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RELATIONSHIP BETWEEN THE FORMS OF PELAGIC FISH DISTRIBUTION AND NICTEMERAL PERIODS. A TENTATIVE MODEL OF BEHAVIOUR

Abstract

Pelagic fish behaviour in relation to sunlight.

5825 echograms, collected in the Adriatic in 5 echosurveys, have been classified with reference to the forms of spatial distribution of pelagic fish and analyzed for 4 different intervals over 24 hour period. An attempt to model fish behaviour using Duffin's equation is proposed

Key-words: Adriatic sea, echosurvey, catastrophe model, fish behaviour, nictemeral period.

Introduction

Acoustic surveys have been carried out by I.R.PE.M. in the North and Middle Adriatic sea since 1976. At present all the acoustic data collected in the surveys have been stored in a data base system, that permits a large number of users to have access to them and ask a wide variety of questions.

The paper illustrates an application derived from the use of the data base: the classification of the echograms in regard to the spatial distributions of small pelagic fish and sunlight.

The different forms of pelagic fish distribution considerably affect the commercial catch.

One benefit of processing data in this way is to provide clues to select the type of fishing gear (driftnets, nets for trawling and purse-seining) and their dimensions.

In the same way, the forms of pelagic fish distribution affect the statistics of the received echosignals, therefore they must be considered in processing acoustic data for biomass assessment.

Other potential users of the forms of spatial distribution are: ecologists; mathematicians; modellers.

Definitions and assumptions

The spatial distributions of small pelagic fish have been classified (see note 1) in three main forms: disperse, schooled, in accumulation.

Each form has been labeled «local», if limited within a nautical mile; «scattered», if extended beyond a nautical mile. All these forms and types are schematically shown in Fig. 1.

A *disperse distribution* of fish means that single fish or small groups of few individuals are isolated from each other and are not bound up by any kind of uniform behaviour.

Usually small pelagic fish are found dispersed after spawning, when they are feeble and in a passive physiological state. The areas occupied by a disperse distribution extend generally for many miles (*scattered disperse distribution*); a *local disperse distribution* is fairly rare and occurs only in case of an unfavourable habitat. Fish dispersed over a large area are of no interest to fishermen. However fairly good catches can be obtained by driftnets.

A *schooled distribution* is formed by grouping of fish of the same species, similar in size and identical in their biological state. Schooling behaviour is typical of small pelagic fish for a large part of their life, but the causes of grouping mechanisms (reactions to predator and/or facilities offered by a social behaviour in a certain environment) are unknown. Here it is assumed that schooling is mostly a defending strategy against predators.

The shape, size and density of the schools may vary appreciably from species to species and, within a species, from age class to age class. Usually small schools are scattered over large areas (*scattered schooled distributions*). In this case particularly good catches are obtained by trawling and purse-seining.

An *accumulation* is a non homogenous union of single fish or an aggregation of schools.

This mixing of single fish or schools destroys the uniformity of behaviour, whereas a school is characterized by synchronized behaviour.

Scattered accumulations are often formed by fish during migration to the feeding or spawning areas; they have usually low density and give stable but not large catches. *Local accumulations* arise, probably, in places where fish, during migration, linger for feeding; they are very important for trawling.

The definitions of the main forms of fish distribution and the assumptions of the physiological state related to them can be summarized in the following two cases:

physiological state:

form of distribution:

1) PASSIVE: after spawning

DISPERSE

2) ACTIVE: defending

SCHOOLED

feeding, migrating, spawning

IN ACCUMULATION

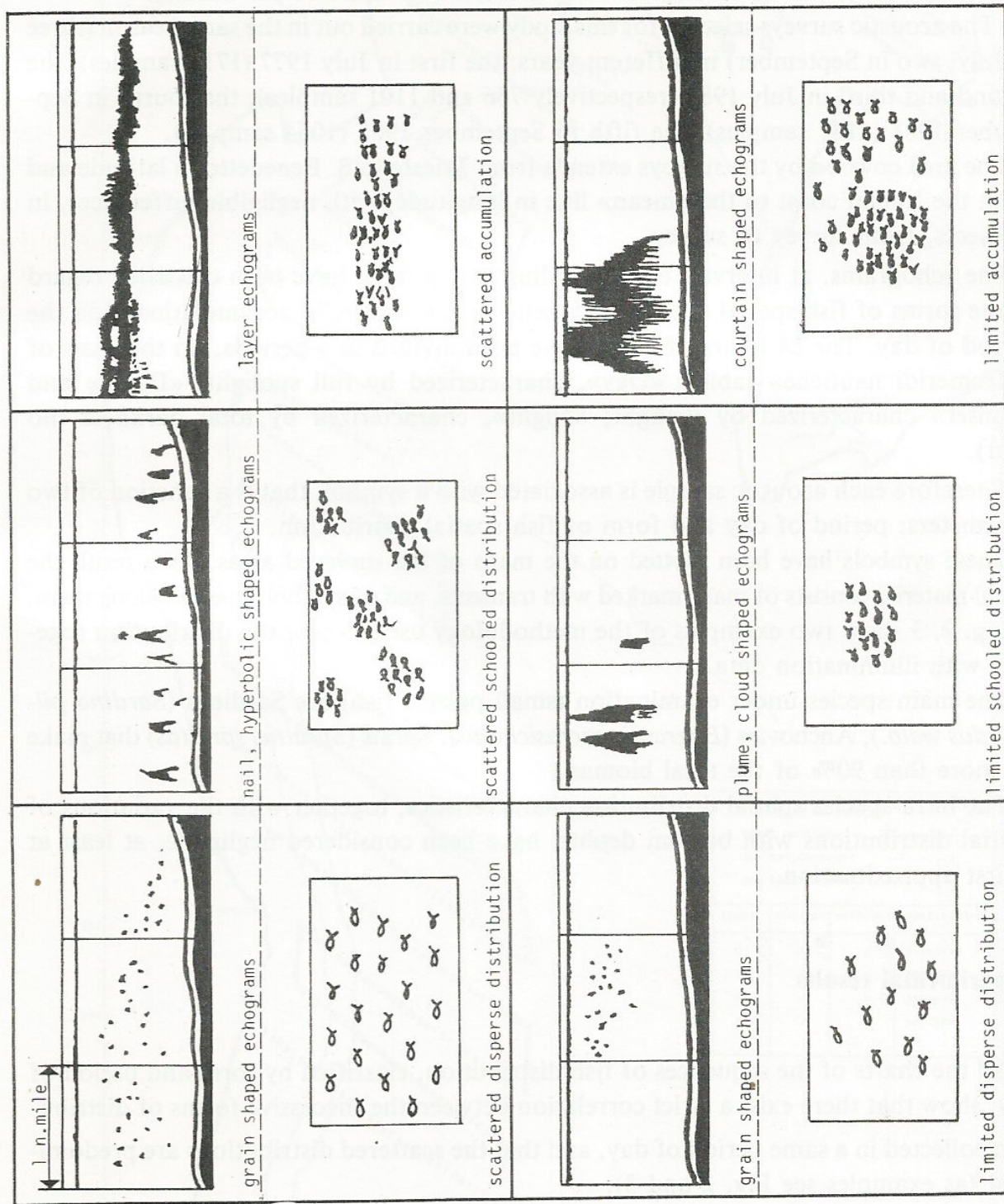


Fig. - 1 - Main forms of pelagic fish distributions detected by hydroacoustic instruments and relatives echogram.

Methods and materials

The acoustic surveys use line sampling technique, that takes the form of uninterrupted transects in space and time. An elementary sample is a unit distance of 1 nautical mile (E.S.D.U.), that is usually sailed at 8 knots (7.5 minutes per n.mile).

The acoustic surveys selected for this study were carried out in the same season (three in July, two in September) in different years: the first in July 1977 (1713 samples), the second and third in July 1980 (respectively 766 and 1101 samples), the fourth in September 1981 (1181 samples), the fifth in September 1982 (1064 samples).

The area covered by the surveys extends from Trieste to S. Benedetto in latitude and from the Italian coast to the «mean» line in longitude, with negligible differences, in transects, from survey to survey.

The echograms, at intervals corresponding to 1 n.mile, have been classified regard to the forms of fish spatial distribution (schooling, dispersed, in accumulation) and the period of day. The 24 hours of a day have been divided in 4 periods, on the basis of «Effeimeridi nautiche» tables: «Day», characterized by full sunlight, «Dawn» and «Sunset» characterized by twilight; «Night», characterized by total darkness (no light).

Therefore each acoustic sample is associated with a symbol, that is a function of two parameters: period of day and form of fish spatial distribution.

These symbols have been plotted on the maps of the surveyed areas. As a result the initial material consists of maps marked with transects, and of symbols marked along them.

Fig. 2, 3 show two examples of the methodology used to plot the distribution together with illumination data.

The main species under examination (small pelagic fish) are Sardines (*Sardina pilchardus walb.*), Anchovies (*Engraulis encrasicolus*), Sprats (*Sprattus sprattus*) that make up more than 90% of the total biomass.

The intra-species spatial distribution characteristics, together with the variations of spatial distributions with bottom depths, have been considered negligible, at least at a first approximation.

Experimental results

All the charts of the sequences of fish distribution, classified by form and period of day, show that there exist a strict correlation between the successive forms of distribution collected in a same period of day, and that the scattered distributions are predominant (as examples see Fig. 2 and 3).

The persistence of schooled distributions for the hours characterized by full sunlight and of accumulations during the night is evident in these maps. Tables 1, 2, 3, 4, 5 and relative histograms indicate that schooled distribution is the predominant frequency class during the light period (July '77: 61.4%; July '80: 45.1%; July '80: 52.0%; Sept. '81: 73.0%; Sept. '82: 64.0%), whereas this behavioural pattern is almost inaccessible during the night.

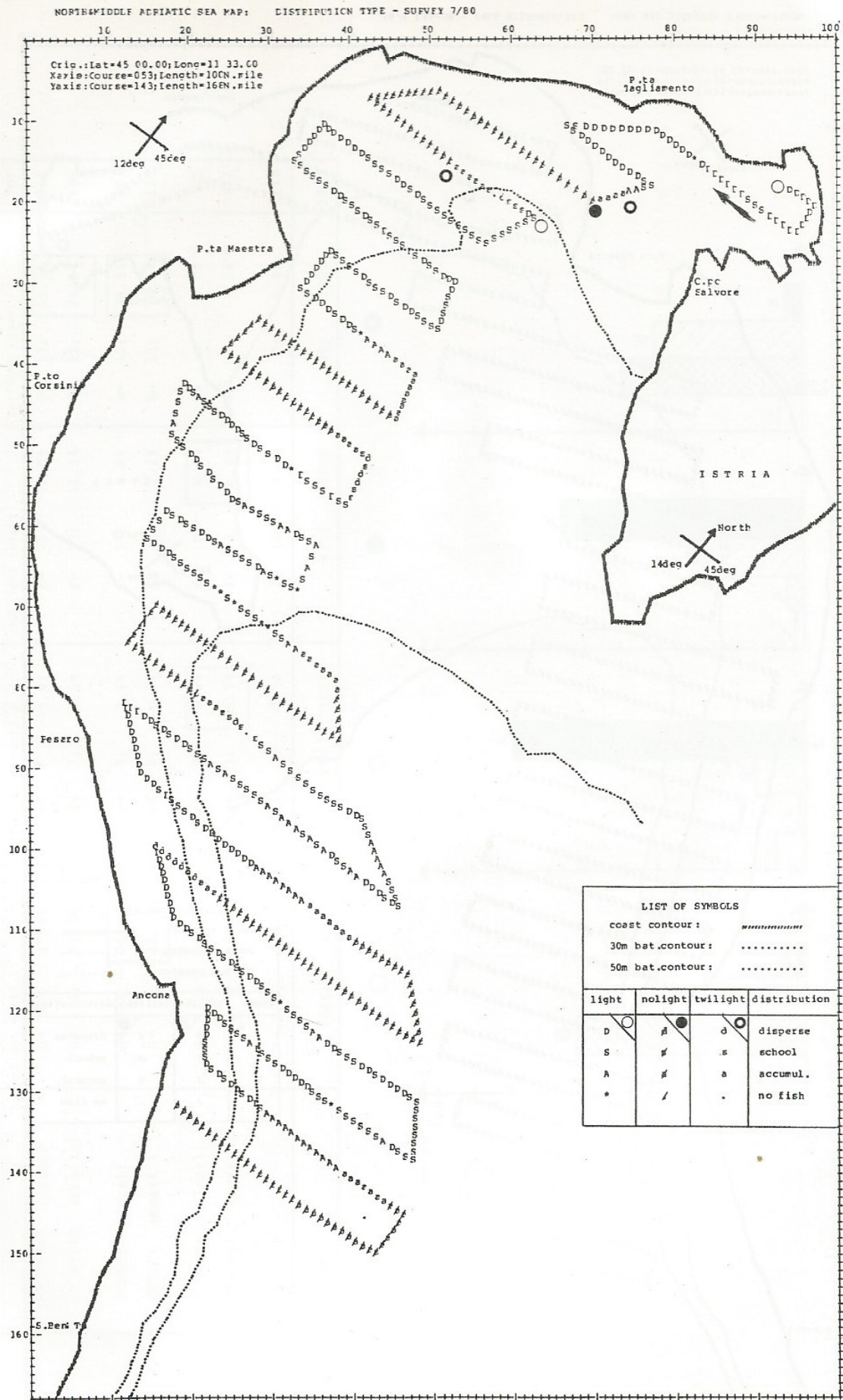


Fig. 2 - July 1980: forms of distributions of pelagic fish in the survey area, every nautical mile, by periods of day.

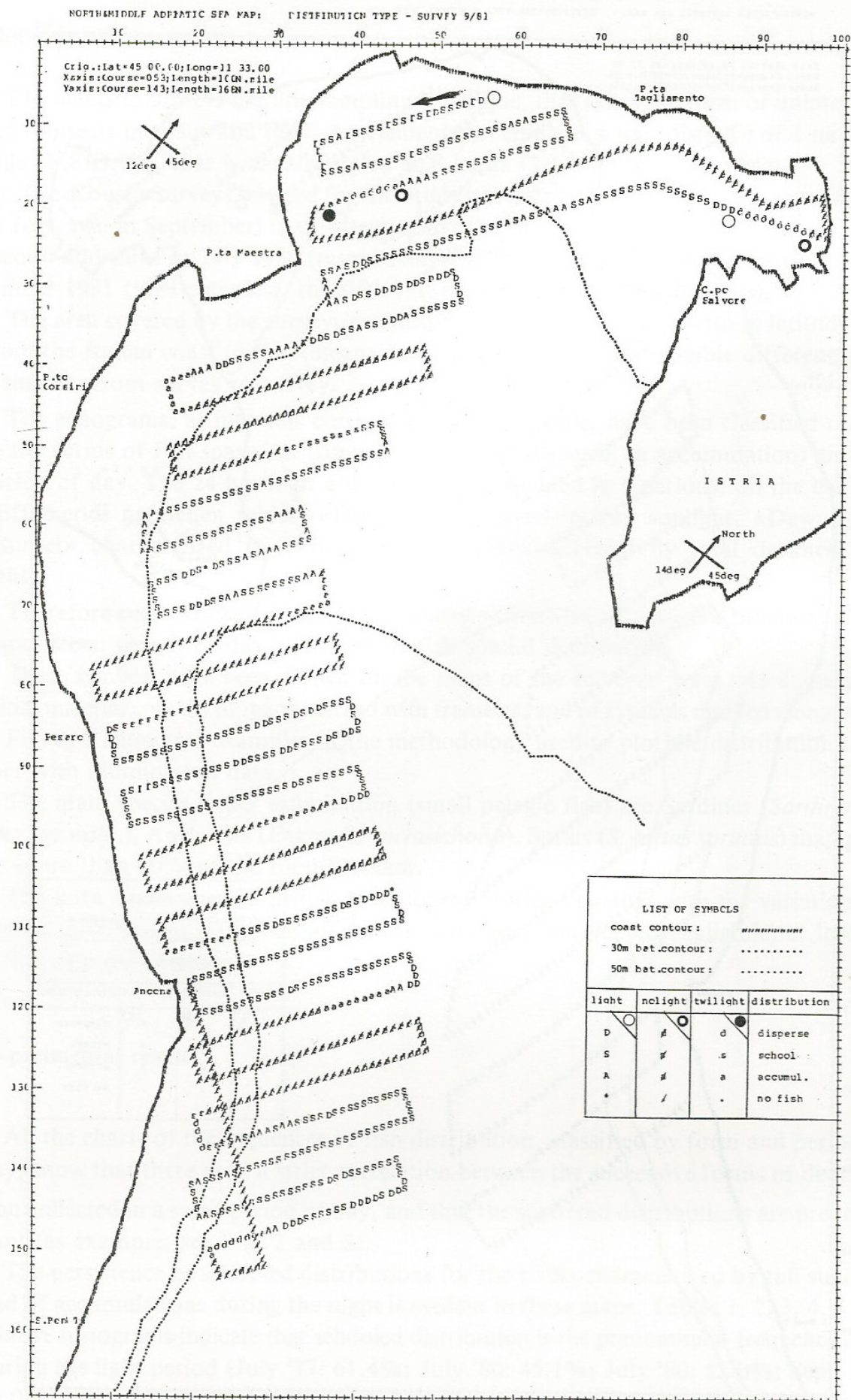
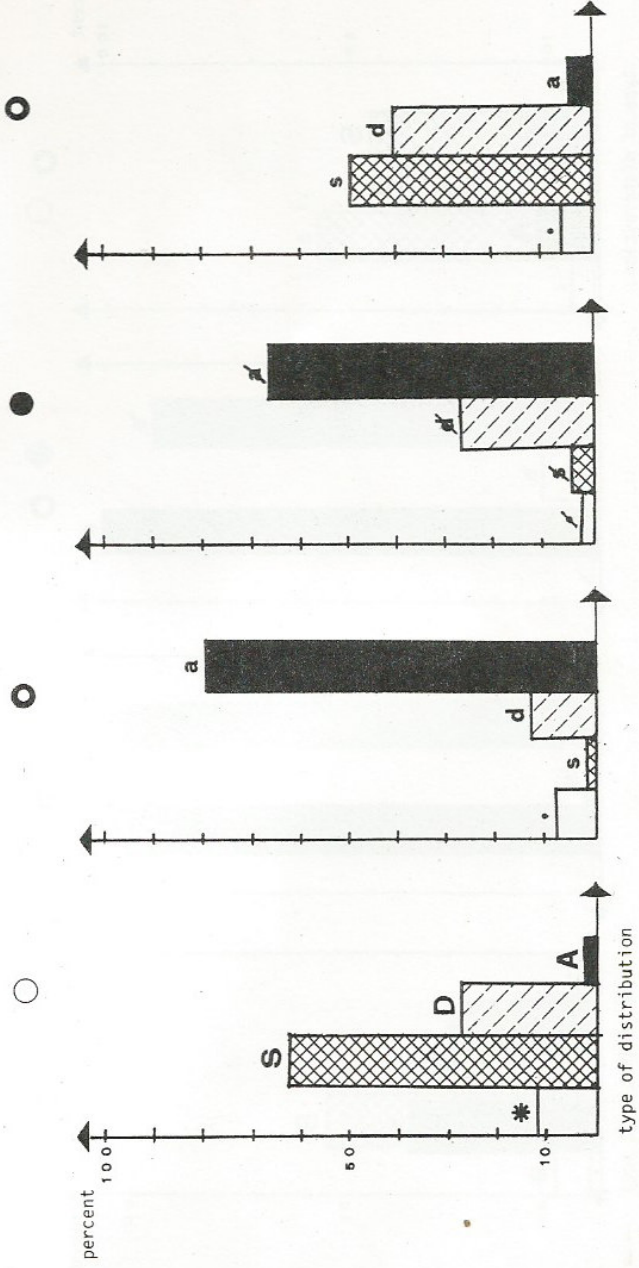


Fig. 3 - September 1981: forms of distributions of pelagic fish in the survey area, every nautical mile, by periods of day.

ANALYSIS OF DISTRIBUTION TYPE: 7/77 RESULTS

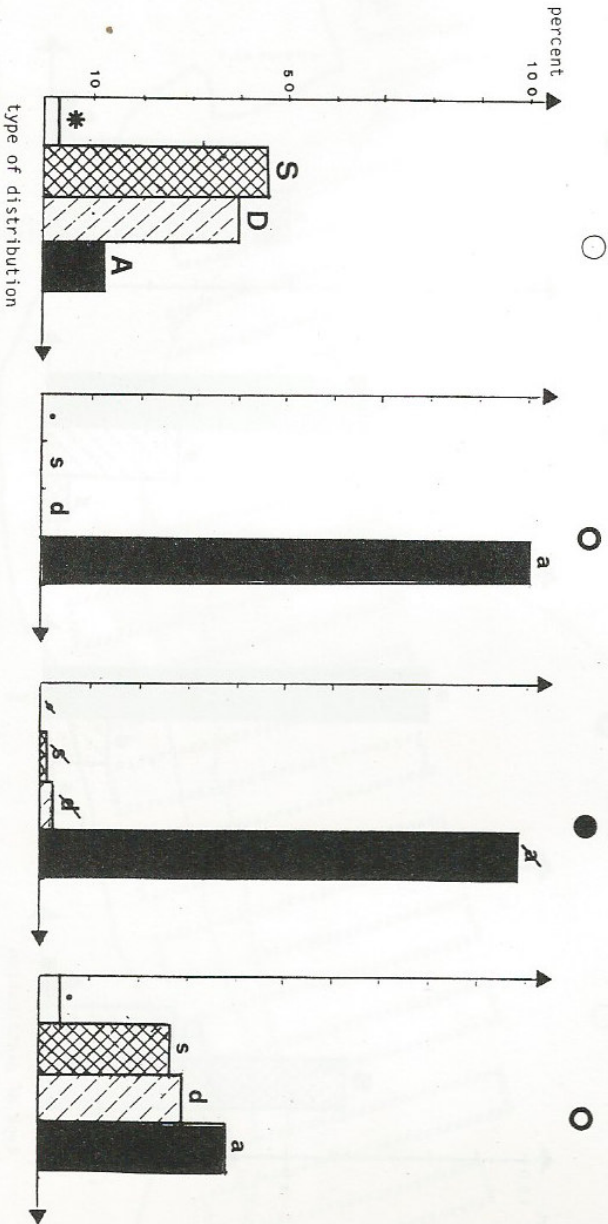
	light (day)	twilight (sunset)	no light (night)	twilight (dawn)	Tot
DISPERSE (local)	D= 165; 15.9%	d= 5; 5.4%	d= 73; 15.5%	d= 17; 15.6%	260
DISPERSE (scatt.)	D= 111; 10.7%	d= 7; 7.5%	d= 53; 11.3%	d= 27; 24.8%	198
SCHOOL (local)	S= 528; 50.8%	s= 1; 1.1%	s= 13; 2.8%	s= 42; 38.5%	584
SCHOOL (scatt.)	S= 110; 10.6%	s= 0; 0.0%	s= 5; 1.1%	s= 11; 10.1%	126
ACCUMUL. (local)	A= 5; 0.5%	a= 0; 0.0%	a= 0; 0.0%	a= 0; 0.0%	5
ACCUMUL. (scatt.)	A= 5; 0.5%	a= 73; 78.5%	a= 311; 66.0%	a= 5; 4.6%	394
NO FISH	*= 116; 11.2%	= 7; 7.5%	= 16; 3.4%	= 7; 6.4%	146
TOTAL	1040; 100%	93; 100%	471; 100%	109; 100%	1713



Tab. 1 - July 1977: analysis and histograms of the forms of pelagic fish distribution by periods of time (day, sunset, night, dawn).

ANALYSIS OF DISTRIBUTION TYPE: 7/80 RESULTS

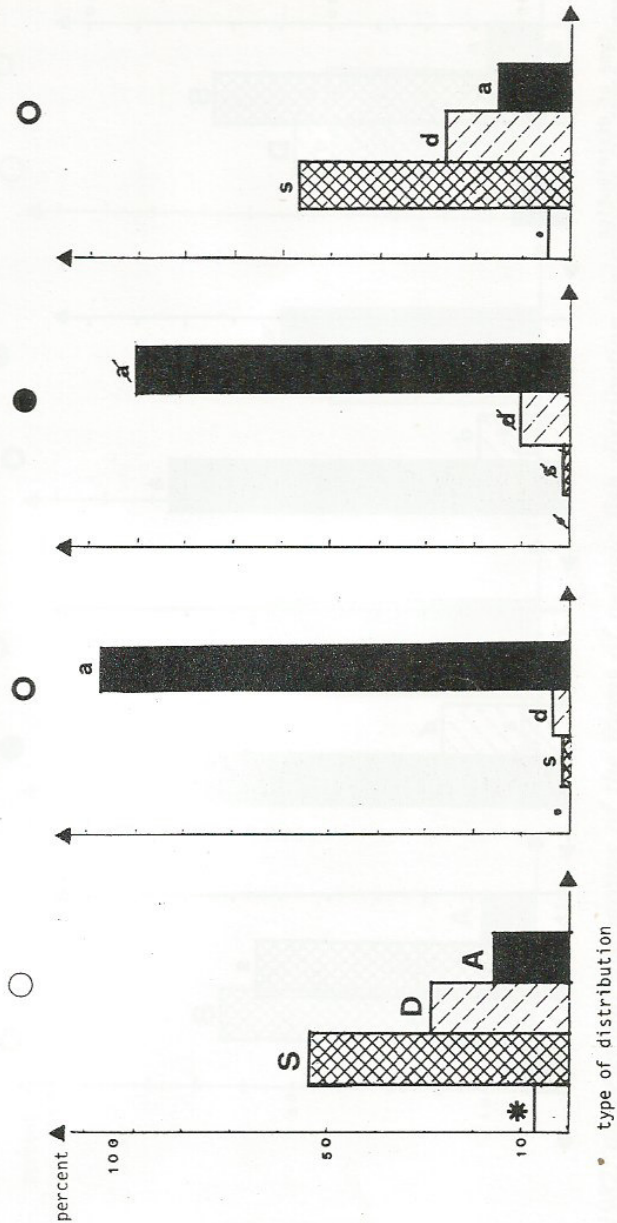
	light (day)	twilight (sunset)	no light (night)	twilight (dawn)	Tot
FISPERFI (Jccal)	r = 132; <div>27.8%</div>	d = 0; 0.0%	f = 0; 0.0%	d = 6; <div>14.6%</div>	138
FISPFPIF (scatt.)	D = 59; <div>12.4%</div>	d = 0; 0.0%	d = 4; 1.9%	d = 6; <div>14.6%</div>	69
SCHCCL (Jccal)	S = 175; <div>36.5%</div>	s = 0; 0.0%	f = 1; 0.5%	s = 6; 14.6%	182
SCHCCL (scatt.)	S = 39; <div>8.2%</div>	s = 0; 0.0%	f = 0; 0.0%	s = 5; 12.2%	44
ACCUMUL. (Jccal)	A = 27; 5.7%	a = 0; 0.0%	f = 12; 5.6%	a = 6; <div>14.6%</div>	45
ACCUMUL. (scatt.)	A = 30; 6.3%	a = 36; <div>100.0%</div>	f = 198; <div>52.1%</div>	a = 10; <div>24.4%</div>	274
NO FISH	* = 12; 2.5%	. = 0; 0.0%	/ = 0; 0.0%	. = 2; 4.9%	14
TOTAL	474; 100%	36; 100%	215; 100%	41; 100%	766



Tab. 2 - July 1980: analysis and histograms of the forms of pelagic fish distribution by periods of time (day, sunset, night, dawn).

ANALYSIS OF DISTRIBUTION TYPE: 7/80 RESULTS

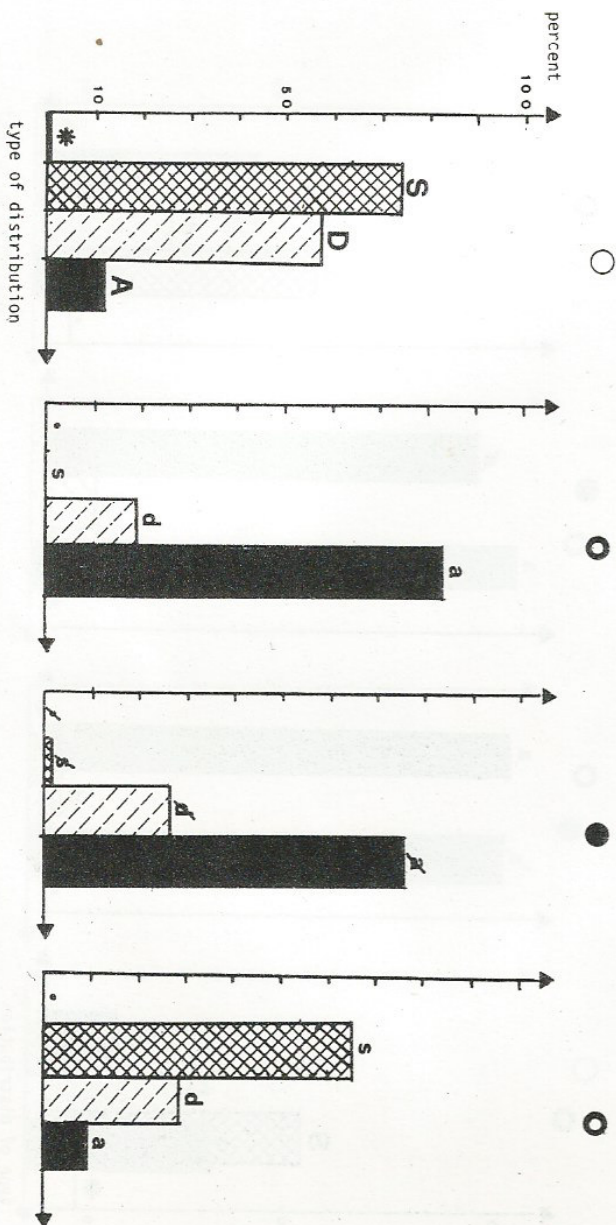
	light (day)	twilight (sunset)	no light (night)	twilight (dawn)	Tot
DISPEPSE (lccal)	D= 134; 18.6%	0= 0; 0.0%	16= 16; 6.1%	0= 10; 19.2%	160
DISPEPSE (scatt.)	D= 64; 8.9%	0= 2; 5.0%	11= 11; 4.2%	0= 3; 5.8%	80
SCHOCL (lccal)	S= 204; 42.3%	1= 1; 1.5%	3= 3; 1.1%	S= 22; 42.3%	330
SCHOCL (scatt.)	S= 70; 9.7%	0= 0; 0.0%	0= 0; 0.0%	S= 7; 13.5%	77
ACCUMUL. (lccal)	A= 74; 10.3%	0= 0; 0.0%	1= 1; 0.4%	0= 3; 5.8%	78
ACCUMUL. (scatt.)	A= 33; 4.6%	0= 64; 95.5%	232= 232; 88.2%	0= 5; 9.6%	334
NO FISH	*= 40; 5.6%	0= 0; 0.0%	0= 0; 0.0%	2= 2; 3.8%	42
TOTAL	719; 100%	67; 100%	263; 100%	52; 100%	1101



Tab. 3 - July 1980: analysis and histograms of the forms of pelagic fish distribution by periods of time (day, sunset, night, dawn).

ANALYSIS OF DISTRIBUTION TYPE: 9/81 RESULTS

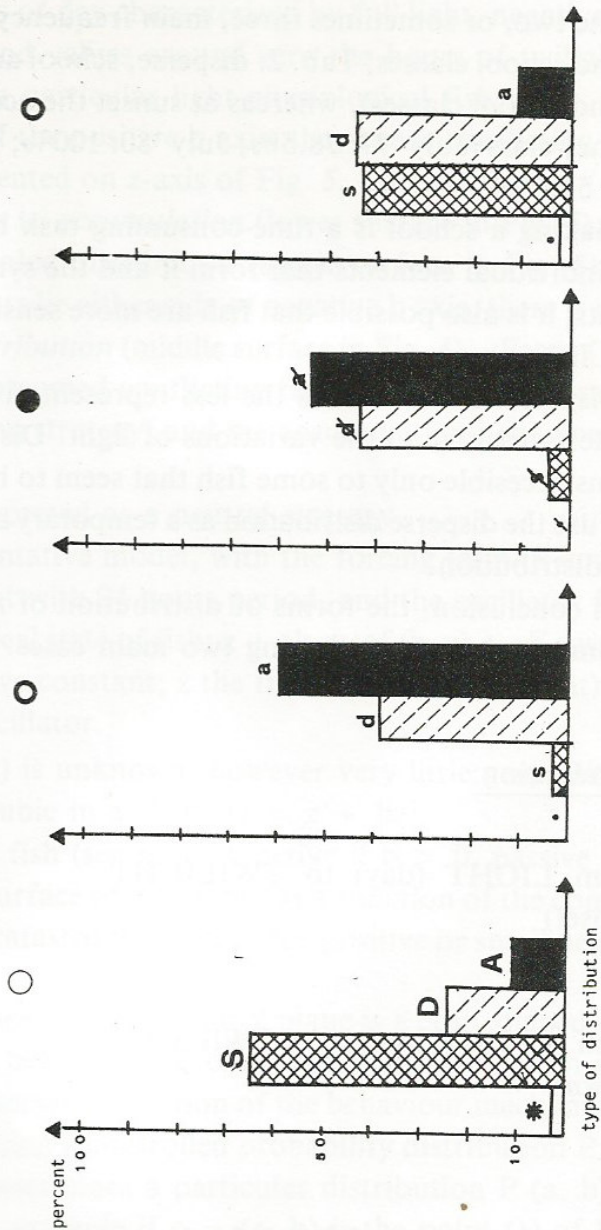
	light (day)	twilight (sunset)	no light (night)	twilight (dawn)	tot
FISFESE (1ccal)	P = 59; 5.6%	Q = 0; 0.0%	R = 8; 1.7%	Q = 2; 4.3%	69
FISFESE (scatt.)	D = 37; 6.0%	Q = 10; 10.5%	R = 109; 23.5%	Q = 11; 23.4%	167
SCICCL (1ccal)	S = 244; 39.6%	E = 0; 0.0%	R = 1; 0.2%	E = 4; 8.5%	249
SCICCL (scatt.)	S = 206; 33.4%	E = 0; 0.0%	R = 3; 0.6%	E = 26; 55.3%	235
POCCMUL. (1ccal)	A = 51; 8.3%	E = 0; 0.0%	R = 0; 0.0%	A = 2; 4.3%	53
POCCMUL. (scatt.)	A = 17; 2.8%	A = 44; 81.5%	R = 343; 73.9%	A = 2; 4.3%	406
NO FISH	* = 2; 0.3%	. = 0; 0.0%	R = 0; 0.0%	. = 0; 0.0%	2
TOTAL	616; 100%	54; 100%	464; 100%	47; 100%	1181



Tab. 4 - September 1981: analysis and histograms of the forms of pelagic fish distribution by periods of time (day, sunset, night, dawn).

ANALYSIS OF DISTRIBUTION TYPE: 9/82 RESULTS

	light (day)	twilight (sunset)	no light (night)	twilight (dawn)	Tot
DISPERSE (local)	D= 62; 15.2%	d= 5; 10.6%	δ= 38; 8.5%	δ= 5; 9.3%	130
DISPERSE (scatt.)	D= 46; 8.6%	d= 13; 27.7%	δ= 142; 33.4%	δ= 19; 35.2%	220
SCHOCI (local)	S= 229; 42.6%	S= 0; 0.0%	δ= 2; 0.5%	S= 11; 20.4%	242
SCHCOL (scatt.)	S= 115; 21.4%	S= 1; 2.1%	δ= 15; 3.5%	S= 12; 22.2%	143
ACCUMUL. (local)	A= 48; 8.9%	A= 0; 0.0%	δ= 3; 0.7%	A= 4; 7.4%	55
ACCUMUL. (scatt.)	A= 10; 1.9%	A= 28; 59.6%	δ= 223; 52.5%	A= 2; 3.7%	263
NO FISH	*= 8; 1.5%	*= 0; 0.0%	δ= 2; 0.5%	*= 1; 1.9%	11
TOTAL	530; 100%	47; 100%	425; 100%	54; 100%	1064



Tab. 5 - September 1982: analysis and histograms of the forms of pelagic fish distribution by periods of time (day, sunset, night, dawn).

In the darkness the accumulations predominate and, in some years, are almost the only frequency class present (July '77: 60.0%; July '80: 97%; July '80: 88.6%; Sept. '81: 73.9%; Sept. '82: 53.2%).

Therefore fish make sudden behaviour changes in the short periods of day characterized by twilight (dawn and sunset last about 1 hour). However, while the school patterns dissolve into accumulations suddenly at sunset, at dawn the delay before making the change from accumulation to school patterns is appreciable. This is demonstrated by the two, or sometimes three, main frequency classes present at dawn (Tab. 1: disperse and school classes; Tab. 2: disperse, school and accumulation classes; Tab. 5: disperse and school classes), whereas at sunset the accumulation is clearly the only main frequency class (July '77: 78.5%; July '80: 100%; July '80: 95.5%; Sept. '81: 81.5%; Sept. '82: 59.6%).

Making a school is a time-consuming task because of the need of homogeneity of the individual elements that form it and the synchronization of their swimming movements; it is also possible that fish are more sensitive to decreasing rather than to increasing light.

Disperse distribution is the less representative class (except at dawn), but it is also the less sensitive to the variations of light. Disperse distribution, as stable behaviour, seems accessible only to some fish that seem to be unable to react to environment. Most fish use the disperse distribution as a temporary and unstable behaviour to jump to schooled distribution.

In conclusion, the forms of distribution of most pelagic fish related to light can be summarized in the following two main cases:

illumination:

form of distribution:

From LIGHT (day) to TWILIGHT
(sunset)

SCHOOLED DISTRIBUTION, most
of time; sudden change towards AC-
CUMULATION

From NO LIGHT (night) to TWILIGHT
(dawn)

ACCUMULATION, most of time;
change with delay towards SCHOOLED
DISTRIBUTION.

A tentative model of fish behaviour and conclusions

What has been said so far is an attempt, in addition to systematize and classify the types of records, to relate behaviour of fish, indicated by their spatial distributions, to both their physiological state and the external oscillation of light.

The persistence of fish behaviour for many hours, the sudden behaviour changes, the difference of delays before making these changes, the possibility of divergent behaviour under similar illumination (twilight) have suggested the use of a catastrophe model.

The proposed model assumes that the rhythm of day and night represents the «normal-factor» (a axis in Fig. 4) and the physiological state of fish represents the «split-factor» (b axis in Fig. 4) in the control plane C, that represents the «cause» of a particular behaviour.

Positive values of b indicate an active physiological state (such as defending, migrating, feeding etc.), increasing in intensity with b. Negative values of b indicate a passive physiological state (such as insensitiveness to external stimuli).

Positive values of a indicate the hours of day characterized by full light, negative values of a indicate the hours of night and values around zero the hours of twilight.

A point $c = (a, b)$ in C represents a particular light-physiological fish state.

If the control factors lie either side of the positive b axis, they cause conflicting tendencies in the behaviour of fish, represented on z-axis of Fig. 5. The left factors ($-a, +b$) try to attract the fish behaviour on to *accumulation* (lower surface in Fig. 5), the right factors ($+a, +b$) on to the schooled distribution (upper surface in Fig. 5).

On the other hand if the control factors lie either side of negative b axis, there is only an attracting behaviour: *the disperse distribution* (middle surface in Fig. 4). «Fear» ($+a, +b$) and «Hunger» ($-a, +b$) may be assumed conflicting factors attracting, respectively, the schooled behaviour (a defending strategy) and the accumulation behaviour (a feeding strategy).

The disperse behaviour may be interpreted as a neutral strategy.

Let us take Duffin's equation as a tentative model, with the forcing term ($F \cos at$) representing the external rhythm of light with 24 hours period, and the oscillator $f(b, z)$ the diurnal variation on the physiological state of fish: $\ddot{z} + \epsilon k z + f(b, z) = \epsilon F \cos(at)$.

Where: t is time; ϵ, k are small positive constant; z the fish behaviour; $F \cos(at)$ the forcing term; $f(b, z)$ the biological oscillator.

The restoring biological force $f(b, z)$ is unknown, however very little generality is lost by assuming for it the following cubic in z : $f(b, z) = z + bz^3$.

Where b is the physiological state of fish (see note 2), active if $b > 0$, passive if $b \leq 0$. If so, Duffin's equation gives the surface of behaviour as a function of the control parameters b and a (Fig. 5); it is a cusp catastrophe surface for positive or small negative values of b .

The projection of the behaviour surface onto the control plane is a cusp-shaped curve, that marks the boundary where the behaviour becomes bimodal (bifurcation set).

The above discussion is only a rigid oversimplification of the behaviour mechanisms; this rigidity can be modified by introducing a controlled probability distribution $P = P(a, b, z)$. Each point $c = (a, b)$ in C determines a particular distribution $P(a, b)$ of the behaviour-space z (see note 3). For example if $c = (a, b)$ is the point (1) of Fig. 4, $P(a, b)$ is a unimodal distribution, with a unique maximum at point (1) on the behaviour-surface of Fig. 5; on the other hand if $c = (a, b)$ is the point (2) of Fig. 4, $P(a, b)$ is a bimodal distribution with two maxima at the points (2) on the behaviour surface of Fig. 5. $P(a, b, z)$ can be assumed smooth and generic (see note 4), that enables us to use catastrophe theory. Moreover the behaviour surface is smooth, since P is smooth.

Returning to the fish behaviour, a point on the control plane $c = (a, b)$ gives the

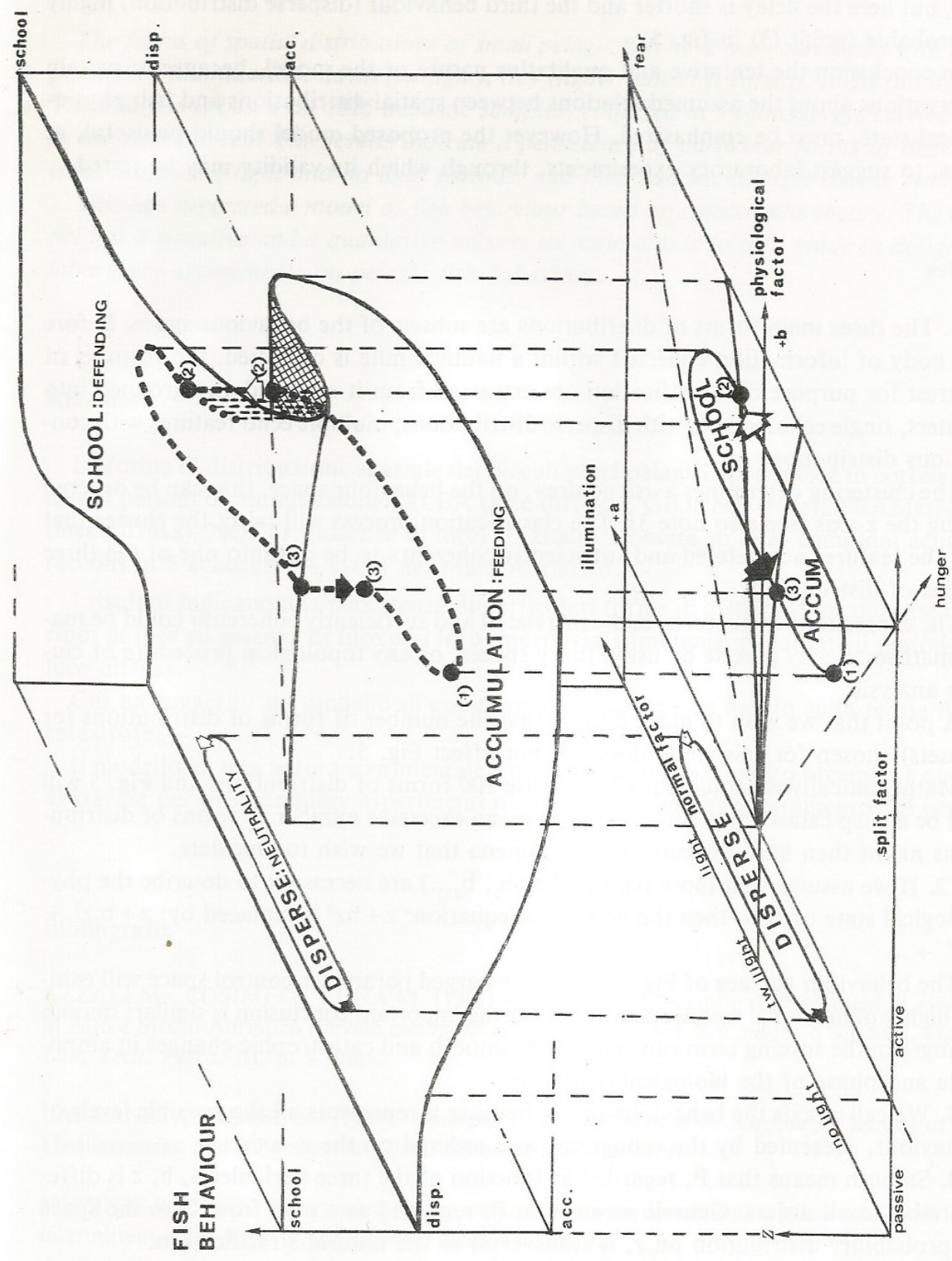


Fig. 5 - The surface of fish behaviours: the paths on the surface indicate the evolution of fish behaviours due to gradually changing of the illumination and physiological factor.

A similar change happens when the external stimuli decreases towards twilight (sunset), but here the delay is shorter and the third behaviour (disperse distribution) highly improbable (point (3) in fig. 5).

In conclusion the tentative and qualitative nature of the model, because of certain reservations about the assumed relations between spatial distributions and fish physiological state, must be emphasized. However the proposed model should be useful, at least, to suggest laboratory experiments, through which its validity may be tested.

Notes

1. The three main forms of distributions are subsets of the behaviour-space. Before the body of information collected within a nautical mile is classified, the features of interest for purpose of classification are extracted from it analysed and grouped into clusters, single echofeatures with disperse distributions, multiple echo features with continuous distributions etc...

The clustering determines a «structure», on the behaviour space, that can be ordered along the z-axis (see also note 3). The classification process will select the cluster that has the features «correlated and sufficiently coherent» to be put into one of the three forms of distributions.

The expressions «structure» and «correlated and sufficiently coherent» could be made mathematically precise by using fuzzy spaces, or any topological procedure of cluster analysis.

A point that we wish to make clear is that the number of forms of distributions (or subsets) chosen for this study does not not affect Fig. 5.

Mathematically we could equally well use 100 forms of distributions and Fig. 5 will still be a cusp catastrophe surface; however, an excessive number of forms of distributions might then have obscure the phenomena that we wish to elucidate.

2. If we assume that more parameters (b_1, b_2, \dots) are necessary to describe the physiological state of fish, then the non-linear equation: $z + bz^3$ is replaced by: $z + b_1z^3 + b_2z^5 + \dots$

The behaviour surface of Fig. 5 over the enlarged parameter control space will exhibit higher dimensional catastrophes, however the important conclusion is similar: smooth changes in the forcing term can cause both smooth and catastrophic changes in amplitude and phase of the biological oscillator.

3. We call z- axis the behaviour-space, because it represents all the possible levels of behaviour, presented by the echograms and ordered on the z- axis.

4. Smooth means that P, regarded as function of the three variables a, b, z is differentiable to all orders. Generic means that P, regarded as a map from C to the space of probability distribution on z, is transversal to the natural stratification.

Smooth generic Ps are open dense in the space of all smooth Ps, which are dense in the space of all continuous Ps.

Therefore any continuous P can be approximated arbitrarily close to a smooth generic P, justifying the use of smooth generic models.

Summary

The forms of spatial distributions of small pelagic fish have been correlated with four periods of illumination: dawn (twilight), day (light), sunset (twilight), night (no light). The analysis is based on 5825 acoustic samples, collected in 5 echosurveys carried out in the Adriatic sea. The results indicate a persistence of particular forms of distributions during the light and no light periods, and their sudden changes during twilight.

This has suggested a model of fish behaviour based on catastrophe theory. The model has a tentative and a qualitative nature; its main aim is to be a guide in designing laboratory experiments on pelagic fish behaviour.

Riassunto

Le forme di distribuzione spaziale dei piccoli pesci pelagici sono messe in correlazione a 4 periodi di illuminazione: ALBA (luce diffusa), GIORNO (luce), TRAMONTO (luce diffusa), NOTTE (assenza di luce). L'analisi è basata su 5825 campioni acustici raccolti in 5 echosurveys svolti nel Mare Adriatico.

I risultati indicano una persistenza di particolari forme di distribuzione durante i periodi di luce ed assenza di luce ed i loro improvvisi cambiamenti durante il periodo di luce diffusa.

Ciò ha suggerito un modello di comportamento del pesce basato sulla teoria della catastrofe.

Il modello ha una natura sperimentale e qualitativa; il suo compito precipuo è quello di traccia per programmare esperimenti di laboratorio sul comportamento del pesce.

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