli holdt tilbake i (b) et gunstig oppvekstområde)

Location of spawning is to a large extent determined by the large scale migration pattern of the stock and the homing instinct of the individual fish. The probability of passing on their genes to the next generation is determined by these instincts. However, there will always be opportunists waiting for better chances if the conditions changes in new or recolonized areas.

EGG/LARVAL SIZE

Fish have a given amount of eggs to spawn, depending on their life history strategies, if they are pulse spawners, «big-bang» spawners taking everything on one card as an immediate response to changes in the environment or patch spawners.

The given amount of eggs is in addition to this depending on the age and nutritional status of the fish (Kjesbu et al., 1991). However, in this part I will not talk about maternal effects, but stress the importance of other mechanisms and try to show that there is indications of a strong and indirect relationship between mortality and size in the marine pelagic ecosystem.

Further I will talk about size selective mortality on the spawning products, the eggs and larvae, and show that there is a direct relationship between growth and mortality and at last discuss why most fish are producing huge clutches of eggs since only two must survive to replace their parents.

The last part with help of the interesting model of Winemiller and Rose (1993) presented in the paper they have called; « Why do most fish produce so many tiny offspring?».

Peterson and Wroblewski(1984) showed that as a general phenomenon mortality rate decrease with size. They meant that a general theory for mortality of fishes based on broad marine ecosystem processes may be helpful.

Therefore they derived a size-dependent equation for mortality rate of fish sized particles in the pelagic marine ecosystem based on the following assumptions:

1. Ecosystems are size structured.

2. Declines in biomass and numbers as a function of size are predictable.

3. Predation is the principal cause of loss.

4. Prey size is a fixed proportion of predator size.

The equation they estimated yields estimates that are close to the observed ones: w=100 µg, M(w) ≈ 5% per day

w=1g, M(w) ≈0.5% per day
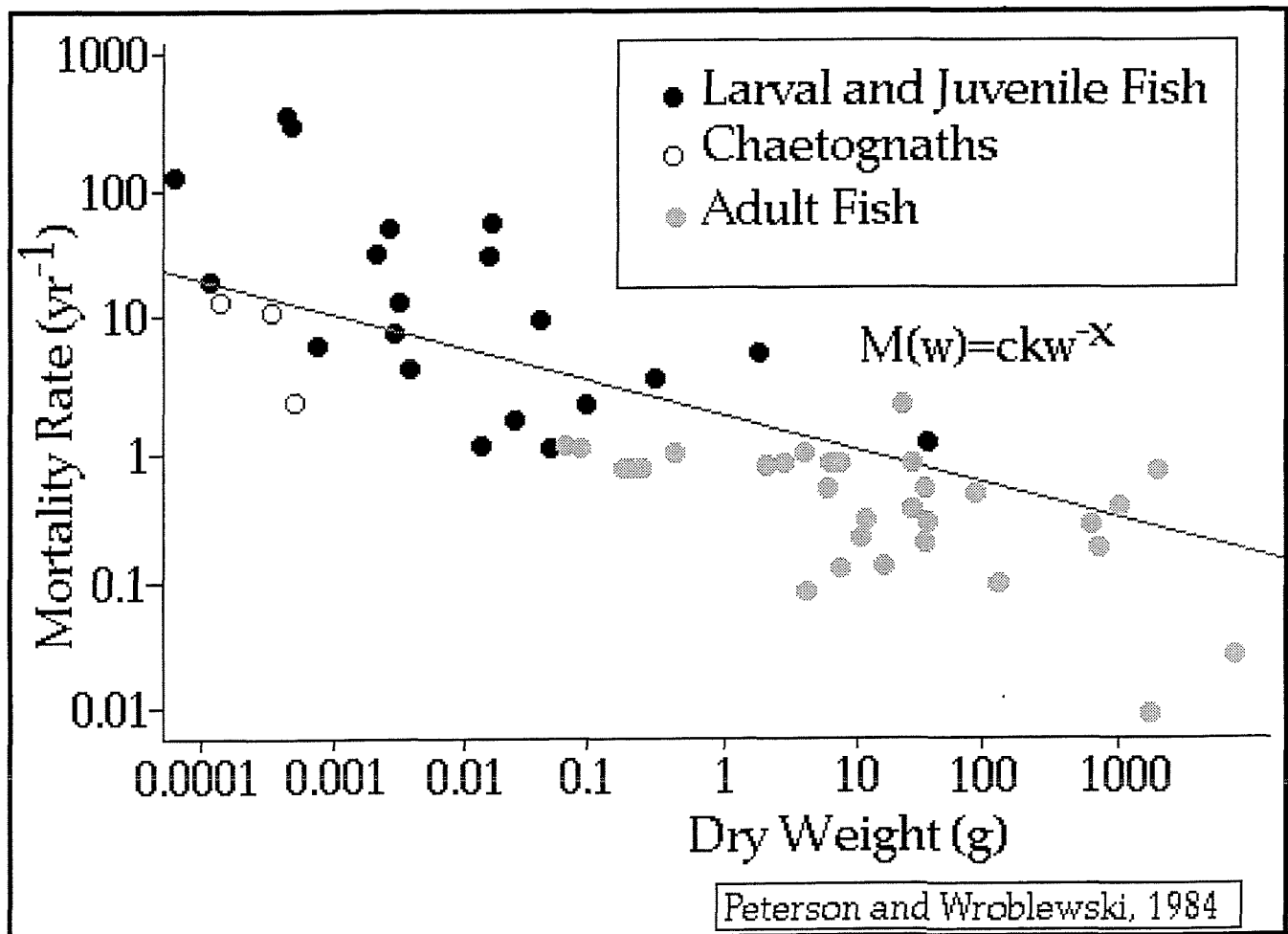
w=10kg, M(w) ≈ 0.05% per day

Fig. 7. Natural mortality rate vs. dry weight.

(Et plott som viser hvordan den naturlige dødeligheten av organismer i havet som et generellt fenomen avtar med økende partikkelstørrelse)

McGurk included data for invertebrates and whales as well. His conclusion was that the natural mortality was higher in fish eggs and larvae than expected from the trend of mortality rates with dry weight in the sea, and that this was positively correlated with the patchiness of their spatial distribution (Fig. 8).
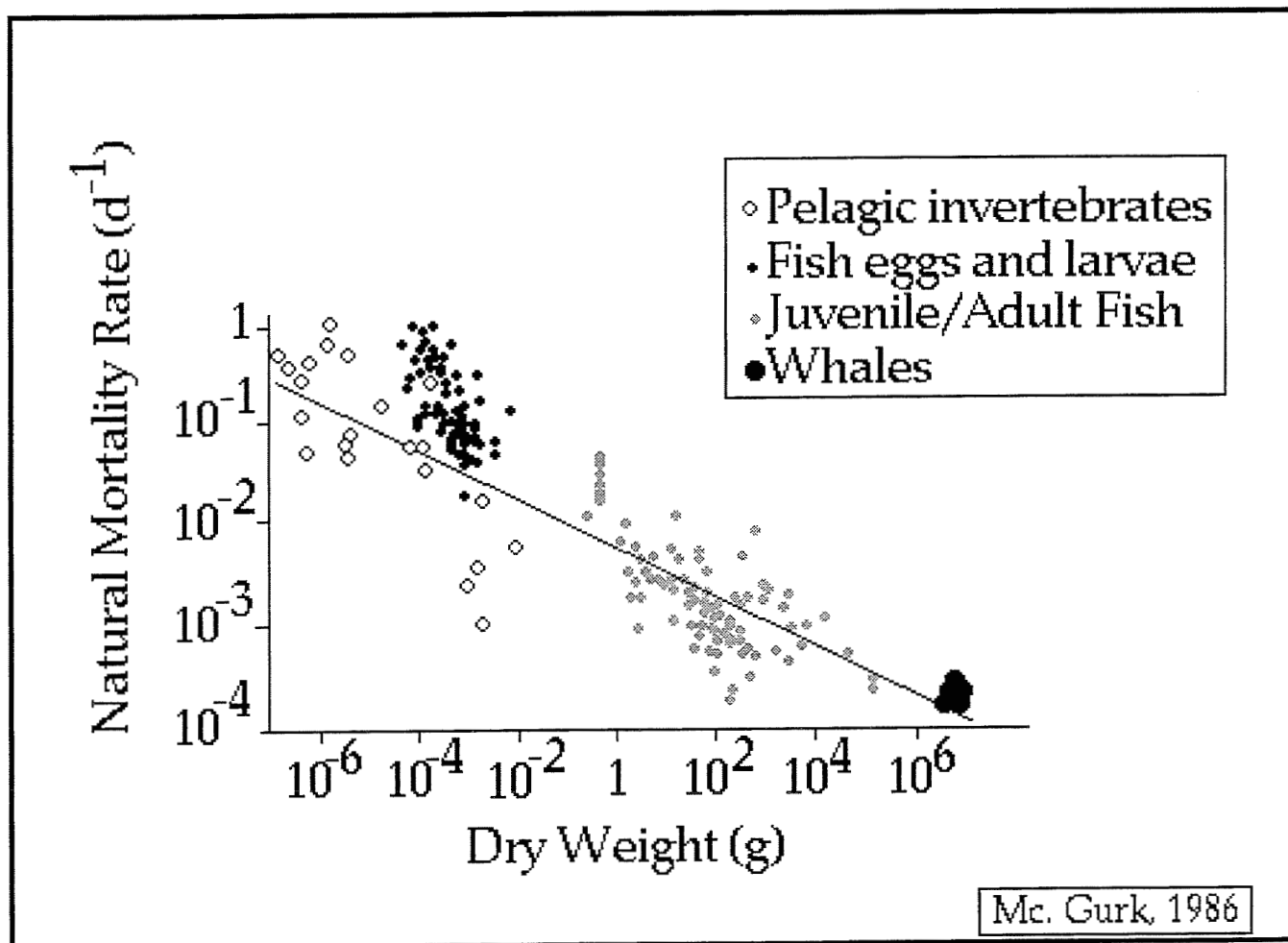

Fig. 8. A plot of natural mortality rate vs. dry weight including other types of organisms.
(Et plott med flere typer organismer viser hvordan den naturlige dødeligheten av organismer i havet som et generelt fenomen avtar med økende partikkelstørrelse)

Another explanation can be that sampling problems can give too high estimates of natural mortality especially in the larval stage, or perhaps fish eggs and embryos are very tasty as indicated by the title of a paper by Orians and Janzen (1974) «Why are embryos so tasty?».

Organism size has long been used as a scaling factor for such biological processes as growth and metabolism. The assumption that mortality comes

from predation agrees well with small particles, but not with the larger ones which is obviously controlled by other factors as disease.

This is only a general tendency, since different species of course have different and stage specific vulnerability to predation. But, that mortality is size-dependent is in any case a strong working hypothesis. I will further analyze what is happening to different sized eggs and larvae when they are entering the ecosystem.

According to Miller et al. (1988) length at hatch do vary among species with over an order of magnitude, and initial weight may vary by three or more orders of magnitude. The effect on size are profound, looking at feeding, activity, and predation risk in species in the size range between 1.6 to 17.6 mm at hatch. They tested three different hypothesis:

1) Time to first feeding is a negative function of larval size at hatching:
Time to first possible feeding varied by a factor of 24 (Fig. 9), white croaker with the smallest larvae (1.8 mm at hatch) fed first after 3 d, while the largest species, garfish 13.5 mm fed first already after 5 h. The hypothesis holds even if there is some noise in the material.

2) Time to PNR is a positive function of body length at hatching:
They found a significant relation between hatch size and time to PNR (Fig. 10). Linear model gave best fit to the data. 3.4 d for the smallest (lined sole, 1.9mm) to 18d in the largest (lake herring, 9.4mm).

3) The difference between PNR and first possible feeding is an index of the flexibility allowed in timing of first feeding. Larvae hatching at large size experiences a greater «window of opportunities»:
The time window when larvae first feed increase and become more variable with increased hatching size. Even small increases in body size at hatching
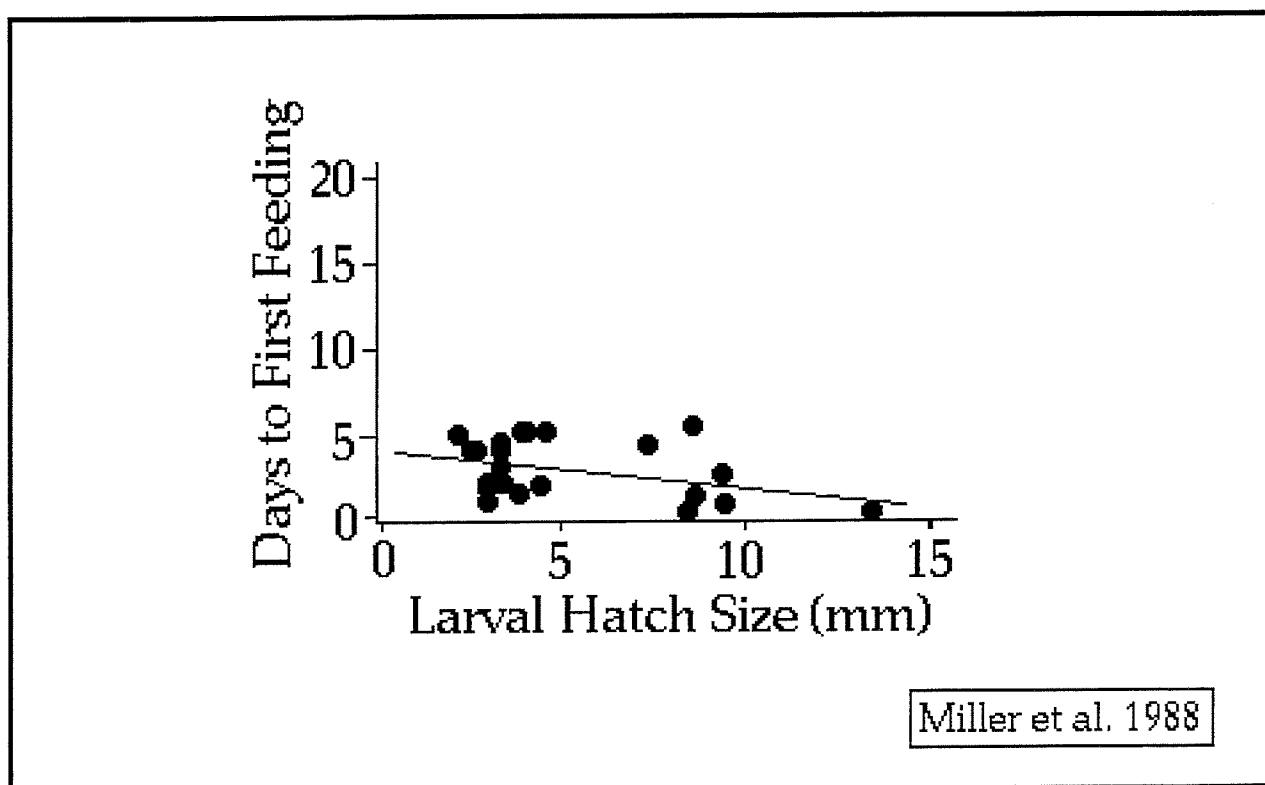
Fig. 9. Time to first possible feeding.
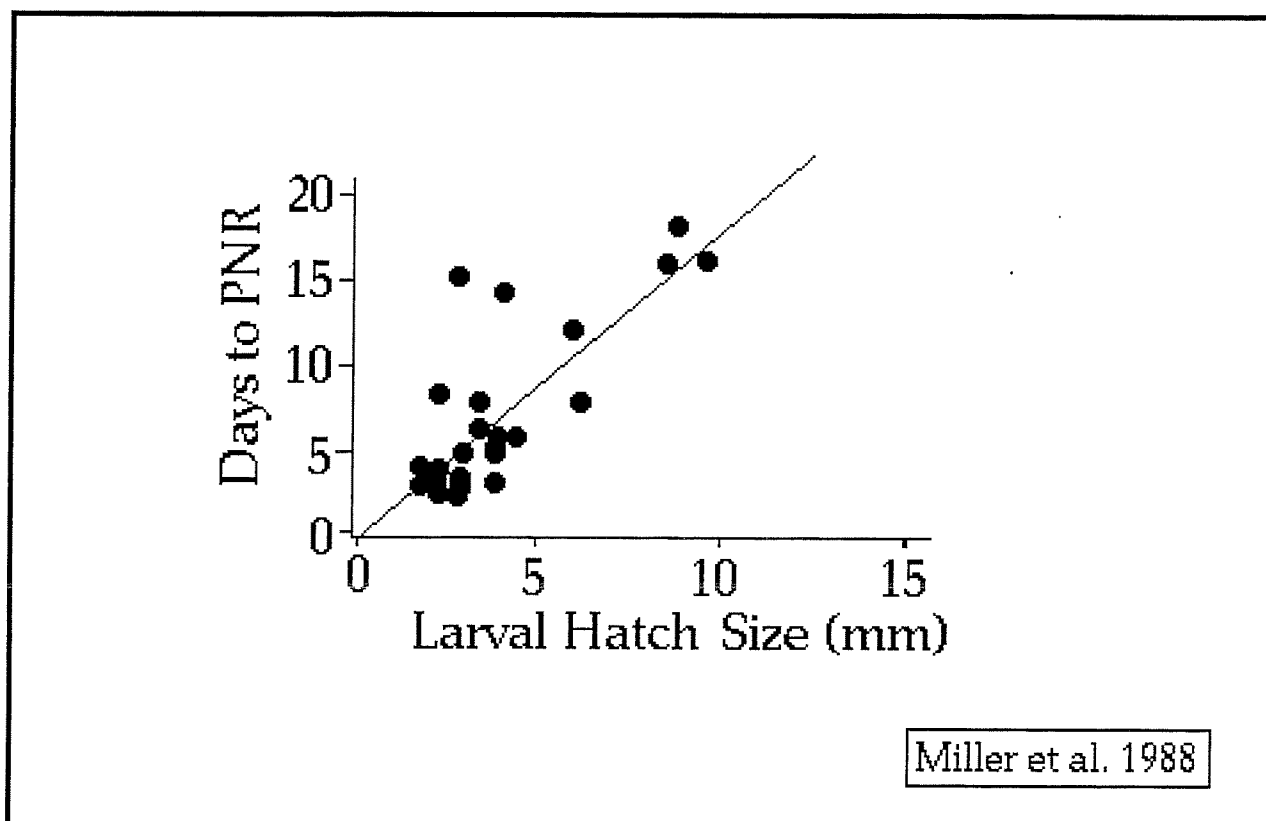
(Tid til første næringsopptak)

Fig. 10. Time to PNR.

(Tid til irreversibel utsulting)

apparently confer large benefits in terms of flexibility in time to first feeding. For every 0.1 mm increase in length at hatching larvae gain about 6 h in which to find food. This means that a 8.2mm long herring larvae and a 6.5mm capelin larvae have 9.25 and 5 days extra time respectively to find food compared to a cod larvae with a total length of 4.5mm at hatching.

Time to 50% mortality shown in Fig. 11, is found by Miller et al (1988) to increase with larval size. Regardless of species at any given length they found greater or equal time to 50% mortality in the larvae that had been dependant on their yolk reserves only.
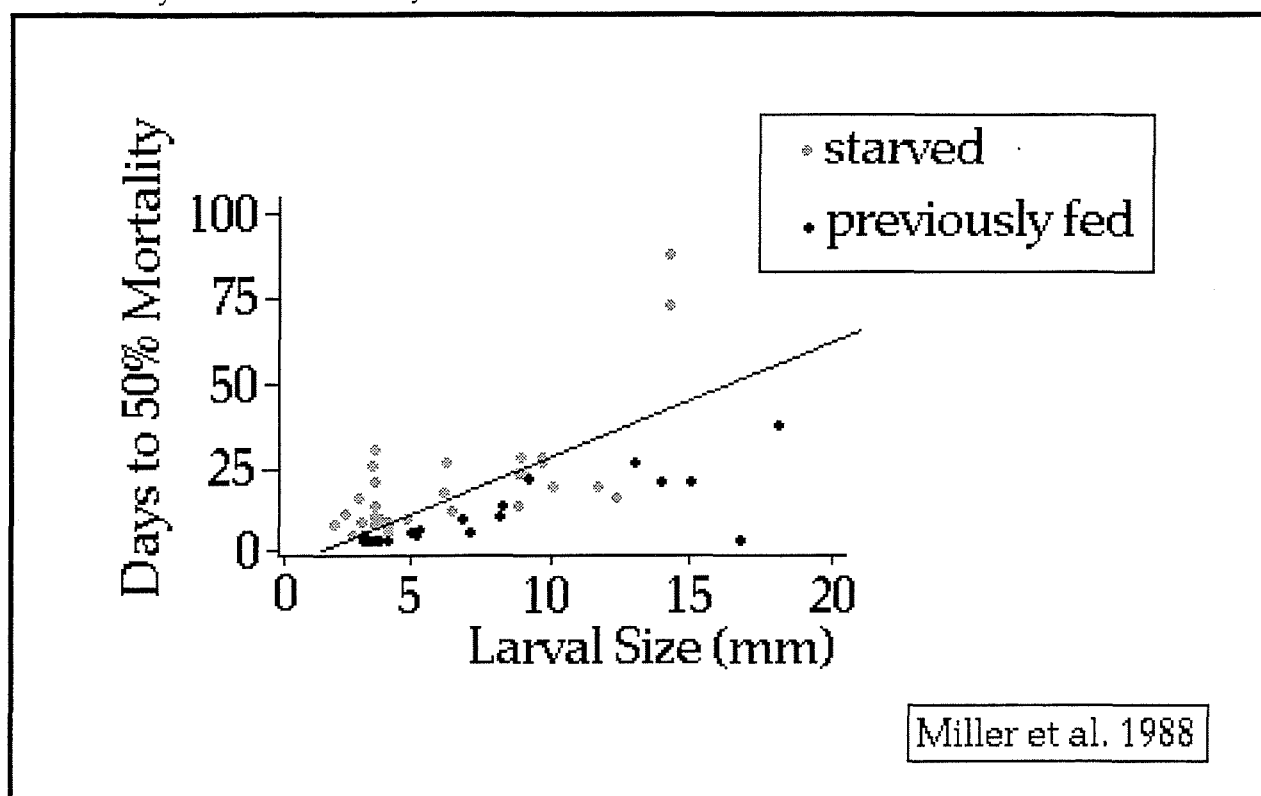

Fig. 11. Days to 50% mortality for a cohort of starved larvae as a function of larval total length at hatching.

(Tid til 50% dødelighet av en cohort av larver som sulter mot larvens lengde ved klekking)

This suggests that first-feeding larvae are no more vulnerable to starvation than larvae of similar size that have fed and subsequently starve. Larvae appears more susceptible to starvation at first feeding only because that is when they are smallest. Larger larvae at hatch are generally more active and better to avoid attacks than smaller larvae and e.g. 2.9mm northern anchovies do not

reach maximum activity until they are 4 days old while 9.5 mm bloaters actively swim 100% of the time after 6 h, but the data on activity are scarce.

In sum they suggest that a larger hatching size in fish confers resistance to starvation as a result of an increased time to 50% mortality, increased time to PNR, and increased flexibility in the timing of first feeding. Large or better more experienced larvae have according to Pepin(1991) better capture success and can also search larger volumes of water. The mean length in the period investigated, also according to Pepin(1991), is significantly correlated to the foraging ability of the larvae.

The size of the larvae at hatch is also negative correlated to the larval stage duration and time to metamorphosis. The application of this is that when the larval stage increase, the cumulative mortality increase (Fig. 12) and the recruitment variability also increase, agreed upon by Pepin & Meyers (1991), Houde (1987) and Beyer (1989).
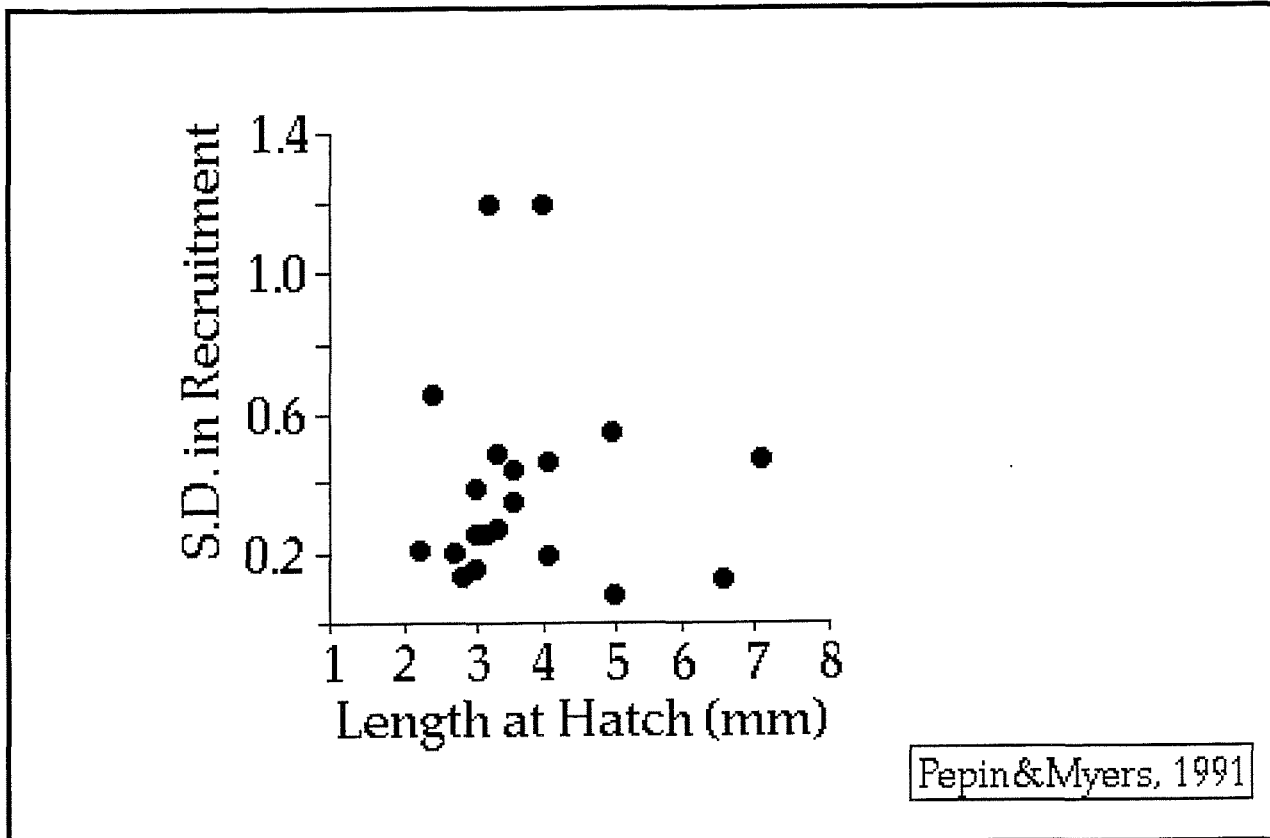

Fig. 12. A scatter plot of the standard deviation in recruitment in relation to lengt at hatch.
(*Et plot av variasjonen i rekruttering mot lengden ved klekking*)

Declining in mortality with increasing length at hatching and as the fish grow
has been reported for a number of marine fish species and is based on the
premise that developing fish pass through various predatory fields. This
phenomenon was clearly demonstrated by Folkvord and Hunter (1986)(Fig. 13).
They demonstrated that the percentage of larvae escaping attack by various
predators increased with increasing larval size, and the escape response was
species specific, with escape from some predators quickly increasing to 100% as
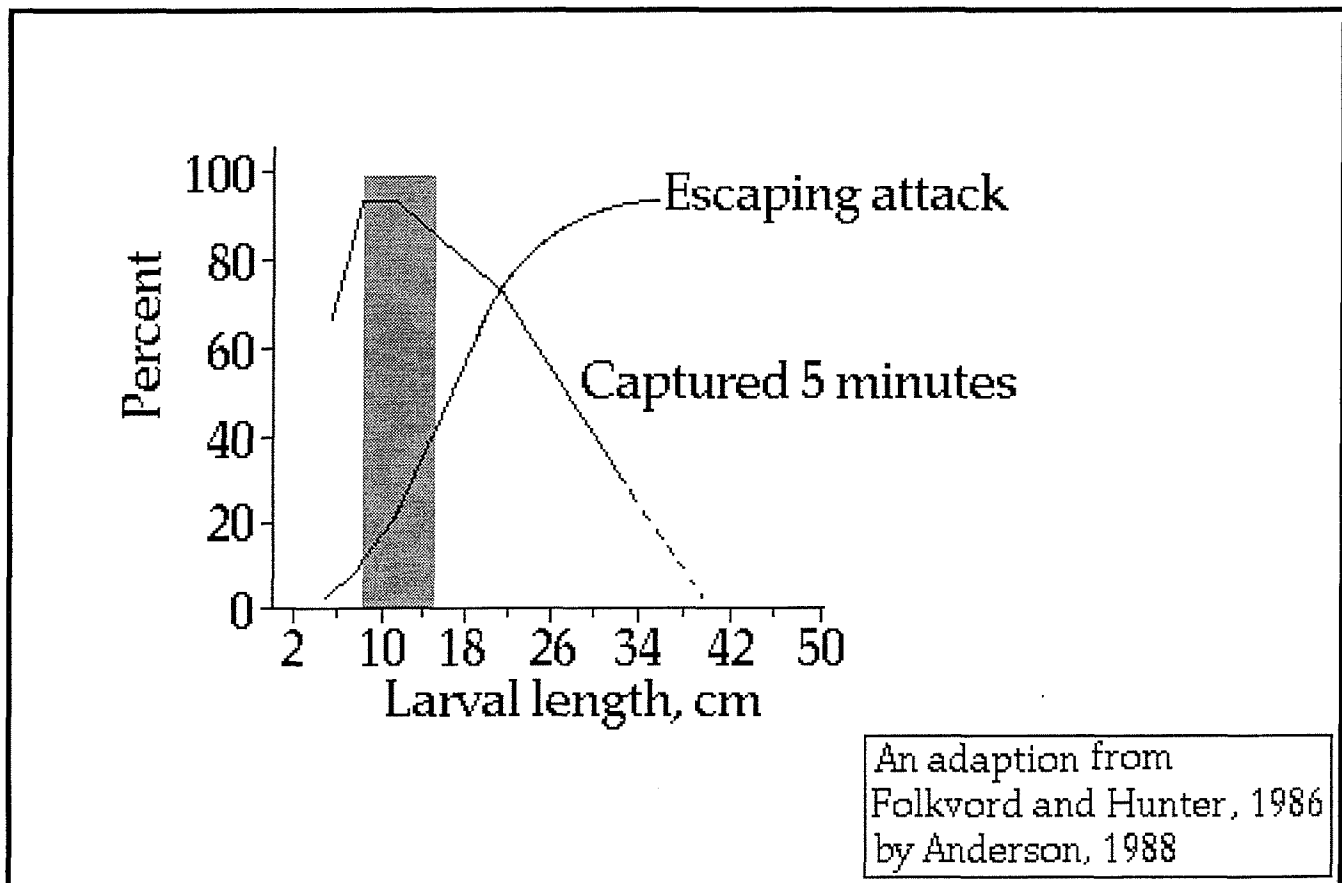larvae grew.

Fig. 13. Mean percentage of anchovy larvae escaping attack and percentage eaten in 5 minutes by
adult anchovy. The shaded area represents the length range of highest predation rate.
*(Andelen ansjoslarver som unnviker et angrep fra voksne ansjos og andelen som blir spist i en 5
minutters periode. Det skyggelagte området er lengdeintervallet med høyest predasjon)*

In addition they observed that vulnerability of larval anchovy to predation by
adult Northern anchovy was highest for larvae 8.5-15 mm in length, attributed
to larvae of this length being more visible to the adults but still having a low
escape response . Thus larval anchovy move through a definite size window
where their vulnerability to cannibalism is highest. Pepin et al. (1987) have

demonstrated that this is generally true for vertebrate and invertebrate predators.

Miller et al. (1988) showed (Fig. 14) that larger predators are less affected by average larval prey size. E.g. predators 120mm long are not affected by small changes in larval prey size while the capture success of a predator of 50mm is critical affected by the size of the prey. However, even though a 190mm mackerel can take a 10mm anchovy larvae «as a piece of cake», they may not select these prey in the field if alternative prey are available.
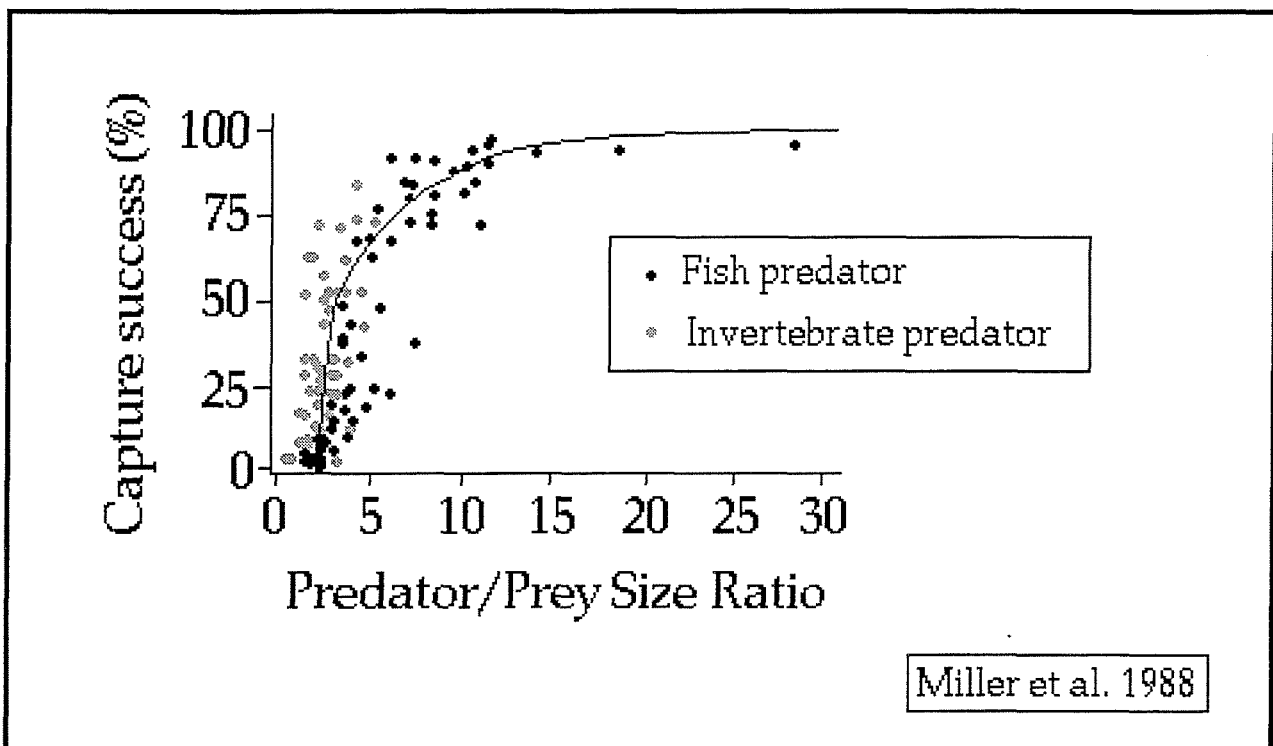

Fig. 14. Capture success as a function of predator to prey length ratio.
(Fangstsuksess som en funksjon av størrelsesforholdet mellom predator og byttedyr)

No substantial differences between evertebrate and vertebrate predators was seen. In summary, the incidence of predation is affected both by predator size and prey size. Larvae may drastically reduce their susceptibility to smaller predators by outgrowing them. But there seems to be no larval size refuge from predators that are 15 or more times the size of the larval prey.

Up to now I have shown that there is a negative relation between size and mortality and that large larvae have higher activity, better foraging ability and larger flexibility when they start to feed. They can also search larger volumes of water, they have fewer predatory fields and shorter time to reach metamorphosis.

My conclusion from this is that if your parents have been so stupid that they did not select for large egg size you better grow at an accelerated rate. However, what are the cost of growth at a maximal rate since the optimal strategy was to have minimum mortality per unit growth. The problem is that instantaneous daily growth and mortality rates are linked (Fig 15) this is also commented by Ware (1975), Anderson (1988) and Houde and Zastrow (1993).
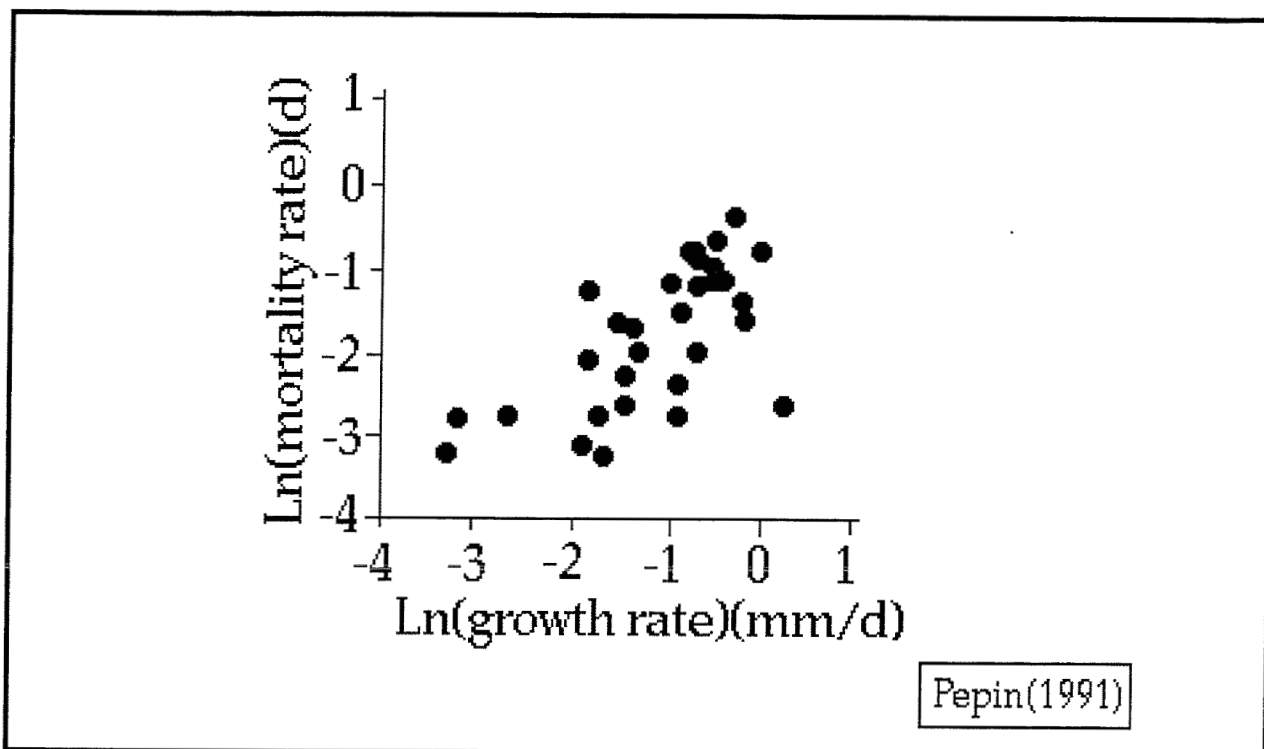
Fig. 15. Daily mortality rates of postlarval fish vs. average daily growth rates.
(Et plott av den daglige øyeblikkelige dødelighetsraten mot den daglige vekstraten)

It follows that in order to grow rapidly, organisms must increase activity levels to encounter and ingest a greater number of prey items. Increased activity will lead to increased encounter rates with both prey and predators (Gerritsen and Strickler 1977) and thus lead to higher growth and mortality rate. In order for a cohort to increase in weight over time mortality rates must be less than growth rates. A plot of the ratio between Z and G is shown in Houde and Zastrow (1993) (Fig 16) for different types of fish larvae from fastgrowing Scombrid larvae to slower growing Percoid larvae and in different types of ecosystem.
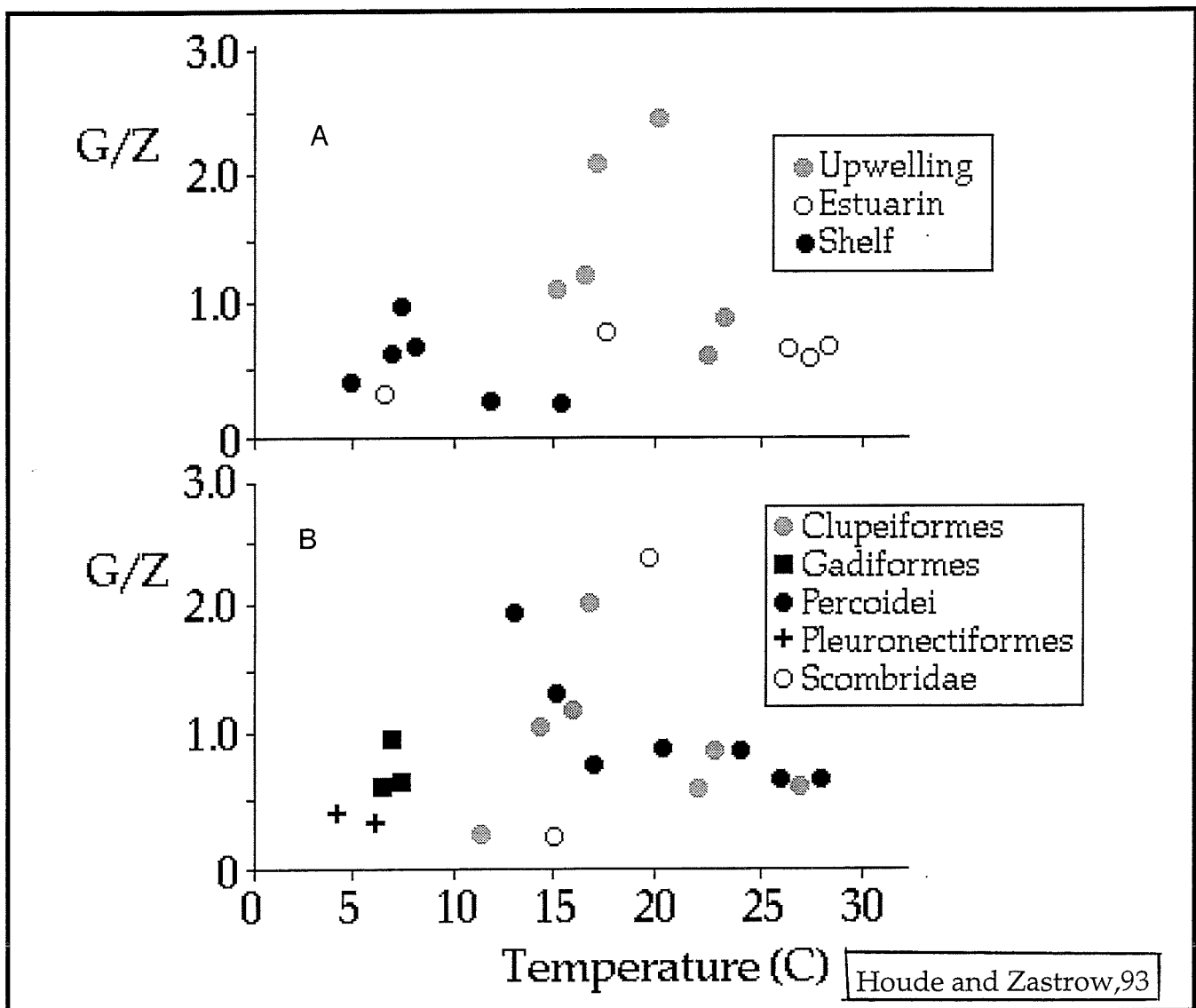

Fig. 16. A, Ecosystem- and B, Taxon-specific, ratio of growth coefficient to mortality coefficient values of teleost larvae in relation to temperature.

(Det økosystem- og slektsspesifikke forholdet mellom vekst og dødelighet i relasjon til temperatur)

There were no significant differences between nighter species nor systems. The overall mean G/Z did not differ from a value of 1.0 indicating that population biomass are relative constant during the teleost larval stage.

Back to scratch, the fate of the tiny larvae is perhaps dependent on that the individual growth rate increase without an concurrent increase in the species specific activity and thus mortality rate, and that this increase is caused by density-independent factors that change both on a spatial and temporal scale.

However, before I make any final conclusions I will present the work by Weinmiller and Rose (1991) called "Why do most fish produce so many tiny offspring?"

There is a general accepted hypothesis that large larvae generally have better early survival especially when the resources are scarce. Therefore a fixed amount of reproductive effort should be positioned into many small offspring in resource-rich habitats or into a few large offspring in resource-poor habitats.

Production of large clutches of small pelagic eggs is the predominant strategy in fishes inhabit offshore environment. Body size appears to be a key characteristic, small larvae seem less likely to forage successfully they have slower growth and are dyeing faster from starvation and predation. Why so selection for tiny eggs?

This model is individually based-density independent, size based model of feeding, growth and survival to examine the effect of spatial variation in environmental quality on survival.

Prey encounters, growth and mortality of individual larvae from first feeding until 20-mm total length are modelled. Two initial conditions were specified: the fixed biomass of spawn and the length of larvae at first feeding.

Comparison 1: Effect on survival related to prey density and larval size

In this first comparison, prey densities were assumed to be randomly
distributed and constant over time under each condition. The spawned
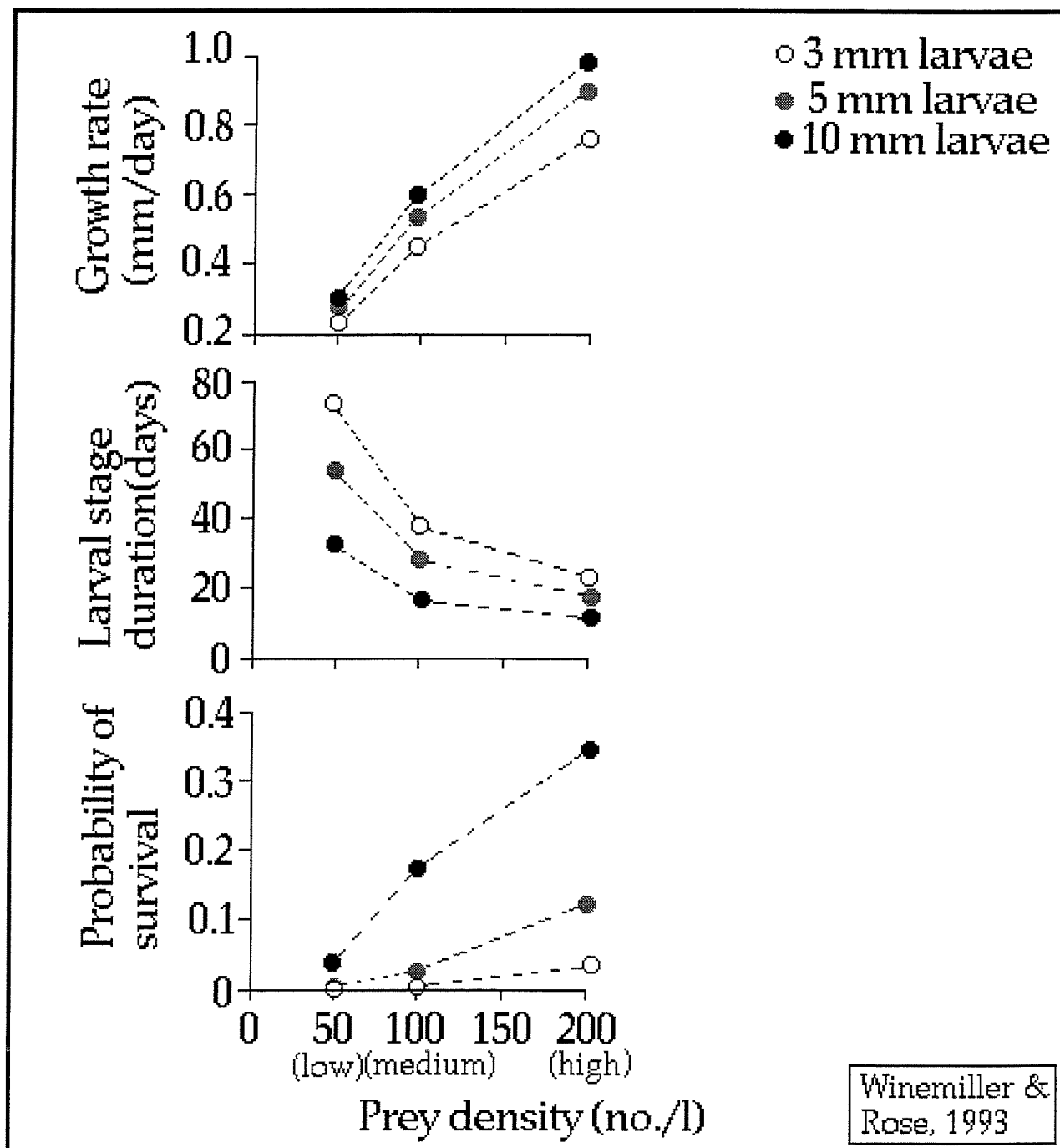

Fig. 17. Daily growth rate, larval stage duration and probability of survival of larvae with 3, 5
and 10 mm hatching length.

*(Daglig vekstrate, stadievarighet og sannsynligheten for å overleve hos larver med 3, 5 og 10 mm
klekkelengde)*

biomass to be allocated into larvae was held constant at 11g dw; that meen

1000000 (3mm), 137500 (5mm), 9565 (10mm) larvae.

Daily growth rate was higher, stage duration was shorter and probability of

survival higher for larger initial size (Fig. 17). Highest parental fitness; highest

number of survivors per 11g dw spawn for small larvae at medium to high
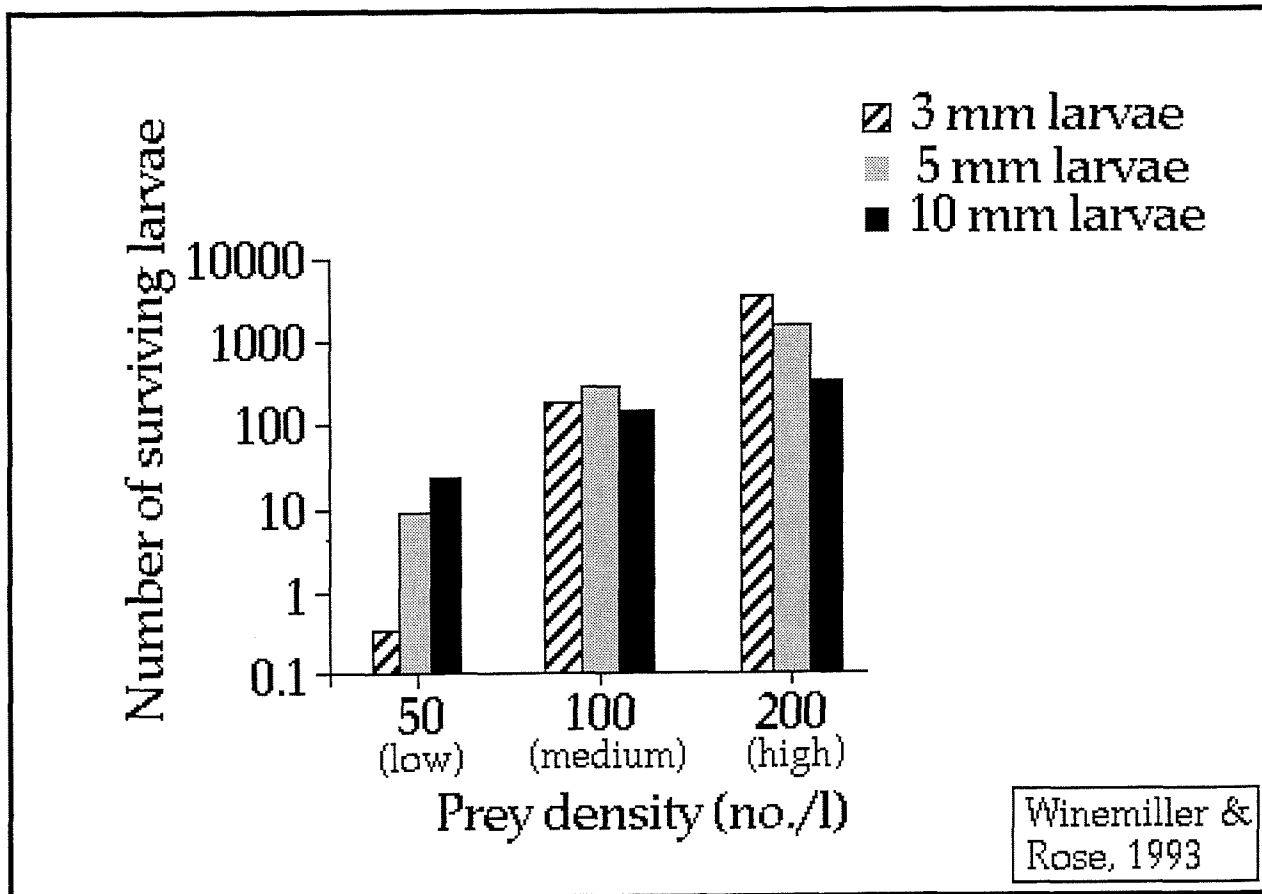
prey density (Fig. 18).

Fig.18. Parental fitnes at variable hatching size and prey density.

(Antall overlevende pr 11 g egg (tørrvekt) med variabel klekkelengde og byttedyrtetthet)

Comparison 2: Effect on survival of small-scale prey patchiness

It was generated realized encounter rates on a day to day basis, with prey from a

negative binomial distribution. The negative binomial distribution has been

used to represent spatial patchiness in zooplankton (Owen 1989, e.g. K=1.0

median for Southern California Bight). Simulations with 3 and 10 mm larvae

at 50 and 200 prey/l, 11 gdw of spawn. Simulations involving small larvae in

environments with low prey density gave all few survivors (Fig. 19). Survival decreased monotonically with all other prey density and larval size versus increasing prey patchiness. At the highest prey density the fitness was best with the smallest larvae (Fig. 19).
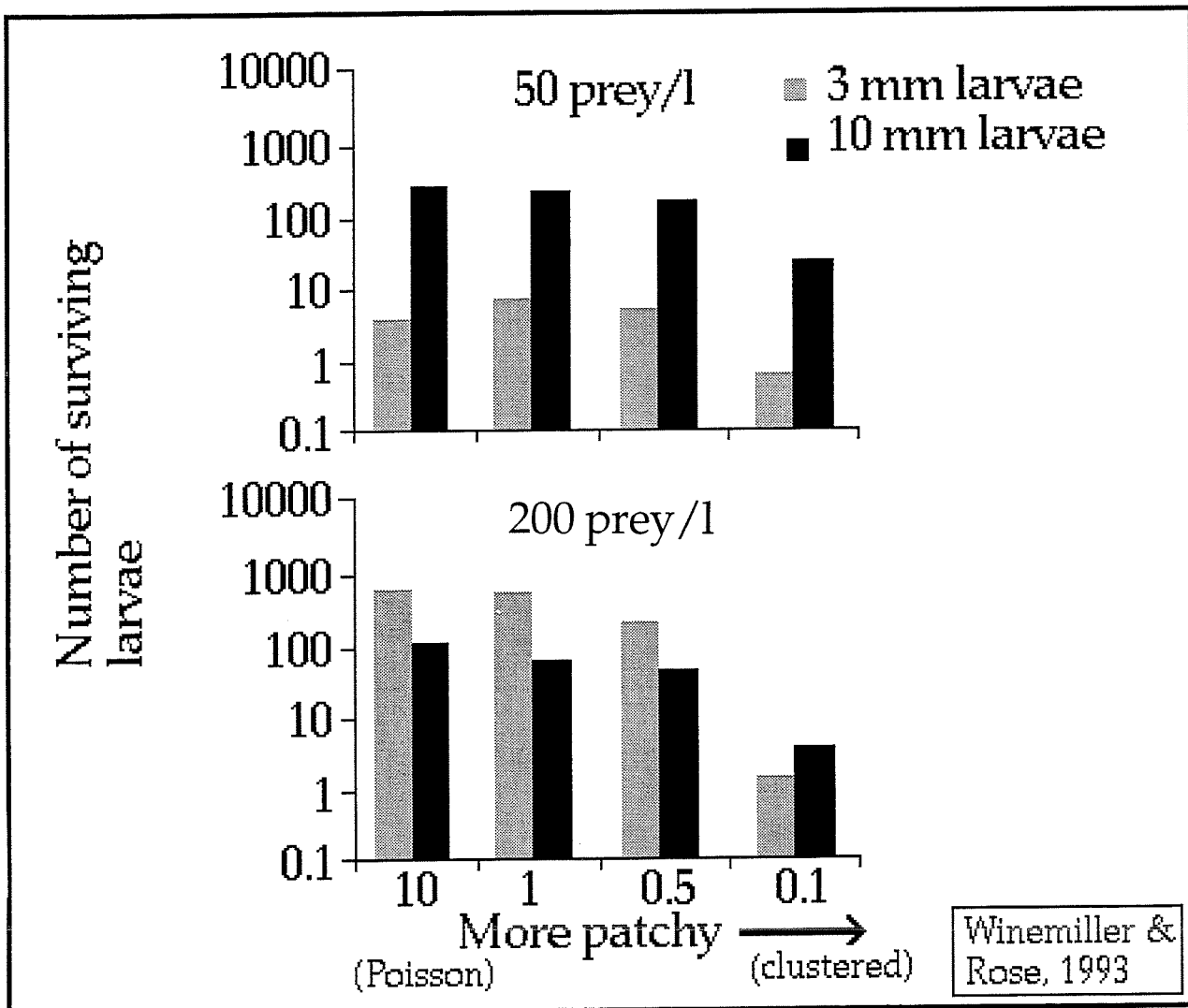

Fig. 19. Parental fitness with larvae of 3 and 10 mm hatching-length and variable degree of prey patchiness.

(Antall overlevende pr 11 g. egg (tørrvekt) når klekkelengden og byttedyrfordelingen forandrer seg)

Comparison 3: Effect of Large-Scale Prey Patchiness.

The assumption was that once the larvae enter a large patch with high density (200/l) found in upwelling areas, frontal zone etc., they stays there for the rest of the larval period. Thus they put forward following question: What percentage of larvae must occur in dense patches if the number of survivors shall be equal for broods comprised of equal biomass of small and large initial sizes at first feeding? Two examples of solutions :

1) If a brood is comprised of equal biomass of 3 and 5 mm first feeding larvae then ≈10% of the larvae must enter the patch if the number of survivors from the two size groups shall be equal. If a larger percentage enter the patch the smallest larvae have best fit.

2) If a brood is comprised of 11 g dw of both 3 and 10 mm first feeding larvae then if 5% of the larvae occupy patches of high prey density (200/l), broods comprised of 3-mm first feeding larvae result in 867 survivors compared to 235 for broods comprised of 10.0 mm first feeding larvae.

SUMMING UP

So perhaps your parents wasn´t that stupid after all. Selection for small eggs can be an adaptation to temporal pulses year in year out in the production of zooplankton. Since relative high prey densities favours small eggs while low prey densities favours large eggs. The same does patchiness if the scale is relative large. A good tactic can therefore be to wait for the good year and select for many small eggs, because even if the survival in years with low prey densities would have been better with large eggs this is more than compensated with the increased survival in years with high zooplankton production. Another conclusion is that the most important selective mechanisms of significance for survival of fish larvae are size based and based on general level of activity of the larvae. However, in the juvenile stage density-dependent mechanisms can be of importance also indicated by Sissenwine (1984). Fish and

bird predators that are only gape size limited can often select positively for size and they can be triggered by increased abundance of fish prey resulting in large and may be controlling impact on the resulting size of the yearclass.

Cod, herring and capelin, the three species in my thesis have very different strategies with respect to selective mechanisms connected to reproduction. The capelin is a opportunist and a one time spawner, the recruitment seem mainly to be density-independent regulated with a typical difference in reproductive success on three orders of magnitude. However , there seem to be year in year out in capelin recruitment depending on the presence of young herring in the system laying a heavy predation pressure on the capelin recruitment.

The herring is a multiple spawner responding to changes in the environment with longer wavelengths with a typical difference in reproductive success on two orders of magnitude. The different herring stocks have evolved several different strategies with respect to reproduction with spawning almost all the year around at distinct spawning grounds. The dry weight of the eggs are dependent on the timing with zooplankton production, with winter and spring spawners having heavier eggs than summer and autumn spawners. The herring have a relative primitive form for larva, metamorphosing in the size interval 40-50 mm thus depending on a long growth season.

The cod larvae grow faster than the herring larvae especially under suboptimal prey conditions, metamorphose at a much smaller size 12-15 mm. However, as a typical top predator the cod abundance is strongly regulated through density-dependent mechanisms resulting in a typical difference in reproductive success on one order of magnitude.

In the future more work should be done on larval growth and mortality. Much of the estimates presented in the literature are according to Pepin (1993) length based estimates and perhaps not accurate enough. He recommend the use of otolith microstructure for ageing purposes and for backcalculating of growth. In addition to such investigations I feel that there is a strong need for more

quantitative sampling equipment, and if we succeed in quantifying our sampling and are able to further develop the otolith microstructure technique I believe that we are in the beginning of a new aura in recruitment inv.

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