

When do environment–recruitment correlations work?

RANSOM A. MYERS

Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1. E-mail: Ransom.Myers@Dal.Ca

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Abstract

I review the role of environmental variability in the survival of juvenile fish and shellfish by examining the success of previously published environment–recruitment correlations when tested with new data. The proportion of published correlations that have been verified upon retest is low. There is one generalization that stands out: correlations for populations at the limit of a species' geographical range have often remained statistically significant when re-examined. An examination of environment–recruitment correlations that were reviewed 13 years ago by Shepherd and co-workers shows that only 1 out of 47 reviewed studies is currently used in the estimation of recruitment in routine assessments. The results suggest that future progress will require testing general hypotheses using data from many populations.

Keywords: correlation, environment, fish, meta-analysis, recruitment, variability

Introduction

The importance of synthetic, but sceptical, approach to the study of population dynamics is a hallmark of the approach of Ray Beverton and Sidney Holt (1957, 1959). Here I apply this approach to study one of the longest-standing problems in fisheries biology: the influence of the environment upon recruitment.

The search for environmental predictors of recruitment is at least a century old (Cushing, 1982). The term 'recruitment' refers to the abundance of the earliest age at which a cohort can effectively be estimated – usually the youngest age that they enter a fishery. The purpose of this review is to examine how past attempts to predict recruitment have fared upon re-examination, and to search for general hypotheses that may help synthesize past research and suggest directions for future research.

I will primarily review studies that have 'retested' previously published environment–recruitment relationships because of the fundamental difficulty of simultaneously carrying out exploratory and confirmatory statistics (Sissenwine, 1984). It is difficult not to find environmental variables that are nominally statistically significant in an exploratory analysis.

I will also review those studies that have systematically tested the same hypothesis on several populations of the same or similar species. These results must be viewed as less reliable than true confirmatory tests, but are certainly much more reliable than studies of single-species searches for environmental correlations.

The chief difficulty I had with this review was the relative rarity in which strictly a priori hypotheses were tested. In some cases, there were over a dozen papers on the same population without a single strictly confirmatory statistical analysis taking place. Part of the problem was my inability to make sense of the complex results in many cases; I apologize to those scientists if I have not included their work in this review. I do not attempt to review all work on recruitment, as there are three excellent recent reviews (Cushing, 1980; Heath, 1992; Bakun, 1996).

Methods

COLLECTION OF DATA

I attempted to collect all cases where previously published environment–recruitment correlations were tested with new data. Cases of environmentally induced changes in migration that may affect local production, e.g. migration of Atlantic cod (*Gadus morhua Gadidae*) to west Greenland in warm periods (Cushing, 1980), will not be considered in this review.

A fundamental difficulty of any attempt at research synthesis is publication bias (Cooper and Hedges, 1994), i.e. statistically significant and non-significant results may not be published equally. For example, environmental correlations that fail may simply not be used by biologists in future assessments. This is the case for the published correlations of Atlantic menhaden (*Brevoortia tyrannus*, Clupeidae; Nelson *et al.*, 1977). The recruitment data were reanalysed by one of Nelson's collaborators, W. Schaaf, and it was found that the proposed mechanism, Ekman transport, could not be used to predict recruitment (D.S. Vaughan, National Marine Fisheries Service, North Carolina, pers. comm.). However, the retest was never published, so the paper by Nelson *et al.* is still being cited as a success.

To reduce this source of bias, I searched forward from past reviews, e.g. Shepherd *et al.* (1984), for retests, both published and unpublished. I did this by contacting experts in the individual stocks that had been previously studied. I also attempted to collect all the studies where correlations had been purposely retested.

I classified retests into verified or not (+ or –) in Tables 1–3. I generally accepted the criteria of the author carrying out the retest as to whether the prediction was verified or not. I was less concerned with the nominal statistical significance of the results than if the pattern was as predicted by the original study. Thus, the retest was not necessarily statistically significant. I included the results from a previous meta-analysis (Drinkwater and Myers, 1987) as a special case. I have denoted these studies by a †.

In some cases, there was more than one retest; I have used the most recent one if all the results were consistent. Sometimes, a retest initially appeared to be consistent with the exploratory test, but then failed when more data were collected. I have denoted these by asterisks in Tables 1 and 2.

In some studies, an environment–recruitment correlation was re-examined but only the results for the combined exploratory and confirmatory analysis were presented. These were not included in the review unless the raw data could be obtained so an analysis could be carried out only on the new portion of the data.

The results were categorized by the proposed mechanism that was hypothesized to affect recruitment. Temperature, salinity and wind were the most used environmental data.

I began the analysis by attempting a formal meta-analysis of the results, e.g. combining the correlation coefficient of the predicted relationship (Cooper and Hedges, 1994). Meta-analysis has proved to be very useful for the analysis of specific hypotheses in recruitment studies (Myers, 1997); however, they are not well suited to general reviews where many hypotheses are being examined. One purpose of this study is to encourage fisheries biologists to frame their research and present their results in such a manner that a formal meta-analysis can be carried out.

RELIABILITY OF RETESTS

I considered two aspects of the reliability of the retests. First, the quality of the data are crucial. The least reliable index of abundance is total catch because so many things other than recruitment will affect it. Commercial catch per unit effort (CPUE) is usually a better index of abundance than total catch but is often seriously misleading (Hilborn and Walters, 1992). The most reliable data for estimating recruitment are from research surveys which are independent of the fishery. For example, the numbers at age for marine populations are estimated annually using stratified random surveys. Reconstructed population estimates from catch-at-age data (sequential population analysis (SPA); cohort and virtual population analyses are examples) are usually reliable if the reported catch is well known, but are subject to a number of biases that can lead to spurious trends (Hilborn and Walters, 1992; Myers and Cadigan, 1995).

Second, I examined how the confirmatory tests were carried out. I consider the following classes of retests.

1. Repeat analysis using new data exactly as the original exploratory test was carried out.

2. Updated analysis using new data in a manner similar to the way the exploratory test was carried out.
3. Retest using older data in a manner similar to the way the exploratory test was carried out.
4. Test using another population in a similar manner.
5. Test of link in the hypothesis.
6. Test of the statistical methods.
7. Test using data-splitting (Cox, 1975), i.e. use exploratory tests on part of the data and reserve a portion of the data for confirmatory testing.

The most reliable retests are class 1. Repeating the methods from a published study may be the only way to completely honestly retest an environment–recruitment correlation. There are simply too many choices in the manner in which recruitment and environmental variables can be treated and transformed for any other method to be as reliable.

Class 2 retests are those that are not an exact repeat of an exploratory test. These tests cannot be considered as reliable as class 1 tests. Sometimes, a fair retest is possible because of ignorance of previous research. That is, an exploratory analysis may be by accident a retest of a previously published hypothesis. I have identified such retests as class 2 retests as well.

It is sometimes possible to carry out a retest by obtaining independent data collected prior to those used to generate the hypothesis (class 3 retests). These retests should have similar reliability to class 2 retests because there is almost always some flexibility in constructing recruitment series.

A hypothesis can be tested on a population different from that used to formulate the hypothesis (class 4 retests). This class of retests is probably not very reliable because there is great flexibility in the selection of time series and hypotheses.

An alternative approach (class 5) is to test an assumption for the proposed mechanism of an environment–recruitment correlation. For example, in Cushing's model of the effect of the great salinity anomaly, he predicted a sequence of causal mechanisms, each of which could be tested (Mertz and Myers, 1995).

Class 6 includes retests where the statistical or analytical methods are not appropriate. In these cases, a retest can be carried out without new data.

Finally, it is possible to split the data into two portions (class 7). For example, Sissenwine (1974) developed a model relating temperature to recruitment in yellowtail flounder (*Limanda ferruginea*, Pleuromectidae) using CPUE data, and tested using 5 years of new data from research surveys.

Results on analysis of retests

The results for the retests were, on the whole, dismal (Tables 1–3). The retests that repeated the original tests exactly, class 1, and in which the original test relied upon catch data, i.e. landings, were borne out in only a few cases. The class 1 retests that relied upon more reliable data fared better. Smallmouth bass (*Micropterus dolomieu*, Ceuforarchidae) in Lake Opeongo was a spectacular success, with the relationship between temperature and recruitment persisting for almost 60 years. This hypothesis was first suggested in the 1930s and has held up to the present (Christie and Regier, 1973). It

Table 1. The sign of the proposed relationship with temperature, the species and location of the population of the test, the data used for the analysis (Count, counting fence; CPUE, catch per unit effort; RV, research vessel surveys; SPA, sequential population analysis) the type of retest (see text), the result of the retest (+ implies the correlation held up upon reexamination; if a later test was carried out, the results are marked by an asterisk), the reference for the original experiment and the retest. The results marked by a † denote tests that were not statistically significant when the results were combined in the meta-analysis by Drinkwater and Myers (1987). The scientific names of species are given in Table 4. If a different data type was used to generate and test a hypothesis, both are given and they are separated by a comma

Sign	Species	Location	Data	Type	Result	Reference	Restest
						Original	Restest
+	Alewife	New England	Catch	1	-†	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
+	Butterfish	New England	Catch	1	+†	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
+	Cod	Barents Sea	SPA	2	+	Cushing (1982)	Ottersen <i>et al.</i> (1994)
-	Cod	Labrador	SPA	2	+*	Elizarov (1965)	Rice and Evans (1986)
-	Cod	Labrador	SPA and RV	2	-	Elizarov (1963)	Myers <i>et al.</i> (1992)
+	Cod	Labrador	SPA and RV	3	-	NAFO (1992)	Myers <i>et al.</i> (1992)
+	Cod	Labrador	SPA	6	-	de Young and Rose (1993)	Hutchings and Myers (1994)
+	Cod	S. Grand Bank	SPA and RV	4	-	NAFO (1992)	Myers <i>et al.</i> (1992)
+	Cod	St Pierre Bank	SPA and RV	4	-	NAFO (1992)	Myers <i>et al.</i> (1992)
-	Cod	Flemish Cap	SPA	2	-	Konstantinov (1981)	Rice and Evans (1986)
-	Cod	Browns Bank	CPUE, SPA	2	-	Martin and Kohler (1965)	Frank <i>et al.</i> (1994)
-	Cod	Gulf of St Lawrence	CPUE, SPA	2	-	Martin and Kohler (1965)	Chouinard and Fréchet (1994)
-	Cod	Gulf of Maine	Catch	1	+* †	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
-	Cod	Gulf of Maine	CPUE, SPA	2	-	Martin and Kohler (1965)	Serchuk <i>et al.</i> (1994)
-	Cod	North Sea	SPA and RV	2	-	Dickson <i>et al.</i> (1974)	Dann <i>et al.</i> (1994)
+	Eurasian perch	Windermere	SPA	1	+	LeCren <i>et al.</i> (1977)	Craig <i>et al.</i> (1979)
+	Eurasian perch	Baltic region	Research gillnets	1 and 4	+	Neuman (1976)	Lehtonen and Lappalainen (1995)
+	Haddock ^a	North Sea	SPA	1	-	Shepherd <i>et al.</i> (1984)	thompson and Hilden (1987)
-	Haddock	Georges Bank	CPUE, SPA	2	-	chase (1955)	Sissenwine (1984)
+	Hard-shell clam	New England	Catch	1	-†	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
+	Herring	Sitka sound	SPA	3	+	Zebdi and Collie (1995)	Zebdi and Collie (1995)

Table 1. (Continued).

Sign	Species	Location	Data	Type	Result	Reference	Restest
						Original	
-	Herring	S. British Columbia	SPA	2	+	Tester (1948)	Schweigert (1995)
+	Herring	N. Newfoundland	SPA	1	+	Winters and Wheeler (1987)	Warren (1997)
+	Herring	S. Newfoundland	SPA	1	-	Winters and Wheeler (1987)	Warren (1997)
+	Herring	New England	Catch	1	- ⁱ	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
+	Lake whitefish	S. Georgian Bay	Mark-recapture	4	-	Christie (1963)	Shuter and Regier (1989)
+	Lobster	Maine	Catch	6	+*	Dow (1978)	Fogarty (1988)
+	Lobster	Maine	Catch	1	-	Flowers and Saila (1972)	Drinkwater <i>et al.</i> (1996)
+	Lobster	Nova Scotia	Catch	1	-	Flowers and Saila (1972)	Drinkwater <i>et al.</i> (1996)
+	Lobster	Gulf of St Lawrence	Catch	1	-	Boudreault <i>et al.</i> (1977)	Drinkwater <i>et al.</i> (1996)
+	Menhaden	New England	Catch	1	- ⁱ	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
-	Northern shrimp	Gulf of Maine	Catch, RV	2	+	Dow (1966)	Richards <i>et al.</i> (1996)
-	Pacific hake	NW Pacific	SPA	1	-	Bailey (1981)	Hollowed (1990)
+	Pike	Windermere	SPA	1	-	Kipling (1983)	Kipling (1983)
+	Pikeperch	Baltic region	Research gillnets	1 and 4	+	Svardson and Molin (1968)	Lehtonen and Lappalainen (1995)
+	Pikeperch	Lake IJssel, the Netherlands	RV	1	+	Willemssen (1977)	Buijse (1992)
+	Plaice	Kattegat	RV	1	-	Nielsen and Bagge (1985)	Nielsen <i>et al.</i> (1998)
-	Redfish	Gulf of Maine	Catch	1	- ⁱ	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
+	Sardine	Japan	Catch, SPA	2	-	Kawasaki (1991)	Wada <i>et al.</i> (1995)
+	Sardine	California	SPA	2	+	Marr (1960)	Jacobson and MacCall (1995)
+	Scallops	New England	Catch	1	+ ⁱ	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
+	Sea bass	South Britain	CPUe, CPUe and RV	1	+	Kennedy and Fitzmaurice (1972)	Henderson and Cops (1997)

+	Smallmouth bass	Lake Opeongo	SPA	1	+	christie (1957)	Shuter <i>et al.</i> (1980)
+	Smallmouth bass	N. Lake Huron	SPA	4	+	Fry and Watt (1957)	Christie and Regier (1973)
–	Soft-shell clam	New England	Catch	1	+ [†]	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
–	Sole ^a	North Sea	SPA	1	–	Shepherd <i>et al.</i> (1984)	Thompson and Hilden (1987)
+	Whiting ^a	North Sea	SPA	1	–	Shepherd <i>et al.</i> (1984)	Thompson and Hilden (1987)
+	Whiting ^a	West of Scotland	SPA	1	–	Shepherd <i>et al.</i> (1984)	Thompson and Hilden (1987)
–	Yellowtail flounder	S. New England	Catch	1	+ [†]	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
–	Yellowtail flounder	S. New England	CPUE, RV	7	+	Sissenwine (1974)	Sissenwine (1974)
+	9 stocks ^a	North Sea	SPA	1	–	Shepherd <i>et al.</i> (1984)	Thompson and Hilden (1987)

^aThe first principal component of correlation matrix used for 9 stocks of groundfish (plus herring) in the North Sea and the west of Scotland was used in the original analysis by Shepherd *et al.* (1984). The retest was carried out on each stock individually that was originally statistically significant, as well as the first principal component.

Table 2. Same as Table 1, except that the hypothesis that salinity (or the inverse of rainfall) affects recruitment is tested

Sign	Species	Location	Data	Type	Result	Reference	
						Original	Retest
–	Banana prawn	Gulf of Carpentaria	Catch	1	+	Vance <i>et al.</i> (1985)	D. Dow (pers. comm.)
+	Cod	Eastern Baltic region	SPA	2 and 7	+	Cushing (1982)	Sparholt (1996)
+	Cod	Scottian Shelf	SPA	1	–	Drinkwater (1987)	Frank <i>et al.</i> (1994)
–	Cod	Labrador	SPA and RV	1	+*	Sutcliffe <i>et al.</i> (1983)	Myers <i>et al.</i> (1993)
–	Cod	Labrador	SPA	1	–	Sutcliffe <i>et al.</i> (1983)	Hutchings and Myers (1994)
–	Halibut	Gulf of St Lawrence	Catch	1	– [†]	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
–	Lobster	Gulf of St Lawrence	Catch	1	+* [†]	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)
–	Lobster	Gulf of St Lawrence	Catch	1	–	Sutcliffe <i>et al.</i> (1977)	Drinkwater <i>et al.</i> (1991)
–	Soft-shell clam	Gulf of St Lawrence	Catch	1	+ [†]	Sutcliffe <i>et al.</i> (1977)	Drinkwater and Myers (1987)

Table 3. Same as Table 1, except that a variety of hypotheses are examined

Hypothesis	Species	Location	Data	Type	Result	Reference	Original	Retest
<i>Calanus</i> abundance	Haddock	North Sea	CPUE	1	-	Cushing (1966)		Cushing (1982)
<i>Calanus</i> abundance	Cod	North Sea	SPA	1	-	Cushing (1984)		Brander (1992)
<i>Calanus</i> abundance	Cod	NW Atlantic	SPA	5	+	Cushing (1990)		Myers (1997)
Lagged forcing	Cod, haddock	N. Atlantic stocks	SPA	1	-	Templeman (1972)		Myers <i>et al.</i> (1995b)
Ekman transport	Menhaden	W. Atlantic	SPA	1	-	Nelson <i>et al.</i> (1977)		D.S. Vaughan, pers. comm.
- Offshore Ekman transport	Pacific hake	NW Pacific	SPA	1	-	Bailey (1981)		Hollowed (1990)
Turbulence	Northern anchovy	California coast	SPA	2	-	Lasker (1975)		Peterman and Bradford (1987)
West wind	Haddock	North Sea	CPUE	1	-	Rae (1957)		Savile (1959)
Wind	Plaice	Kattegat	RV	1	+	Nielsen and Bagge (1985)		Nielsen <i>et al.</i> (1998)
Offshore wind	Haddock	Georges Bank	CPUE, SPA	2	-	Chase (1955)		Sissenwine (1984)
+ El Niño	Sockeye salmon	Fraser River	Catch	5	-	Mysak <i>et al.</i> (1982)		Levy and Wood (1992)
+ El Niño	Chub mackerel	California	SPA	1	-	Sinclair <i>et al.</i> (1985)		Prager and Hoening (1989)
+ Upwelling	Coho salmon	Oregon coast	Counts	1	-	Nickelson (1986)		Pearcy (1992)
+ Upwelling	Northern anchovy	California coast	SPA	2	-	Bakun and Parrish (1980)		Prager and MacCall (1993)

may be important that this population is at the northern limit of its range, and excellent data are available. Lake Opeongo is in a park with carefully monitored catches from the only lake exit. Furthermore, it is an introduced population that did not originally inhabit the lake. It is not surprising that correlations based upon reliable data are more likely to be verified.

Environment–recruitment correlations for populations at the geographical limit of a species range were often confirmed if the sign of the predicted correlation was appropriate. For example, the most northern population of cod (the Barents Sea stock) had a consistently positive relationship with temperature. The Baltic Sea cod stock, which is at the limit of its range with respect to salinity, appears to be more productive when there is inflow of high-salinity and high-oxygen water from the Atlantic (Sparholt, 1996). Recruitment of Pacific herring (*Clupea harengus*, Clupeidae) is positively correlated with temperature close to the northern limit of its range in Alaska (Zebdi and Collie, 1995). Northern shrimp (*Pandalus borealis*) is negatively correlated with temperature at its southern limit in the Gulf of Maine (Richards *et al.*, 1996). Freshwater species, i.e. smallmouth bass and Eurasian perch (*Perca fluviatilis*, Percidae), show positive correlations with temperature at the northern limits of their ranges in Canada and the Baltic Sea respectively.

Note that nearly all the temperature correlations that held up upon re-examination were associated with populations close to the northern limit (these were all in the Northern Hemisphere; with positive correlations) or at the southern limit (with negative correlations) of the species range. Lehtonen and Lappalainen (1995) studied recruitment of over 22 brackish water or freshwater populations in Finland. They found that pikeperch (*Stizostedion lucioperca*, Percidae) and Eurasian perch populations that were close to the northern limit of their range has recruitment that was positively correlated with temperature. They found no such relationship for whitefish (*Coregonus lavaretus*, Salmonidae), which occurs well to the north and south of the study area. Several other studies have consistently found a positive relationship with temperature during the first year of life for perch and pikeperch in Northern Europe.

The published correlations with wind fared poorly (Table 3), perhaps because of the very different mechanisms whereby wind may affect recruitment (Myers and Drinkwater, 1989) and the suggestion that the relationship may in general be non-linear (Cury and Roy, 1989). For example, Hollowed and Bailey (1989) proposed that survival of Pacific hake (*Merluccius productus*, Gadidae) larvae in the California upwelling system was enhanced by weak upwelling in the winter followed by strong upwelling in March. Such complex hypotheses have not yet been fully tested on new data. Correlations with salinity or rainfall also performed poorly.

SUMMARY OF RETESTS

To summarize the results of the retests with temperature, I plotted the results of the retests versus the relative latitude of the population. To scale the latitude, I used the latitude of spawning for the population relative to the range of latitudes of spawning for comparable populations of that species (see below next paragraph).

To improve the use of latitude as a proxy for temperature, I only considered the populations on the eastern or western sides of each ocean basin. For example, the latitude of spawning of North Sea cod is 55°N. This latitude was compared with the range of spawning latitudes for cod populations in the eastern North Atlantic. These

ranged from 48° for cod in the English Channel to 68° for Barents Sea cod. This gave a relative latitude for North Sea cod of 0.35 (i.e. $55 - 48 = 7$; $68 - 48 = 20$; $7/20 = 0.35$). Note, however, that this is an approximation. Small populations of cod spawn in the fjords of northern Norway, which is north of the main spawning location at Lofoten. For freshwater populations, I used the latitude range for the continent-wide distribution for the species. Also, note that all the populations from Table 1 are from the Northern Hemisphere. In this summary I used only studies that were retested with methods more reliable than catch data.

The results clearly show the pattern of confirmed relationships at the edge of the species range (Fig. 1). The relationship in Fig. 1 is highly statistically significant (logistic regression, $p < 0.001$).

Systematic tests on many populations of the same species

The approach of comparing many populations of the same or similar species has been used most intensively in the eastern boundary current upwelling systems (Bakun, 1996). In particular, the optimal environmental window (OEW) hypothesis relates recruitment with the environment in upwelling systems (Cury and Roy, 1989). It suggests a dome-shaped relationship between the recruitment success and the upwelling intensity. Cury and Roy (1989) developed their hypothesis using data for the Peruvian anchoveta (*Engraulis ringens*, Euphrasidae), the Pacific sardine (*Sardinops sagax caerulea*, Clupeidae) and the West African sardines and sardinellas. A similar domed shape has been found in the anchovy (*Engraulis encrasicolus*, Euphrasidae; Roy *et al.*, 1995) and sardine (*Sardina pilchardus*, Clupeidae; Borja *et al.*, 1996) off the Iberian Peninsula, the Chilean sardine (Serra *et al.*, 1997), the Californian anchovy (*Engraulis mordax*, Euphrasidae; Cury *et al.*, 1995), and southern Africa anchovy (*Engraulis capensis*, Euphrasidae; Boyd *et al.*, 1997).

Gibson and Myers (1988) analysed the effects of winter and summer river discharge on the survival of Atlantic salmon (*Salmo salar*, Salmonidae) eggs and juveniles for six rivers in Eastern Canada. There were positive relationships between either winter discharge or temperature and survival for five rivers. For all rivers combined, survival

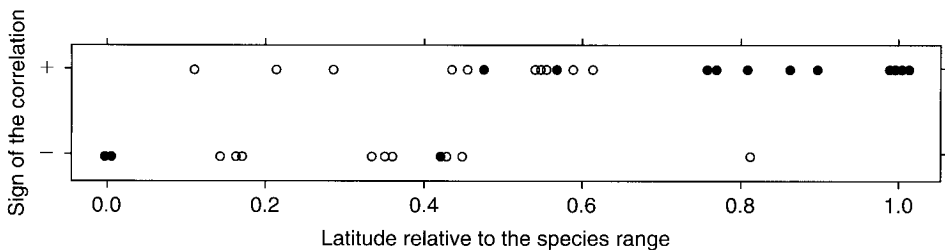


Fig. 1. The confirmed (solid circles) and unconfirmed (open circles) environment–recruitment correlations versus the spawning latitude of a population relative to the species range. A relative latitude of 0 indicates the southern limit of the species range and a relative latitude of 1 indicates the northern limit of the species range. The data have been slightly ‘jittered’ to improve visibility of overlapping observations.

and winter discharge were related. The hypothesis that summer discharge was unrelated to survival could not be rejected. However, there was evidence that summer discharge enhances survival in the Miramichi and Northwest Miramichi rivers of New Brunswick. In general, the results indicated that summer discharge was critical in the southern portion of the range and winter discharge was more important in the northern limit of the range.

Recently, much attention has been focused on changes in the North Pacific that occurred in the mid 1970s. Adkinson *et al.* (1996) studied sea survival from all major sockeye salmon (*Oncorhynchus meyka*, Salmonidae) populations in Bristol Bay, Alaska, and the Fraser River, British Columbia. The Bristol Bay stocks showed an increase in survival in the 1970s, which was assumed to be related to a climate change, but the Fraser River stocks did not.

Myers and Drinkwater (1989) analysed the influence of Gulf Stream warm core rings on the recruitment from 25 populations of fish and shellfish. There is evidence that increased warm core ring activity reduces recruitment in the 17 groundfish stocks examined, with the exception of cod from Georges Bank. A similar analysis of seven pelagic stocks and one shellfish stock showed no consistent evidence that warm core rings reduce their recruitment.

Each of these studies is suggestive, and carries much more weight than single-population studies; however, they must be tested in a truly confirmatory fashion.

Are environmental correlations used to predict recruitment in practice?

In the review by Shepherd *et al.* (1984), a list of 47 studies on 42 stocks in the North Atlantic and north-east Pacific was compiled (Tables 1–4 in Shepherd *et al.*, 1984). If these correlations were considered to be of practical use by assessment biologists, then they would be routinely used to predict recruitment in the assessments.

I obtained the latest available assessment for each of these populations, e.g. those carried out in 1996, and determined if the environmental correlation with recruitment was used to predict recruitment. In only one case, that of the positive influence of sea surface temperature on Pacific sardine recruitment (Jacobson and MacCall, 1995), was any of the 42 studies used in the assessments to modify management action. I know of one other case, i.e. the relationship between rainfall and banana prawn (*Penaeus merguensis*) recruitment in the Gulf of Carpentaria (Vance *et al.*, 1985), where an environment–recruitment correlation has been retested and is now routinely used in assessments.

The reluctance of assessment biologists to include environment–recruitment correlations into their predictions of recruitment is not because they are unduly conservative. For example, 5 years after there were claims that recruitment of northern cod could be partially predicted from the environment, i.e. that cold water led to a greater probability of good survival of cod juveniles (Rice and Evans, 1986; Rice, 1987), the collapse of the stock was being blamed on cold water (NAFO, 1992).

Although environment–recruitment correlations are rarely used to predict recruitment, there has been limited use of environmental data in stock assessment models for maturity for northern anchovy off California. This is important for using ichthyoplankton-based abundance indices (Methot, 1989); the distribution/migration (US–Canada) of Pacific hake (Dorn, 1995); and the growth of Pacific hake (Dorn, 1992).

Table 4. Scientific names for species listed in Tables 1 to 3

Common name	Scientific name
Alewife	<i>Alosa pseudoharengus</i> (Clupeidae)
Atlantic halibut	<i>Hippoglossus hippoglossus</i> (Pleuromectidae)
Banana prawn	<i>penaeus merguensis</i>
Butterfish	<i>Peprilus triacanthus</i> (Stromateidae)
Capelin	<i>Mallotus villosus</i> (Osmeridae)
Chub mackerel	<i>Scomber japonicus</i> (Scombridae)
Cod	<i>Gadus morhua</i> (Gadidae)
Coho salmon	<i>Oncorhynchus kisutch</i> (Salmonidae)
Eurasian perch	<i>Perca fluviatilis</i> (Percidae)
Haddock	<i>Melanogrammus aeglefinus</i> (Gadidae)
Hard-shelled clams	<i>Mercenaria mercenaria</i>
Herring	<i>Clupea harengus</i> (Clupeidae)
Lake whitefish	<i>Coregonus clupeaformis</i> (Salmonidae)
Lobster	<i>Homarus americanus</i>
Menhaden	<i>Brevoortia tyrannus</i> (Clupeidae)
Northern shrimp	<i>Pandalus borealis</i>
Northern anchovy	<i>Engraulis mordax</i> (Eugravilidae)
Pacific hake	<i>Merluccius productus</i> (Gadidae)
Peruvian anchoveta	<i>Engraulis ringens</i> (Eugravilidae)
Pike	<i>Esox lucius</i> (Esocidae)
Pikeperch	<i>Stizostedion lucioperca</i> (Percidae)
Plaice	<i>Pleuronectes platessa</i> (Pleuromectidae)
Pollock or saithe	<i>Pollachius virens</i> (Gadidae)
Redfish	<i>Sebastes</i> sp. (Scorpaenidae)
Sardine	<i>Sardinops sagax</i> (Clupeidae)
Scallop	<i>Placopecten magellanicus</i>
Sea bass	<i>Sebastes flavidus</i> (Scorpaenidae)
Smallmouth bass	<i>Micropterus dolomieu</i> (Centravchidae)
Sockeye salmon	<i>Oncorhynchus nerka</i> (Salmonidae)
Soft-shelled clams	<i>Mya arenaria</i>
Sole	<i>Solea vulgaris</i> (Soleidae)
Whiting	<i>Merlangius merlangus</i> (Gadidae)
Yellowtail flounder	<i>Limanda ferruginea</i> ^a (Pleuronectridae)

^aThe AFS name is *Pleuronectes ferrugineus* - ed.

Discussion

CORRELATIONS AT THE GEOGRAPHICAL LIMIT OF SPECIES RANGE

There is a remarkable consistency of the results: the recruitment of freshwater species at the northern limit of their range is almost always positively correlated with temperature. This is part of the general pattern of confirming environment–recruitment correlations at the limit of a species range, and is reflected by the frequent failure of environmental correlations with recruitment near the centre of a species range. It is remarkable that not one solid environment–recruitment correlation has been found in such well-studied regions as the North Sea or Georges Bank.

If populations at the limit of a species range are more susceptible to density-independent factors than those at the centre, as has been suggested (Huffaker and Messenger, 1964; Richards and Southwood, 1968; Coulson and Whittaker, 1978), then the relative variability in population density should be greater at the limit of a species range than at the centre (Gaston, 1990).

The general results are consistent with long-established patterns of the behaviour of species at the limit of their range. That is, abiotic factors should be more important at the limit of a range (Huffaker and Messenger, 1964) where their influences will generally be simple enough to be understood. This is consistent with the observation that recruitment of cod, haddock (*Melauogrammus aeglefinus*, Gadidae) and herring are more variable at the limit of their range (Myers, 1991). Correlations that were statistically significant when retested generally occurred in populations close to the limit of the species range in which recruitment increased when environmental conditions were moderated.

HOW CAN RESEARCH BE IMPROVED?

The rarity of successful retests of previously published environment–recruitment correlations clearly indicates that different approaches are needed in this research. The following are statistical and analytical approaches that appear to be the most promising.

1. Test general hypotheses. By examining many populations at once, it should be possible to detect general patterns. For example, the sign of the correlation between environmental factors corresponds to that predicted at the limit of the range, i.e. at the colder limit of a species range one would expect a positive relationship with temperature, and a negative one at the warmer limit of the range. The hypothesis that recruitment in upwelling systems should be a dome-shaped function of upwelling intensity (Cury and Roy, 1989) is another general hypothesis. Examining many populations is relatively easy now that much of the world's recruitment data are available in a readily accessible database (Myers *et al.*, 1995a).
2. Separate exploratory from confirmatory analysis. Attempt to test previously published environment–recruitment correlations as closely as possible to the original predictions, and present the results so they can be evaluated in future meta-analyses.
3. Be honest about how many correlations were tested in an exploratory analysis; otherwise it is impossible to assess the reliability of the reported results.
4. Use data-splitting (Cox, 1975) to overcome the difficulty of treating exploratory results as if they were confirmatory. This is, split the data into two portions. The first portion can be used to choose the exact hypothesis to be tested and the second portion evaluates its significance. Cox (1975) analysed this method and found it to be efficient. One of the few examples of this method for analysing environment–recruitment correlations was the analysis of the influence of Gulf Stream warm core rings on recruitment by Myers and Drinkwater (1989). We used a small portion of the data to choose a more narrow hypothesis to test, i.e. that rings would affect recruitment of demersal, but not pelagic, species. However, there were enough other choices to be made in the analysis that the paper cannot fairly be called a retest (we are currently carrying out such a retest).

5. Correct for the loss of degrees of freedom caused by autocorrelation. Unfortunately, although several techniques exist for this, it is always difficult to assess the true pattern of autocorrelation from relatively short time series.
6. Recognize that many patterns may simply be an artefact of fishing (direct or indirect). For example, the large-scale decline of recruitment of cod in eastern Canada in the 1970s, followed by an increase, appears to have been caused by the discarding of small fish (Myers *et al.*, 1997).
7. Use all indices of abundance. Research surveys of abundance are often ignored in recruitment studies in favour of estimates based upon catch-at-age data. There are several reasons for this, e.g. it is more difficult to examine more than one index of abundance. Another reason is that many researchers simply do not understand that output from catch-at-age models, e.g. cohort and virtual population analyses, are simple transformations of the *reported* catch-at-age. If there are trends in discarding, they may dominate the trends in recruitment (Myers *et al.*, 1997).
8. Look for consistency of results across similar ecosystems. This approach has been used by Bakun (1996) and co-workers in eastern boundary current exosystems.
9. Use formal meta-analytic techniques. An excellent reference is Cooper and Hedges (1994). These methods allow statistical significance levels, correlation coefficients, and effect sizes to be combined across studies. Future work of this type would be greatly simplified if authors would clearly separate confirmatory and exploratory statistics. Drinkwater and Myers (1987) used meta-analysis to increase the power of their analysis of the influence of the environment on recruitment in the north-west Atlantic.
10. Correct for spawning abundance. Many trends in recruitment are a result of changes in spawner abundance (Myers and Barrowman, 1996), and in general should be included in any analysis if possible.
11. Carry out predictive models. In some cases it is possible to carry out an analysis in which the validity of a mechanism can be largely eliminated without carrying out a correlational study. For example, Myers and Drinkwater (1988) showed that Ekman transport could not be responsible for a significant amount of recruitment variability for several north-west Atlantic species by constructing a physical oceanographic model driven by 40 years of 6 hourly wind data.

THE ROLE OF CORRELATIONS IN THE STUDY OF RECRUITMENT

The rarity of the use of environment–recruitment correlations is clear evidence against their general usefulness in assessments. Even if an environmental variable is important, it does not mean that it is key to the management of the fishery. Even though there does appear to be a weak relationship between sea temperature and recruitment in the Barents Sea (Ottersen *et al.*, 1994), very large catches were obtained in the late 1800s when the environment was considerably colder than in the latter half of this century (Nakken, 1994). Similarly, for the Labrador or ‘northern’ cod stock, very large catches were obtained in the late 1880s during a relatively cold period (Hutchings and Myers, 1994). When correlations with the environment have held up over time (Richards *et al.*, 1996), this does not mean that spawning biomass is not important as well.

There are theoretical reasons to doubt that recruitment can be predicted with sufficient accuracy from environmental data to be useful for management (Bradford,

1992; Mertz and Myers, 1995). The basis of the simulations by Bradford (1992) and the analytical models of Mertz and Myers (1995) is the distribution of mortality across life-history stages that is typically observed (Bradford, 1992; Bradford and Cabana, 1997) and the strength of density-dependent mortality in the juvenile stages (Myers and Cadigan, 1993). When these factors are combined, the ability to predict recruitment from environmental factors is very limited, even if the principal mechanism determining interannual survival during the egg and larval stage is well understood (which is seldom the case). The utility of spending large amounts of public research funding to establish predictions of recruitment based upon environmental indices should therefore be questioned (Walters and Collie, 1988; Walters, 1989).

However, there are other strong justifications for studying recruitment mechanisms. This information may be crucial for multispecies management and predicting the long-term consequences of climate change. Furthermore, much of this work could be justified on purely scientific basis.

The emphasis on the search for environmental correlations of recruitment may have led to the neglect of other important processes. For example, the relationship between spawner abundance and subsequent recruitment is usually not clear for any one population, but is very clear if viewed across many populations (Myers and Barrowmen, 1996). Both biotic and abiotic factors need to be studied if we are to understand recruitment variability; in both cases, we need to take a synthetic approach in which processes are studied in many populations as if they were realizations of a natural experiment.

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