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Spawning biomass and recruitment relationships as additional indices of ocean fishes abundance dynamics and their possible application in fishery management strategy development

V.A. Rikhter and P.A. Bukatin

Atlantic Research Institute of Marine Fisheries and Oceanography (AtlantNIRO)
5, Dm. Donskoy Str., 236022 Kaliningrad, Russia
Tel. 007 (4012) 925547, Fax 007 (4012) 219997, E-mail: rikhter@atlant.baltnet.ru

ABSTRACT

The relationship between spawning biomass and recruitment of 69 populations (stock units) of bottom and pelagic fishes of the Atlantic and Pacific Oceans and adjacent seas has been researched using a special approach. This research results confirmed that the pattern of above said relationship demonstrated by indices Ir and Il is a population feature rather than specific. On the basis of the data obtained the opinion has been expressed that these indices may satisfactorily reflect some peculiarities of fish stocks dynamics important for fishery management. At the same time, both relationship pattern and stock dynamics, including density dependence effect, are mainly determined by the environment conditions and species interactions in the ecosystems specific to each population. In respect to the practical applicaton of the obtained results, it seems that the above said indices values may be used as reference points (indicators) facilitating the search of an optimal approach in the ocean populations fishery management. In the view of the prospects of further researches in this direction, the ecosystem approach seems to be the most appropriate method in researching the problem indicated in the title of this paper.

INTRODUCTION

Since the time of the classic work by Ricker (1954), a lot of papers have been published, which seems to cover all aspects of the problem sufficiently comprehensively. However, the replacement of only one word in the latter title (“relationship” instead of “dependence”) has somewhat shifted the emphasis attracting more attention to the necessity of the complex interpretation of the factors, which determine the researched relationship pattern.
In the earlier published paper (Rikhter, 2008), some aspects relevant to the problem, unclear and disputable moments are considered and some ideas are proposed, which needs more convincing support on the basis of more abundant material.

In this paper the attempt is made to provide the more comprehensive insight into the role of the environment conditions and the spawning biomass value in formation of commercial fish year-classes abundance in the Atlantic and Pacific Oceans and adjacent seas during respective time periods; to assess as possible the extent of the above factors impact on the process, and finally to answer the question whether it is possible to judge from the considered relationship pattern about abundance dynamics and approaches to ocean species fishery management.

MATERIAL AND METHODS

Sixty nine populations (stock units) of commercial fishes of the Atlantic and Pacific Oceans and adjacent seas became the subject of study. The retrospective estimates of recruitment abundance and spawning biomass (SSB) necessary for analysis were obtained from NAFO research documents (the Northwestern Atlantic), reports of ICES working groups (the Northeastern Atlantic, the Arctic, the North and the Baltic Seas) and the database formed by the Canadian scientist Myers (R.A. Myers, Department of Biology, Dalhousie University, Halifax, Canada, http://fish.dal.ca/welcome.html). The list of species and populations and respective sources of information are presented below. The numbers and letters after species names are referred to NAFO and ICES statistical areas.

Populations (stock units)	**Sources**
Northwestern Atlantic Ocean (NAFO area)	**NAFO Documents**
Cod (*Gadus morhua*), 2J+3KL	Baird and Bishop, 1986
Cod, 3NO	Morgan et al., 2007
Greenland halibut (*Reinhardtius hippoglossoides*), 2+3	Healy and Mahe, 2005
American plaice (*Hippoglossoides platessoides*), 3LNO	Dwyer et al., 2005
Northeastern Atlantic Ocean, Arctic and adjacent seas (ICES area)	**ICES Reports**
Cod, I and II	ICES, 2006a
Haddock (*Melanogrammus aeglephfinus*), I and II	
Pollock (*Pollachius virens*), I and II	
Greenland halibut, I and II	
Cod, 347d	ICES, 2006b
Haddock, IV and IIIa	
Pollock, IV, VI and IIIa	
European plaice (*Pleuronectes platessa*), (North Sea)	
Cod, 25-32	ICES, 2006c
Norwegian spring-spawning herring (*Clupea harengus*)	ICES, 2007a
North Sea herring	ICES, 2007b
Atlantic herring, VIa (S) and VIIbc	
Western Baltic herring, IIIa and 22-24	
European pilchard (*Sardina pilchardus*), VIII and IXa	ICES, 2007c
Atrlantic mackerel (*Scomber scombrus*), (Northeastern Atlantic Ocean)	

Below the list of populations is presented, for which the respective information is available in Myers database:

Cod, NAFO 3M Cod, NAFO 3Ps Cod, NAFO 4RS Cod, NAFO 4VsW Cod, NAFO 4X Cod, NAFO 5Z Haddock, NAFO 4TVW Haddock, NAFO 5Ze Silver hake (*Merluccius bistraightis*), NAFO 4VWX Silver hake, NAFO 5Ze Silver hake, NAFO 5Zw+6 White hake (*Urophycis tenuis*), NAFO 4T Yellowtail flounder (*Limanda ferruginea*), NAFO 5Zw+6 Striped bass (*Morone saxathilis*), the USA eastern cost Red porgy (*Pagrus pagrus*), the USA eastern cost Dogfish (*Squalus acanthias*), NAFO 4-6 Lane snapper (*Lutjanus synagris*), Cuba area Bluefish (*Pomatomus saltatrix*), the USA eastern coast Weakfish (*Cynoscion regalis*), the USA eastern coast Cod, Iceland area, ICES Whiting (*Merlangus merlangus*), ICES IV and VIId Common dab (*Limanda limanda*), ICES (the Belt Sea) Norway pout (*Trisopterus esmarkii*), ICES (the Northern Sea) Capelin (*Mallotus villosus*), ICES (the Barents Sea) Capelin, ICES (Island area) Blue whiting (*Micromesistius poutassou*), ICES (the northern part) Atlantic herring, ICES VIa (the northern part) Cape hake (*Merluccius capensis*), the South Africa area Pacific hake (*Merluccius productus*), the western coast of Canada and USA	Walleye pollock (*Theragra chalcogramma*), the eastern Bering Sea Pacific cod (*Gadus macrocephalus*), the western coast of Canada Longhead dab (*Limanda proboscidea*), shelf of the western Kamchatka Sakhalin sole (*Limanda sakhalinensis*), shelf of the western Kamchatka Yellowfin sole (*Limanda aspera*), shelf of the western Kamchatka Alaska plaice (*Pleuronectes quadrituberculatus*), shelf of the western Kamchatka Flathead flounder (*Hippoglossoides elassodon*), shelf of the western Kamchatka Rock sole (*Lepidopsetta bilineata*), the western coast of Canada Greenland halibut, the eastern Bering Sea Pacific halibut (*Hippoglossus stenolepis*) Black Sea turbot (*Psetta maeotica*), Black Sea Pacific ocean perch (*Sebastes alutus*), the western coast of USA Pacific ocean perch, the Aleutian Islands area Chillpepper rockfish (*Sebastes goodei*), the western coast of USA Sable fish (*Anaplopoma fimbria*), the western coast of USA Atka mackerel (*Pleurogrammus monopterygius*), the eastern Bering Sea Pacific herring (*Clupea pallasii*), the eastern Bering Sea Chub mackerel (*Scomber japonicus*), Japan area Peruvian anchovy (*Engraulis ringens*) Southern blue whiting (*Micromesistius australis*), New Zealand area Cape horse mackerel (*Trachurus capensis*), the South Africa area

The above presented list is sufficiently extensive to assume fulfilled the conditions required to continue researches in the chosen direction.

A special approach (Rikhter, 2005), slightly modified later, was applied in analysis of the spawning biomass-recruitment relationship. The ratio between the mean SSB values favorable to production of abundant year-classes and high and low SSB values were denoted as Ir and Il (Rikhter, 2008). The relationship analysis was carried out to estimate the degree of relationship between recruits abundance and SSB value, starting from SSB level corresponding to the point of the maximum recruitment and below up to the lowest size observed. For the purpose to provide comparability Ir and Il in the considered populations, the deviations to the higher and lower values from the long-term mean recruitment abundance and biomass exceeding 20% were assumed as a criterion of strong year-classes and high and low SSB areas.

Besides, in the work the index of density dependence, such as the ratio between SSB corresponding to the maximum recruitment abundance (SSBrec) and SSB highest value (SSBmax) was tested.

RESULTS

Before consideration of the above mentioned indices for all listed populations, it is useful to recall some results of the previous study (Rikhter, 2008). In spite of small number of species sampled for analysis, estimated indices Ir and Il may apparently be used as the basis for populations grouping by the degree of environment factors and SSB value impact on the pattern of the relationship considered. For this purpose the following classification of indices values is proposed:

For Ir criterion

1. 0.81 and above: The effect of compensation factors (CF) is weak or actually absent. The recruitment dependence on SSB is mostly high and straight actually over the whole range.
2. 0.61-0.80: The effect of CF is from weak to moderate. The degree of the considered relationship (inverse) effect in the upper part of the biomass range varies from weak to moderate. In the lower part the degree of the considered relationship (straight) effect may be different.
3. 0.60 and below: The effect of CF is strong. The recruitment dependence on SSB is inverse and high in the upper part of the range. In the lower part the degree of the considered relationship (straight) effect may be different.

For Il criterion

1. 3.0 and above: The recruitment dependence on SSB is significant and straight. The environment conditions during a certain period remain relatively stable – mostly average for year-classes abundance formation.

2. 2.1-2.9: The environment conditions play an important role in the recruitment variability reducing its dependence on SSB value.

3. 2.0 and below: The environment conditions play the major role in formation of year-classes abundance and its fluctuations. The recruitment dependence on SSB is very weak or actually absent.

Then grouping of the populations was made by above mentioned criteria according to the proposed categories (Tables 1 and 2).

The presented data indicate that the same groups include populations of different species inhabiting areas located at considerable distance from each other, sometimes in different oceans. At the same time, populations of the same species often occur in different groups.

As expected, grouping the populations on the basis of Il criterion revealed similar peculiarities as the data from Table 1. Therefore, the preliminary conclusions made earlier on the basis of analysis of rather restricted material (Rikhter, 2008) have been confirmed.

Ir and Il values appeared rather high in some populations (0.81 and above, 3.00 and above, respectively) to assume availability of significant dependence of recruitment abundance on SSB value (Rikhter, 2005). For the species with above said indices values the relationship coefficients (Table 3) were estimated starting from the biomass level corresponding to the maximum recruitment and up to the lowest observed value. Eighteen stock units were selected for the relationship analysis.

The data presented evidence that, except for Pacific rockfish, the relationship varied from significant to strong, while the statistical confidence exceeded 99%. In 6 populations the coefficient of determination (r^2) constituted 0.50 and more indicating considerable effect of SSB value in year-classes abundance variability. The stock-recruitment relationship of populations listed in Table 3 is shown in Fig.1, where arrows indicate biomass levels corresponding to the maximum abundance of recruits during the observation period, and the horizontal dotted line represents the boundary above which the area of strong (according to the criterion adopted) year-classes is located.

Evidently, abundant recruitment was formed in most cases at average and high SSB levels. The pattern of the considered relationship in populations with the lowest Ir and Il is shown in Fig. 2, where the opposite picture is observed.

Strong year-classes are observed there mostly in the area of low and average SSB values. Apparently, in this case we could not speak about any more or less straight density dependence. At the same time, the compensatory factors role in some populations may be rather considerable.

Now we consider the ratio SSBrec/SSBmax in respect to its application as an additional index. The data presented in Table 4 indicate that mostly high values are typical to cod and haddock populations of the Northwestern Atlantic and Pacific species of Sebastes, while the lowest values were observed in flatfish of the western Kamchatka shelf. To provide the picture of probable relationship between the considered index and Ir and Il indices, SSBrec/SSBmax values were arranged in three groups (high – 0.71-1.00, average – 0.70-0.51, low – 0.50 and below) and the mean values were estimated for each group and compared to the mean estimates of the above mentioned indices (Table 5).

Apparently, the data presented evidence the existence of a certain relationship between the considered values, the statistical reliability of which is indicated by the relationship coefficients: SSBrec/SSBmax and Ir – r=0,59, p=<0,001; SSBrec/SSBmax and Il – r=0,22, p=0,065. While in the first case the relationship is considerable with high statistical significance, in the second case it is weak and statistically unreliable.

To verify the assumption of considerable role of compensatory factors in some populations, several populations with low Ir were selected and coefficients of relationship between SSB were estimated (starting from average and up to the high values) and respective recruitment (Table 6).

As could be seen, the high and statistically significant dependence between recruitment and spawning biomass in the upper part of the range is observed in Greenland halibut and Chub mackerel only.

According to the results of the previous research, the pattern of SSB-recruitment relationship is determined mostly by the environment conditions (Rikhter, 2008). On this basis the assumption was made that the more observation period resulted in the higher probability of that the above said relationship would not remain stable during the entire period considered. To verify this assumption, the populations were selected with data covering the period more than 40 years. Further these periods were subdivided into shorter time intervals approximately corresponding to a certain state of SSB dynamics (Fig. 3).

Then Ir and Il were estimated for each interval indicated with vertical dotted lines (Table 7). Judging from the results obtained, the above made assumption is valid. As could be seen, indices estimated for the shorter time intervals differ from the estimates obtained for the whole observation period. The most considerable differences occurred in cod and haddock populations from NAFO area (3NO and 5Ze respectively) and Norwegian spring-spawning herring.

DISCUSSION

At first, let consider the data presented in Tables 1 and 2. The results of previous researches of the indicated subject (Rikhter, 2005, 2007, 2008) allow to interpret the new information as follows. In Table 1 all populations are grouped on the basis of the compensatory factors effect, starting from a certain (sufficiently high) SSB level and up to the maximum observed value. High (close to 1) Ir values (group 1) evidence that the compensatory factors effect is weak or actually absent and the probability of rather considerable dependence of recruitment on SSB value with the range from the maximum and minimum. At the same time, according to Nikolskiy (1974) the considered relationship is straight and indicates that regulatory mechanisms are normally working. It should be noted also that the straight relationship is clearly pronounced only during the periods of relative stability of environment factors affecting year-classes abundance formation (Rikhter, 2008), and is hardy relevant to the above said regulatory mechanisms. Zasosov (1976) noted the availability of appropriate relationship between abundances of ancestors and their offspring, which could be replaced by fluctuations and this does not contradict to the above considerations. The compensatory factors role in year-classes abundance formation in populations of groups 2 and 3 are assessed as moderate and considerable, respectively.

In general, Ir index provides a certain idea about the pattern of recruitment and SSB dynamics in the area of SSB high values.

Grouping the populations by Il criterion (Table 2) indicates that group 1, where the environment conditions are assumed relatively stable (average or unfavorable for young fish survival) during the observation period, is the less numerous, and when the effect of straight relationship should be pronounced. At the same time, in addition to unfavorable environment factors, sufficiently intensive fishery is likely to become a kind of trigger of the above said situation. As a result, sometimes the stock abundance decreased to the critically low level (collapse). The problem of such stocks recovery will not be discussed here. It is possible only to note, that this process required the environment conditions especially favorable to fish survival at the early life stages (Rikhter, 2007, Rikhter, 2008). As the history of researches shows, such events have appeared very seldom, and stocks recovery took a long period, sometimes several decades.

Judging from Il values, fluctuations of population abundance in group 3 are mostly determined by respective biotic and abiotic factors (Rikhter, 2005). Therefore, the role of fishery in depression of the considered stocks seems to be relatively insignificant. In these populations strong year-classes appeared not rarely even at the lowest SSB levels, which may be explained only by sharp inter-annual fluctuations of this fish group living conditions. Fish included into group 2 occupy the intermediate position according to the pattern of the relationship considered.

In general, Il index provides a certain idea about the dynamics of recruitment and SSB in the area of the latter parameter reduction from high to minimum values. The data presented in both tables confirm the preliminary conclusion made earlier (Rikhter, 2008), that the pattern of stock-recruitment relationship is a population characteristic, not a specific one, and is mostly determined by the impact of respective environment conditions (biotic and abiotic factors).

Considering the problem of the density dependence degree, it is useful to cite Dementieva (1976): "… the difficulties arise in determining the degree of interdependency between abundance of recruitment and producers. The word "degree" should be emphasized, since recommendations on fisheries management, stocks assessment and prediction improvement depend on evaluation of the degree or closeness of this relationship". It seems that Ir and Il indices, which allow to evaluate the degree of SSB and environment factors impact on recruitment value, are the development of the idea expressed in the above citation.

The above considerations evidence that the pattern of considered factors dynamics is the prime cause determining the degree of dependence between producers and offspring. The data presented in Table 3 indicate that the density dependence role appeared very important and sometimes even basic in year-classes abundance formation in 17 out of 69 populations. However, in most populations this role may be evaluated as a secondary one, which agrees with Dementieva's opinion (1976).

Now let consider Figs. 1 and 2. The information contained in them allows to conclude that the indices used in this work satisfactorily reflects the pattern of recruitment and SSB dynamics of the populations researched. As a rule, high values of Ir and Il are associated with the total absence of strong year-classes at low SSB and vice versa. Besides, the points scatter in Fig. 2 provides the basis for assumption of considerable impact of compensatory factors (predation, cannibalism, food deficiency, diseases, etc.) on year-classes abundance, which, in turn, assumes probable in some cases approximation of the stock-recruitment relationship by Ricker's equation. In general, it seems that the abundance dynamics of populations with low Ir and Il is almost totally determined by the impact of biotic and abiotic environment factors.

Judging from the data of Tables 4 and 5, the ratio SSBrec/SSBmax deserves attention as an index supplementing Ir. As regards the area of low biomasses, the sharp fluctuations of SSBrec appear here as a result of environment factors impact on recruitment value. Therefore, application of this ratio as an index characterizing the stock-recruitment relationship could be hardly recommended.

Concerning the role of compensatory factors in the year-classes abundance formation, it should be noted that the unquestionable confirmation of their notable impact was obtained for population of Greenland halibut in the Northwestern Atlantic Ocean (NAFO 2+3) only. It seems that the idea of the inverse relationship between this stock and SSB value starting from a certain level of biomass and above, was expressed for the first time in 2005 (Rikhter, 2005). Its validity was confirmed with the results of the recent researches by Canadian scientists (Morgan et al., 2008). Most probably, the above mentioned relationship plays a serious role in dynamics of the chub mackerel stock (Table 6). It is hardly possible to say anything definite about the degree of compensatory factors impact in other populations, where the available data at best allow to speak about availability of the inverse relationship at a qualitative level only. However, even on the basis of two statistically reliable estimates only, it is possible to express a view on considerable role of compensatory factors in recruitment formation in some stocks. This condition is directly related to development of the optimal strategy of fisheries management. Unfortunately no proper attention has been paid to researching this aspect. At all levels, including the international one, uncontrolled increase of abundance and biomass of any commercial stock unit has been until now interpreted a'priori only as a factor favorable to the long-term maintenance of fish resources in good condition. This one-sided approach may appear incorrect in some cases.

Certainly, the species biological parameters also affect the stock dynamics. Thus, in species with long life cycle and late maturation the processes of abundance reduction and recovery proceed considerably slower than in species with the opposite characteristics. In the latter species the abundance fluctuations will be undoubtedly significantly stronger and more frequent even at relatively similar conditions of year-classes abundance formation. However, if the species with a short life cycle lives in relatively stable conditions during a certain period, while the environment of the long-living species during the same period has changed considerably, the abundance fluctuations of the second species during the considered period will be more pronounced as compared to the first species.

It seems that in general the discussion of the obtained results allows to assume that SSB and recruitment dynamics, which becomes apparent in peculiarities of these parameters relationship, is basically determined by the environment conditions specific for each population, and as such is a population feature rather than specific. Naturally, the dynamics implies both processes of reduction and recovery of population abundance, while Halliday and Fanning (2006) noted the key role of environment variability only in connection with fish stocks collapse.

It remains to comment briefly the information shown in Table 7 and Fig. 3. Evidently, dealing with sufficiently long series of observations (above 40 years in our case), it is necessary to ascertain if the shorter intervals with different trends of biomass dynamics in individual populations are available within the time period considered. If these differences are revealed, the further analysis of the stock-recruitment relationship should be fulfilled for the each period separately. It is hardly possible to accept the opinion by Cushing (1979) that plotting the Ricker's curve requires data on recruitment abundance for very many years. As our data indicate, the pattern of this relationship may vary several times for these "very many years".

In respect to the ocean stocks fishery management, the group of populations with high Ir and Il deserves special attention. The strong relationship of these fishes recruitment and SSB dictates the necessity to maintain the spawning biomass at sufficiently high level (probably, above the mean level) and to take urgent measures aimed at the fishery intensity reduction (up to the total cessation) if the indications of SSB decline appear. Otherwise, the probability of the stock collapse is very high and further recovery of the stock will be impossible even at environment conditions relatively favorable (average) to year-classes abundance formation (Rikhter, 2007, 2008). In such cases even the total fishery cessation will not save the situation, as has been demonstrated by the history of cod fishery and researches in the Northwestern Atlantic Ocean. Several decades may pass before the environment conditions become so favorable, that at least one sufficiently abundant year-class will appear and the recovery process will start. However, the longer is the depression period, the higher is probability, that unfavorable changes for collapsed population will occur in the ecosystem, e.g. partial replacement of one species by another. In this case, the chance of getting a way off the above said situation will be minimal (Rikhter, 2007).

In the framework of the ecosystem approach to the fishery management, which currently becomes the main one in the international fisheries organizations activities, this risk should be taken into consideration. Besides, the changes may affect also the pattern of the stock-recruitment relationship (abundance dynamics) of individual or several populations, and as a result, probably the necessity appears to transfer these populations into other groups with new Ir and Il values. Accordingly, the approach to these populations fishery management will be different. The probability of events development according to this scenario is not very high, but it exists. On the other hand, low indices values evidence a relatively weak impact of fishery on the stock state, and as regards Ir, low values of this index evidence also considerable role of compensatory factors in year-classes formation. In this case estimation of the biomass limiting reference point in its low values area, denoted earlier as Blim (low) (Rikhter, 2005), is hardly required. If the trend to the biomass decline appears, it will be enough to reduce the fishing effort, maintaining the fishing mortality rate at the level optimal to the new population abundance levels (Rikhter, 1981). If the biomass of the population with respective Ir value has attained the level when the compensatory factors begin to act at their full potential towards off-spring abundance reduction, it is necessary to increase fishery intensity for the purpose to bring back the producers biomass to the optimal level (Barkova et al.; Rikhter, 2005, 2007). As regards the populations with intermediate indices values (mostly group 2, Table 1 and 2), they need a more flexible approach using, as necessary, the management strategy elements mentioned above.

The authors would like to warn against attempts to use for the practical purposes the above recommendations for the populations with time series (data on the stock and recruitment) finished in the 20th century. The results of researches (Table 7, Fig. 3) evidence probable considerable long-term changes in the pattern of commercial stocks dynamics, and consequently in SSB-recruitment relationship. Therefore, it is necessary at first to obtain the information covering the recent time period.

In conclusion it seems necessary to speak briefly about the prospects of further researches of ocean fish population dynamics in the interpretation proposed by us (Rikhter, 2005, 2007, 2008, this paper). In this respect, the authors would like to cite some statements from the last chapter of the classic work by Nikolskiy (1974): "In the general form, the prospective task of the biological fishery science seems to me as revelation of biological regularities and development of methods for managing dynamics of commercial species populations abundance and biomass for the purpose of their productivity improvement" and "… a special attention should be paid to research of the interrelations, which appear between different populations in the ecosystem, studying the "elasticity", i.e. the degree of ecosystem sustainability and variability in different water basins. The research of this range of problems should be directed to the development of water ecosystems management methods on the basis of regularities existing in the nature". From the above considerations it appears that the final purpose of the biological fishery science, in the authors' opinion, is to attain the level providing the efficient management of not only commercial species abundance and biomass but also the water ecosystems. Accepting in general the formulation of tasks in the field of fish dynamics research, it seems that the above goal is hardly achievable in the nearest future with reference to the sea and ocean areas. Certainly, identification of biological regularities will provide the necessary scientific basis for the optimal fisheries management in the indicated areas only. However, even solution of this problem is not simple and extremely important matter.

It is useful to recall, that G.V.Nikolskiy had actually developed and formulated the basic principles of the ecosystem approach to research of fish stocks dynamics and fishery management already in 1970s. Since then many years had passed. The new century has begun before the above mentioned approach has been implemented into the common practice by scientists from different countries and international fisheries organizations as the basic method used in solution of strategic tasks for living resources conservation and fishery management.

As regards the research direction developed in this work, it hardly may be considered finished. The idea of considerable and even decisive impact of environment factors and species interactions in oceanic ecosystems on the stock-recruitment relationship pattern and dynamics of fish populations abundance, confirmed to a certain degree by the results obtained, needs comprehensive and purposeful research of the influence exerted by the above said factors and interactions on the living resources dynamics. Evidently, it is again the question of the ecosystem approach to this problem research, the implementation of which requires the joint work of specialists from different fields.

CONCLUSIONS

The results of this research confirmed that the stock-recruitment relationship pattern is a population characteristic (not species). At the same time, indices Ir and Il (and to a certain degree the ratio SSBrec/SSBmax) provide satisfactory picture of some features of the spawning biomass and recruitment dynamics, which are very important for fishery management. The latter features apparent in characteristics of the indicated ratio (Ir and Il values), are mainly determined by the environment conditions (abiotic and biotic factors) specific for each population. Therefore, it is apparently possible also to speak about population specific of fish stocks dynamics. It is likely, that the above said conditions determine to a considerable degree also the role of density dependence in the year-classes abundance formation.

In general, on the basis of the data obtained it is possible to assume that Ir and Il values may be used as reference points (indicators) facilitating elaboration of the optimal approach to ocean fishery management. At the same time the occurrence of different populations and species in one group, stipulated by similar impact of environment on their abundance dynamics, assumes approximately similar approach to the management strategy, which in any case should take in consideration the impact of respective ecosystem elements on commercial stocks dynamics.

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Table 1. Populations (stock units), grouped by Ir criterion

Populations (stock units)	Ir	Il
	0.81 иand more	
Cod, NAFO 2J+3KL	1.03	4.68
Cod, NAFO 3NO	1.01	4.11
Cod, NAFO 3M	0.91	3.59
Cod, NAFO 4VsW	0.82	1.95
Haddock, NAFO 4TVW	0.86	3.93
Haddock, NAFO 5Ze	0.86	4.00
Silver hake, NAFO 5Ze	1.09	7.67
Silver hake, NAFO 5Zw+6	0.91	5.89
Dogfish, NAFO 4-6	0.85	2.52
Red porgy, the USA eastern coast	0.89	2.48
Striped bass, the USA eastern coast	0.92	3.28
Bluefish, the USA eastern coast	0.94	1.85
Walleye pollock, the eastern Bering Sea	0.88	2.24
Black Sea turbot, Black Sea	0.86	2.38
Pacific ocean perch, the USA western coast	0.88	2.50
Chillpepper rockfish, the USA western coast	0.82	1.47
Greenland halibut, the eastern Bering Sea	1.01	2.57
Greenland halibut, ICES, I and II	0.84	3.20
	0.61-0.80	
Cod, NAFO 4RS	0.69	1.77
Cod, NAFO 3Ps	0.73	1.74
Cod, NAFO 4X	0.75	1.32
Cod, NAFO 5Z	0.75	2.43
Silver hake, NAFO 4VWX	0.80	1.35
Greenland halibut, NAFO 2J+3KLMN	0.63	1.97
American plaice, NAFO 3LNO	0.77	3.53
Cod, ICES 347d	0.77	2.40
Cod, ICES, Island area	0.67	2.76
Cod, the Baltic Sea, ICES 25-32	0.77	2.61
Haddock, ICES I and II	0.69	1.74
Whiting, ICES IV and VIId	0.69	1.87
Common dab, ICES, the Belt Sea	0.78	1.42
Norwegian spring-spawning herring	0.68	5.70
Atlantic mackerel, ICES, Northeastern Atlantic	0.67	1.40
Capelin, ICES, Island area	0.79	2.14
Atlantic herring, ICES VIa (south) and VIIbc	0.66	2.19
Western Baltic herring, ICES IIIa, 22-24	0.68	1.45
European pilchard, ICES VIIIc-Ixa	0.71	1.21
European plaice (*Pleuronectes platessa*), ICES, the North Sea	0.77	1.54
Cape horse mackerel, the South Africa area	0.65	1.41
Pacific hake, the western coast of USA and Canada	0.70	1.47
Sakhalin sole, shelf of the western Kamchatka	0.63	1.88
Pacific halibut, the northern part of the ocean	0.69	1.46
Norway pout, ICES, the North Sea	0.71	1.78
Weakfish, the USA eastern coast	0.65	1.91
Lane snapper, Cuba area	0.78	1.72
Sable fish, the USA western coast	0.77	1.49
Southern blue whiting, New Zealand area	0.68	2.13
Peruvian anchovy, Peru area	0.80	2.53
	0.60 and less	
White hake, NAFO 4T	0.50	1.03
Yellowtail flounder, NAFO 5Zw+6	0.44	2.16
Cod, ICES I and II	0.55	2.52
Haddock, ICES IV and IIIa	0.53	2.30

Pollock, ICES I and II	0.56	2.02
Pollock, ICES IV, VI and IIIa	0.56	1.77
Blue whiting, ICES (north)	0.46	1.14
Atlantic herring, ICES, the North Sea southwards of 62°N	0.58	2.98
Atlantic herring, ICES VIa (north)	0.41	1.78
Cape hake, the South Africa area	0.60	1.95
Pacific cod, western coast of Canada	0.58	1.39
Yellowfin sole, shelf of the western Kamchatka	0.29	2.04
Rock sole, shelf of the western Canada	0.47	1.41
Longhead dab, shelf of the western Kamchatka	0.36	1.25
Alaska plaice, shelf of the western Kamchatka	0.46	2.30
Flathead flounder, shelf of the western Kamchatka	0.58	1.87
Pacific ocean perch, the Aleutian Islands	0.38	1.56
Atka mackerel, the eastern Bering Sea	0.60	1.96
Pacific herring, the eastern Bering Sea	0.32	1.87
Chub mackerel, Japan area	0.23	1.49
Capelin, ICES (Barents Sea)	0.54	8.27

Table 2. Populations (stock units), grouped by Il criterion

Populations (stock units)	Il	Ir
	3.00 and more	
Cod, NAFO 2J+3KL	4.68	1.03
Cod, NAFO 3NO	4.11	1.01
Cod, NAFO 3M	3.59	0.91
Haddock, NAFO 4TVW	3.93	0.86
Haddock, NAFO 5Ze	4.00	0.86
Silver hake, NAFO 5Ze	7.67	1.09
Silver hake, NAFO 5Zw+6	5.89	0.91
American plaice, NAFO 3LNO	3.53	0.77
Striped bass, the USA eastern coast	3.28	0.92
Greenland halibut, ICES I and II	3.20	0.84
Capelin, ICES, Barents Sea	8.27	0.54
Norwegian spring-spawning herring, ICES	5.70	0.68
	2.00-2.99	
Cod, NAFO 5Z	2.43	0.75
Yellowtail flounder, NAFO 5Zw+6	2.16	0.44
Dogfish, NAFO 3-6	2.52	0.85
Red porgy, the USA eastern coast	2.48	0.89
Cod, ICES I and II	2.52	0.55
Cod, ICES, Island area	2.76	0.67
Cod, ICES 347d	2.40	0.70
Cod, ICES, Skagerrak /Eastern Channel	2.40	0.70
Cod, ICES IIIa, 25-32	2.61	0.77
Haddock, ICES IV and IIIa	2.30	0.53
Pollock, ICES I and II	2.02	0.56
Atlantic herring, ICES Via (south) and VIIbc	2.19	0.66
Atlantic herring, ICES, the North Sea southwards of 62°N	2.98	0.58
Capelin, ICES, Island area	2.14	0.79
Walleye pollock, the eastern Bering Sea	2.24	0.88
Yellowfin sole, shelf of the western Kamchatka	2.04	0.29
Alaska plaice, shelf of the western Kamchatka	2.30	0.46
Greenland halibut, the eastern Bering Sea	2.57	1.01
Black Sea turbot, Black Sea	2.38	0.86
Pacific ocean perch, the USA western coast	2.50	0.88
Peruvian anchovy, Peru area	2.53	0.80
Southern blue whiting, New Zealand area	2.13	0.68
	2.00 и меньше	
Cod, NAFO 3Ps	1.74	0.73
Cod, NAFO 4RS	1.77	0.69
Cod, NAFO 4VsW	1.95	0.82
Cod, NAFO 4X	1.32	0.75
Silver hake, NAFO 4VWX	1.35	0.80
White hake, NAFO 4T	1.03	0.50
Greenland halibut, NAFO 2J+3KLMN	1.97	0.63
Bluefish, the USA eastern coast	1.85	0.94
Weakfish, the USA eastern coast	1.91	0.65
Lane snapper, Cuba area	1.72	0.78
Pollock, ICES IV, VI, IIIa	1.77	0.56
Whiting, ICES IV and VId	1.87	0.69
Haddock, ICES I and II	1.74	0.69
Common dab, ICES, the Belt Sea	1.42	0.78
European plaice, ICES, the North Sea	1.54	0.77
Atlantic herring, ICES VIa (north)	1.78	0.41
Atlantic herring, ICES IIIa, 22-24	1.45	0.68
European pilchard, ICES VIIIc-IXa	1.21	0.71

Atlantic mackerel, ICES, the Northeastern Atlantic Ocean	1.40	0.67
Blue whiting, ICES (northern part)	1.14	0.46
Norway pout, ICES, the North Sea		
Cape horse mackerel, the South Africa area	1.41	0.65
Cape hake, the South Africa area	1.95	0.60
Pacific cod, the western coast of Canada	1.39	0.58
Pacific hake, the western coast of USA and Canada	1.47	0.70
Chillpepper rockfish, the USA western coast	1.47	0.82
Pacific ocean perch, the Aleutian Islands	1.56	0.38
Pacific halibut, северная часть океана	1.46	0.69
Rock sole, shelf of the western coast of Canada	1.41	0.47
Longhead dab, shelf of the western Kamchatka	1.25	0.36
Flathead flounder, shelf of the western Kamchatka	1.87	0.58
Sable fish, the USA western coast	1.49	0.77
Atka mackerel, the eastern Bering Sea	1.96	0.60
Sakhalin sole, shelf of the western Kamchatka	1.88	0.63
Pacific herring, the eastern Bering Sea	1.87	0.32
Chub mackerel, Japan area	1.49	0.23

Table 3. Assessment of relationship between spawning biomass and recruitment in populations with Ir and Il values assuming sufficiently evident effect of density dependence

Populations (stock units)	r	r^2	*p*
Cod, NAFO 2J+3KL	0.67	0.45	0.002
Cod, NAFO 3NO	0.73	0.53	<0.001
Cod, NAFO 3M	0.63	0.39	0.002
Haddock, NAFO 4TVW	0.63	0.39	<0.001
Haddock, NAFO 5Ze	0.53	0.28	<0.001
Silver hake, NAFO 5Ze	0.71	0.50	<0.001
Silver hake, NAFO 5Zw+6	0.55	0.31	0.002
American plaice, NAFO 3LNO	0.71	0.50	<0.001
Dogfish, NAFO 4-6	0.58	0.33	0.012

Table 4. Relationship between the spawning biomass corresponding the maximum recruitment abundance (SSBrec) and its highest value (SSBmax), and indices Ir and Il

Populations (stock units)	SSBrec/SSBmax	Ir	Il
Cod, NAFO 2J+3KL	0.93	1.03	4.68
Cod, NAFO 3NO	0.74	1.01	4.11
Cod, NAFO 3M	0.66	0.91	3.59
Cod, NAFO 3Ps	0.72	0.73	1.74
Cod, NAFO 4RS	0.62	0.69	1.77
Cod NAFO 4VsW	0.82	0.82	1.95
Cod, NAFO, 4X	0.73	0.75	1.32
Cod, НАФО 5Z	1.00	0.75	2.43
Cod, ICES I and II	0.19	0.55	2.52
Cod, ICES (Island area)	0.23	0.67	2.76
Cod, ICES 347d	0.59	0.77	2.40
Cod, ICES 25-32	0.51	0.77	2.61
Haddock, NAFO 5Ze	0.78	0.86	4.00
Haddock, NAFO 4TVW	0.77	0.86	3.93
Haddock, ICES I and II	0.55	0.69	1.74
Haddock, ICES IV, IIIa	0.28	0.53	2.30
Whiting, ICES IV, VIId	0.57	0.69	1.87
Silver hake, NAFO 4VWX	0.48	0.80	1.35
Silver hake, NAFO 5Ze	0.83	1.09	7.67
Silver hake, NAFO 5Zw+6	0.50	0.91	5.89
Pollock, ICES I and II	0.55	0.56	2.02
Pollock, ICES IV, VI, IIIa	0.96	0.56	1.77
White hake, NAFO 4T	0.37	0.50	1.03
Blue whiting, ICES (northern part)	0.36	0.46	1.14
Southern blue whiting, New Zealand area	0.36	0.68	2.13
Cape hake, the South Africa area	0.64	0.60	1.95
Walleye pollock, the eastern Barents Sea	0.45	0.88	2.24
Pacific cod, the western Canada	0.53	0.58	1.39
Pacific hake, the western Canada and USA	0.45	0.70	1.47
Yellowtail flounder, NAFO 5Zw+6	0.41	0.44	2.16
American plaice, NAFO 3LNO	0.74	0.77	3.53
European plaice, ICES (the North Sea)	0.62	0.77	1.54
Common dab, ICES (the Belt Sea)	0.72	0.78	1.42
Black Sea turbot, the Black Sea	0.67	0.86	2.38
Sakhalin sole, shelf of the western Kamchatka	0.41	0.63	1.88
Alaska plaice, shelf of the western Kamchatka	0.07	0.46	2.30
Yellowfin sole, shelf of the western Kamchatka	0.28	0.29	2.04
Rock sole, shelf of the western Canada	0.31	0.47	1.41
Longhead dab, shelf of the western Kamchatka	0.32	0.36	1.25
Flathead flounder, shelf of the western Kamchatka	0.53	0.58	1.87
Greenland halibut, NAFO 2+3	0.48	0.63	1.97
Greenland halibut, the eastern Bering Sea	0.82	1.01	2.57
Pacific halibut	0.56	0.69	1.46
Pacific ocean perch, the Aleutian Islands	0.99	0.38	1.56
Pacific ocean perch, the western coast of USA	0.95	0.88	2.50
Chillpepper rockfish, the western coast of USA	0.78	0.92	3.28
Striped bass, the eastern coast of USA	0.78	0.92	3.28
Red porgy, the eastern coast of USA	0.71	0.89	2.48
Weakfish, the eastern coast of USA	0.31	0.65	1.91
Lane snapper, Cuba area	0.63	0.78	1.72
Bluefish, the eastern coast of USA	0.91	0.94	1.85
Norwegian spring-spawning herring, ICES	0.47	0.68	5.70
Atlantic herring, ICES VIa, VIIbc	0.37	0.66	2.19
Atlantic herring, ICES VIa (north)	0.38	0.41	1.78

Atlantic herring, ICES (North Sea к югу от 62 с.ш.)	1.00	0.58	2.98
Western Baltic herring, ICES IIIa, 22-24	0.39	0.68	1.45
Pacific herring, the eastern Barents Sea	0.11	0.32	1.87
Cape horse mackerel, the South Africa area	0.41	0.65	1.41
European pilchard, ICES VIII, Ixa	0.63	0.71	1.21
Capelin ICES (Barents Sea)	0.60	0.54	8.27
Capelin, ICES (Island)	0.43	0.79	2.14
Atlantic mackerel, ICES (the northeastern Atlantic Ocean)	0.51	0.67	1.40
Chub mackerel (Japan)	0.18	0.23	1.49
Norway pout, ICES (the North Sea)	0.74	0.71	1.78
Peruvian anchovy (Peru area)	0.52	0.80	2.53
Sable fish, western USA	0.86	0.77	1.49
Atka mackerel, the eastern Barents Sea	0.70	0.60	1.96
Dogfish, NAFO 4-6	0.77	0.85	2.52

Table 5. The mean of three indices of the stock-recruitment relationship by indices groups

Groups	SSBrec/SSBmax	Ir	Il
0.71-1.00	0.83	0.82	2.81
0.70-0.51	0.59	0.69	2.23
<0.51	0.35	0.56	2.04

Table 6. Estimate of relationship degree between spawning biomass in the upper range part and recruitment of populations with low Ir

Populations (stock units)	r	r^2	*p*	Ir
Greenland halibut, NAFO 2+3	-0.92	0.84	<0.001	0.63
White hake, NAFO 4T	-0.42	0.18	0.354	0.50
Blue whiting, ICES	-050	0.25	0.138	0.46
Cape hake, the South Africa area	-0.24	0.06	0.454	0.60
Atka mackerel, the eastern Barents Sea	-0.50	0.25	0.114	0.60
Flathead flounder, shelf of the western Kamchatka	-0.37	0.14	0.290	0.58
Pacific herring, the eastern Barents Sea	-0.06	<0.01	0.860	0.32
Chub mackerel, Japan area	-0.78	0.61	0.022	0.23

Table 7. Stock-recruitment relationship trend and dynamics of spawning biomass of some fish populations by time periods

Populations(stock units)	Period, years	Ir	Il	Dynamics of spawning biomass
Cod, NAFO 3NO	1959-1974	0.71	1.40	Most SSB values are in the range from average to high
	1975-1988	0.65	2.46	Sharp reduction followed by increase to the high level
	1989-2005	0.46	3.12	Sharp reduction followed by stabilization at a very low level
	1959-2005	1.04	7.08	
Cod, ICES I и II	1946-1965	0.67	1.97	Reduction from high to low
	1966-1987	0.72	1.66	Alternation of low and high SSB
	1988-2005	0.62	1.63	Alternation with some increase at the end of the period
	1946-2005	0.55	2.52	
Cod, ICES 347d	1963-1982	0.79	1.27	Most SSB values are in the range from average to high
	1983-2004	0.86	2.50	Reduction followed by stabilization at a very low level
	1963-2004	0.77	2.40	
Cod of Iceland, ICES	1928-1959	0.68	1.30	Within the range from average to high
	1960-1991	0.71	1.96	High values at the beginning of the period with subsequent reduction and stabilization at a low level
	1928-1991	0.67	2.76	
Haddock, NAFO 5Ze	1931-1967	0.74	1.47	Most SSB values are in the range from average to high
	1968-1982	0.70	1.92	Fluctuation from low to average values
	1983-1998	0.57	1.36	Low values with slight increase at the period end
	1931-1998	0.86	4.00	
Pacific halibut	1935-1962	0.61	1.06	Increase and stabilization at a high level
	1963-1981	0.60	1.12	Reduction and stabilization at a low level
	1935-1981	0.69	1.46	
Norwegian spring-spawning herring	1950-1967	0.80	2.90	High values in the period beginning with subsequent decrease to very low values
	1968-1986	1.14	7.00	Low values during the whole period
	1987-2002	0.81	1.85	Increase and stabilization at a high level
	1950-2002	68	5.70	

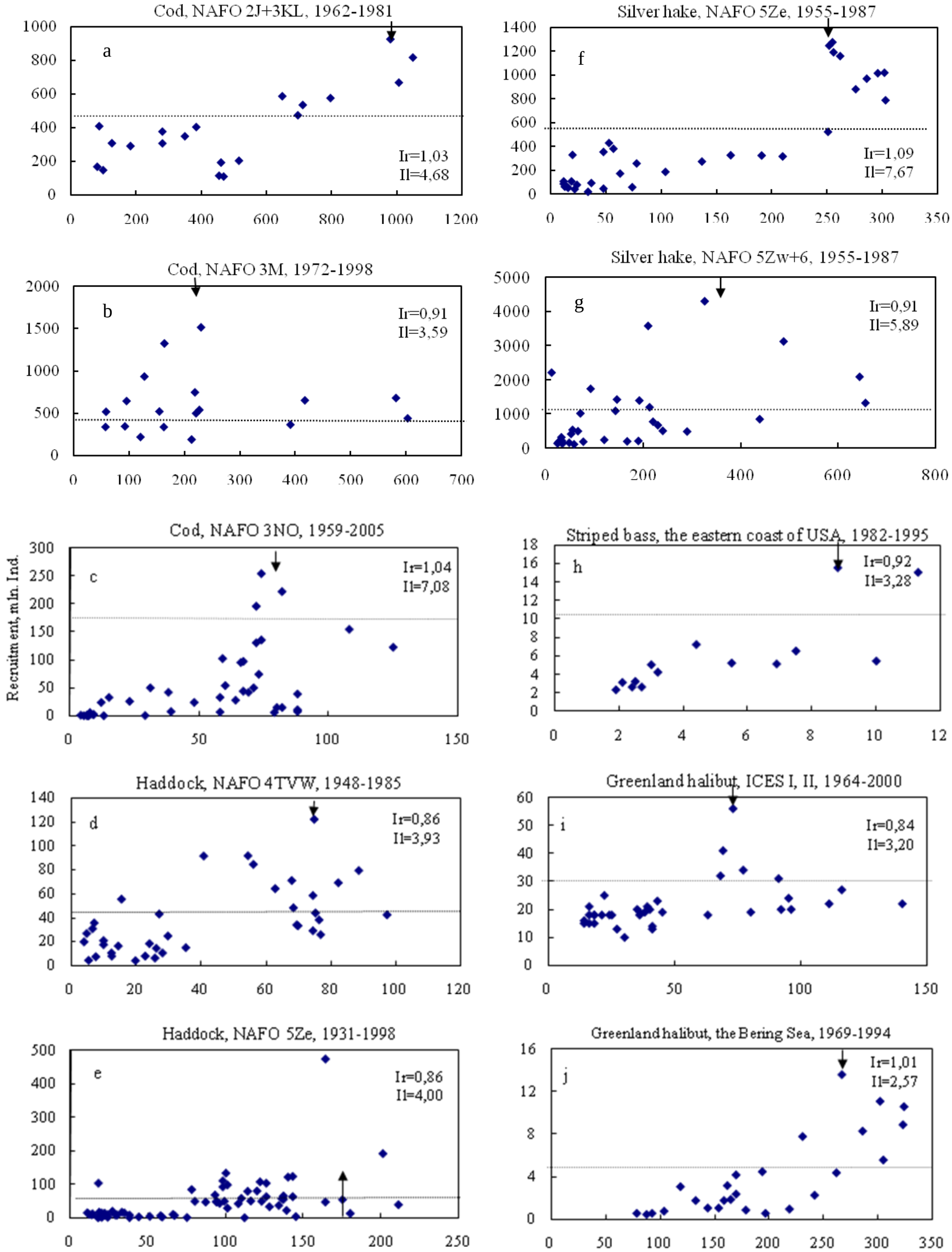

Fig. 1. Relationship of the spawning biomass and recruitment in populations with high Ir and Il.

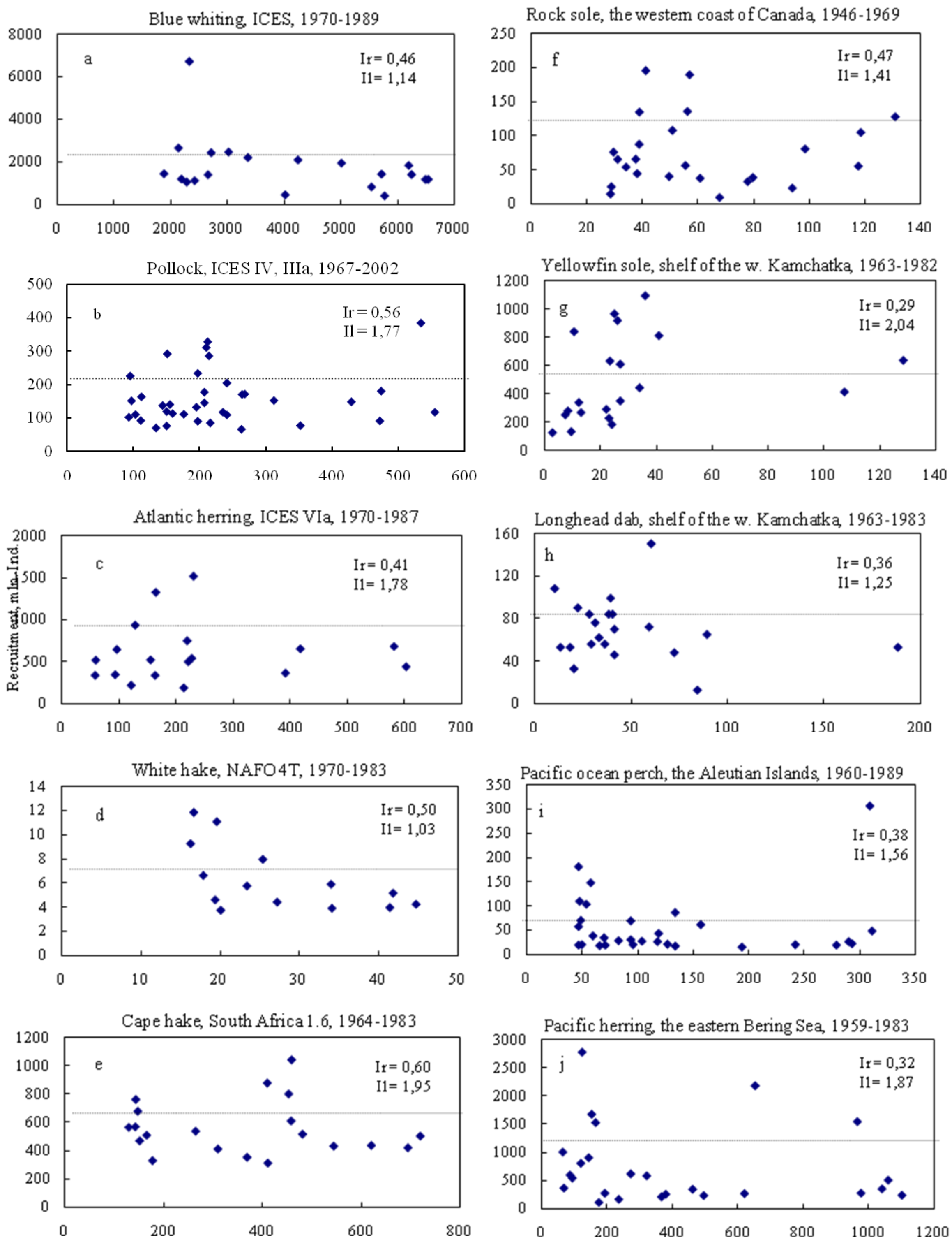

Fig. 2. Relationship of the spawning biomass and recruitment in populations with low Ir and Il.

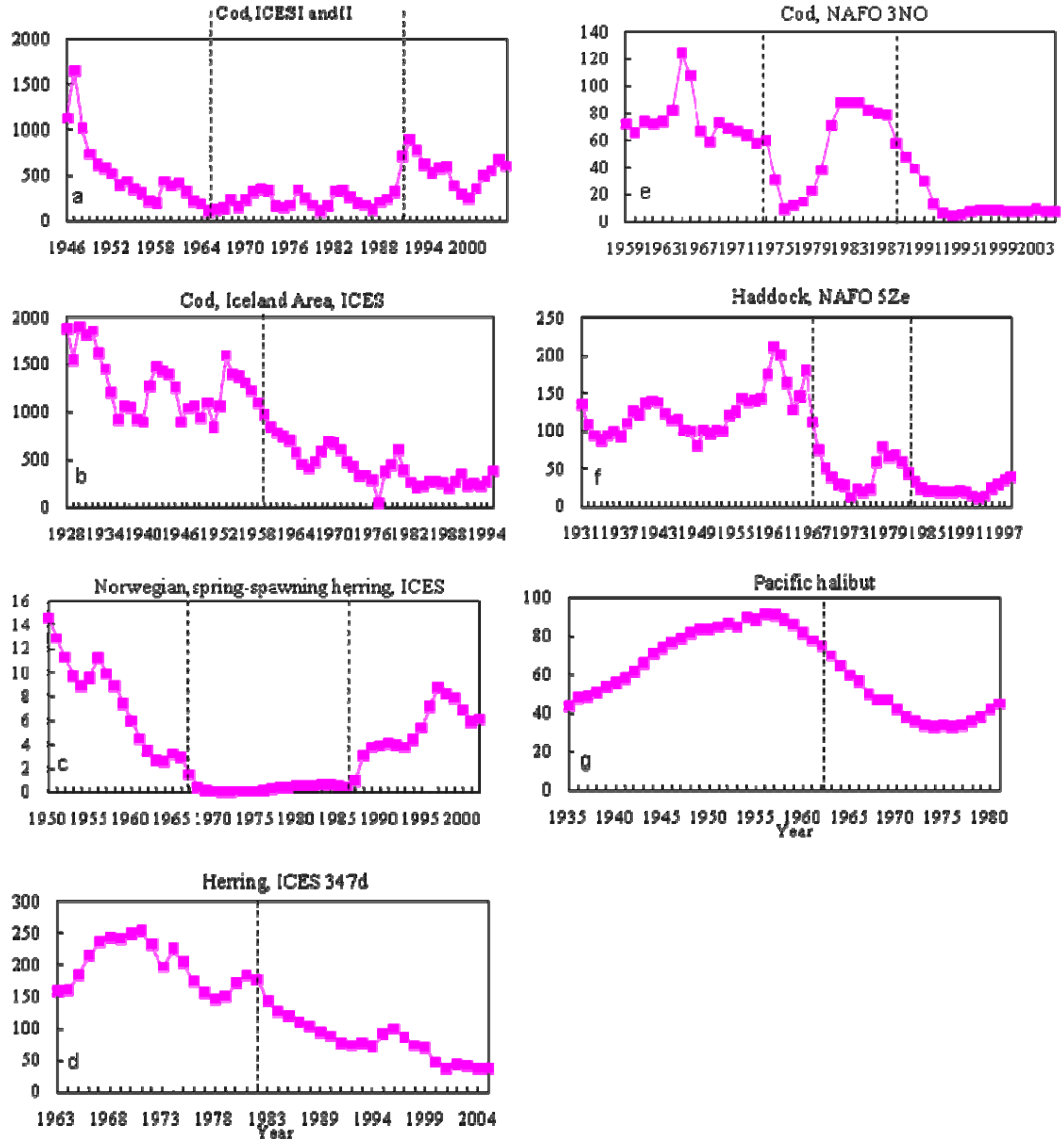

Fig. 3. Spawning biomass dynamics of populations with observation period above 40 years.