FISH and FISHERIES

Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries

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Abstract

Assumptions about the future productivity of a stock are necessary to calculate sustainable catches in fisheries management. Fisheries scientists often assume the number of young fish entering a population (recruitment) is related to the biomass of spawning adults and that recruitment dynamics do not change over time. Thus, managers often use a target biomass based on spawning biomass as the basis for calculating sustainable catches. However, we show recruitment and spawning biomass are not positively related over the observed range of stock sizes for 61% of 224 stocks in the RAM Legacy Stock Assessment Database. Furthermore, 85% of stocks for which spawning biomass may not drive recruitment dynamics over the observed ranges exhibit shifts in average recruitment, which is often used in proxies for target biomasses. Our results suggest that the environment more strongly influences recruitment than spawning biomass over the observed stock sizes for many stocks. Management often endeavours to maintain stock sizes within the observed ranges, so methods for setting management targets that include changes within an ecosystem may better define the status of some stocks, particularly as climate changes.

Keywords Ecosystem-based management, global marine fisheries, population dynamics, recruitment, stock assessment

Introduction

Spawners, recruits and environment

The question of the relationship of recruitment (the number of young fish entering a population after surviving the larval phase) to spawning biomass in exploited marine species has a long history (e.g. Hjort 1914; Ricker 1954; Houde 1987; Cushing 1990). In the 1990s, a database of spawner/recruit observations (Myers *et al.* 1995) allowed meta-analysis of data for hundreds of stocks, but contrasting conclusions were drawn from analyses of these data. Myers and Barrowman (1996) reported that low spawning biomass results in low recruitment, but Gilbert (1997) interpreted the same data as suggesting recruitment shifts between 'recruitment states' in which recruitment varies around a mean. Gilbert proposed that the perceived relationship between spawning biomass and recruitment is due to low recruitment leading to small spawning biomasses when those fish mature rather than small spawning biomass leading to low recruitment. Both hypotheses may be true for different stocks, and recruitment for some stocks may be driven by some combination of these hypotheses. It is clear that some spawners are needed to produce new recruits, but most species produce millions of eggs even at low spawning biomass and larval mortality is very high. Consequently, even small changes in survival can result in highly variable year class sizes (Hjort 1914; Dahlberg 1979).

These two hypotheses have important consequences for management. Fishery managers use expected recruitment to estimate unfished and target spawning biomasses. Common management targets include the biomass (B_{MSY}) and fishing mortality (F_{MSY}) corresponding to 'maximum sustainable yield', both of which rely on an assumed stock–recruit relationship. Proxies for target biomasses that depend on average recruitment have been introduced for use when a stock-recruit relationship is not apparent (e.g. Clark 1991). Regulatory action is often triggered when a stock falls below some threshold proportion of the target biomass. For example, the spawning stock biomass of the canary rockfish, *Sebastes pinniger* (Sebastidae), off the Pacific coast of North America declined beneath its threshold biomass in 1999 at which point allowable catches were reduced from 1045 to 287 mt (Wallace and Cope 2011). Limit biomasses are employed to avoid recruitment overfishing, which occurs when a stock is fished to levels at which recruitment is negatively impacted. Consequently, the rate at which recruitment decreases with biomass (or if it decreases at all) is of great interest to fisheries managers.

Shifts in climate can complicate calculating expectations about future recruitment. Abrupt climatic shifts can precipitate ecosystem 'regime shifts', which have been documented in many regions, for example the North Pacific (Overland *et al.* 2008; Anderson and Piatt 1999), the North Sea (Beaugrand 2004), and the Baltic Sea (Alheit *et al.* 2005). Shifts in climate appear to influence the recruitment of some species, changing the overall productivity of a population (Conners *et al.* 2002; Adkison *et al.* 1996; Duffy-Anderson *et al.* 2005), and therefore should be considered when calculating expected recruitment for management. US fisheries legislation recognizes this by adopting a definition of B_{MSY} (similar to Ricker's 1954 definition) that is relative to 'prevailing environmental

conditions' (Sustainable Fisheries Act 1996). A few US regions account for shifts in climate, but most do not. An exception is Alaska, where average recruitment for demersal fish is calculated only from data gathered after the late 1970s shift in the North Pacific (e.g. Ianelli *et al.* 2012).

We investigate recruitment dynamics for 224 worldwide marine stocks from the RAM Legacy Stock Assessment database (Ricard *et al.* 2012) using cross-correlation to determine if a positive relationship between spawning biomass and recruitment exists and whether recruitment or biomass is 'leading' the dynamics. Shifts in average recruitment are identified for stocks for which spawning biomass does not appear to influence recruitment or a spurious influence of spawning biomass is possible. Synchronies in these shifts within large marine ecosystems (LMEs) are identified and compared to changes in environmental indices to provide starting points for mechanistic studies of regime-like recruitment dynamics.
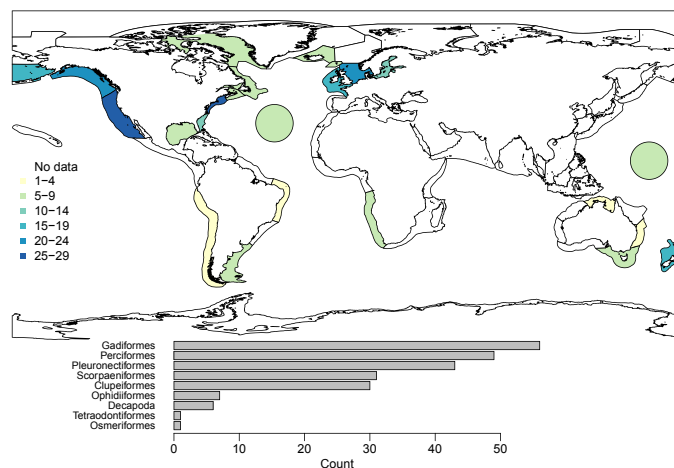
Methods

Data

Time series of recruitment and spawning stock biomass were selected from the RAM Legacy Stock Assessment Database (Ricard *et al.* 2012) after applying two criteria: (i) spawning biomass and recruitment estimates must be available for at least 18 contiguous years and (ii) recruitment estimates must not be derived directly from a stock–recruitment relationship. These stocks represent 10 orders from 29 large marine ecosystems around the world (Fig. 1). Recruitment estimates in the RAM Database were lagged to the year of fertilization and age-at-maturity data were extracted to aid in determining the feasibility of using cross-correlation to infer drivers of recruitment dynamics. Spawning biomass is used as a proxy for reproductive potential here, but it has been suggested that total egg production is a better metric for reproductive potential (Marshall 2009). Although total egg production is likely a better measure, spawning biomass is commonly used to calculate management reference points. Another potential limitation of these data is their restriction to the times during which data are available for assessment, which makes it possible that the maximum observed spawning biomass is some small fraction of virgin spawning biomass. This should not impede identification of an influence of spawning biomass on recruitment because a relationship between spawning biomass and recruitment should be more apparent at lower spawning biomasses.

Cross-correlation and the relationship between spawning biomass and recruitment

Spearman's correlation (Spearman 1904) is used here to calculate the cross-correlation between recruitment and spawning biomass. Spearman's correlation ranks observations before calculating Pearson's correlation for the data, which removes assumptions about linearity, and can therefore identify monotonic relationships (of which the classic Beverton–Holt (1957) stock–recruit relationship is one). Cross-correlation can distinguish
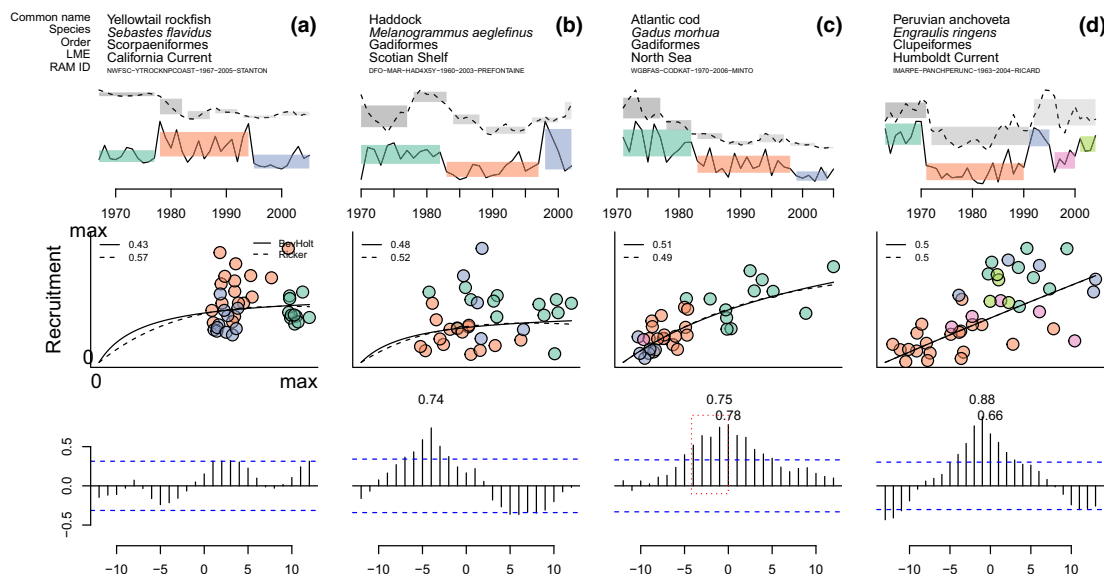

Figure 1 Stocks included in the analysis represented by large marine ecosystem and phylogenetic order.

the impact of recruitment on spawning biomass (Gilbert's thesis) from the influence of spawning biomass on recruitment (Myers' thesis) by providing the strength of correlations at different lags (e.g. Fig. 2). Correlations at zero lag indicate the strength of the influence of spawning biomass on recruitment (because recruitment is lagged to the year of fertilization). Correlations at the 1st, 2nd, 3rd, etc., negative lags indicate the influence of recruitment 1, 2, 3 (etc.) years in the past on spawning biomass in a given year. In this analysis, stocks for which only recruitment significantly influences spawning biomass ($P < 0.05$) or no significant cross-correlations were identified were denoted as environmentally driven. Stocks for which both recruitment and spawning biomass had significant influences on each other ($P < 0.05$) were considered to be potentially environmentally influenced if the influence of recruitment was greater than that of spawning biomass. Stocks for which spawning biomass has a larger (and significant, $P < 0.05$) influence on recruitment than recruitment on spawning biomass were designated as driven by spawning biomass.
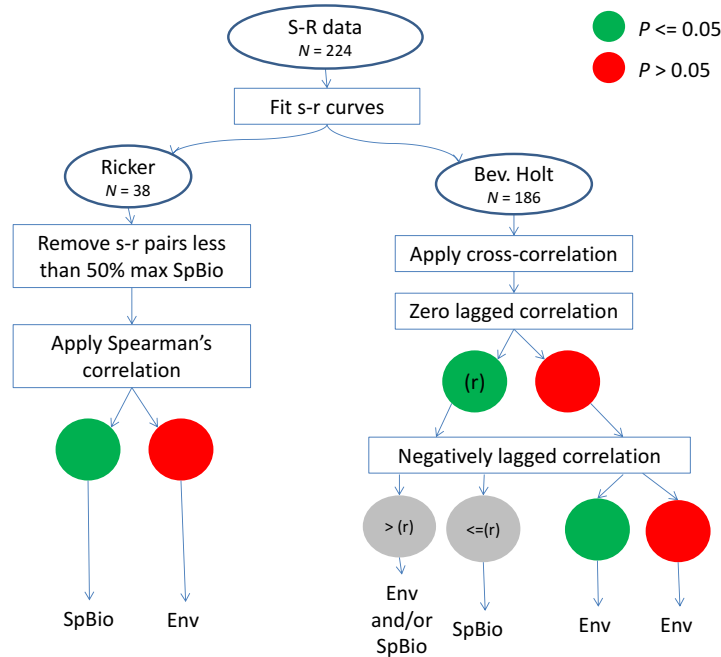
Figure 3 shows a flow chart of the decision-making process for determining recruitment drivers. Dome-shaped dynamics (i.e. overcompensation at high spawning biomasses) will confound the inference of drivers from cross-correlation, so stocks with dome-shaped dynamics are treated separately (see below).

Negatively lagged cross-correlations

The most significant negatively lagged cross-correlation is used here to identify the influence of recruitment on spawning biomass. Choosing the most significant lag *post hoc* elevates the risk of spurious significance through multiple testings. However, age-at-50%-maturity data are available for 122 of the stocks used in the analysis and these data can indicate which lagged recruitment might be expected to have the largest influence on spawning biomass. Time series' of recruitment are lagged such that the 2nd, 3rd, 4th, etc., negatively lagged correlations indicate the influence of recruitment 2, 3, 4, etc., years in the past on a given year's spawning biomass. So, if age-at-50%-maturity

Figure 2 Stocks demonstrating various patterns in cross-correlation. The top row displays regimes in spawning biomass and recruitment (coloured: recruitment; grey: spawning biomass) where box height represents the within-regime, among-year variance, length represents regime length, and the horizontal centre line is the average. Recruitment vs. spawning biomass (middle row) are coloured to match recruitment regime. AIC weights for Ricker and Beverton–Holt curves are given in the legend. Cross-correlation between spawning biomass and recruitment (bottom row) is significant when a vertical line exceeds the dashed horizontal lines; the value of most significant correlation at negative lag and zero lag are indicated above each position. Stocks for which age-at-maturity data are available have a box outlining the window of plausible lagged correlations to describe the influence of recruitment on spawning biomass.

Figure 3 Flow chart describing the decision-making process for assigning drivers. Boxes indicate a 'test' performed on the data, ovals indicate the outcome of that test. The magnitude for the negatively lagged correlations of the stocks that are fit best by a Beverton–Holt curve (right branch) *and* for which there is a significant influence of spawning biomass on recruitment [$P < 0.05$; marked here as '(r)'] are compared to the magnitude of the influence of spawning biomass to identify potentially spurious influence of spawning biomass on recruitment. 'Env' and 'SpBio' denote recruitment dynamics driven by the environment and spawning biomass (respectively) over the observed stock sizes.

occurs during year 3, one might expect the 3rd negatively lagged cross-correlation to reflect this influence (for example). Without the slopes of the maturity ogives, selectivity-at-age or weight-at-age, it is impossible to definitively exclude the possibility that negatively lagged cross-correlations outside of this range are not important. However, 95% of the largest, significant and negatively lagged correlations occur within 2 years on either side of the reported age-at-50%-maturity. Considering the high correspondence with age-at-50%-maturity, the most significant negatively lagged cross-correlation is assumed to adequately represent the influence of recruitment on spawning biomass and is used to determine the influence of recruitment on spawning biomass for all stocks, regardless of the availability of age at maturity data.

Simulation testing of cross-correlation

Stock recruit data were simulated from stock-recruit functions parameterized in terms of the parameters steepness and variability in recruitment (σ_R) to compare the ability of cross-correlation to

identify a stock–recruit relationship relative to that of traditional model-based approaches. Steepness is the proportion of virgin recruitment that is predicted to be produced at 20% of unfished biomass and can assume values from 0.2 to 1 for the Beverton–Holt stock–recruit relationship. The variability around the stock–recruit relationship produced for a given steepness is σ_R. The influence of spawning biomass on recruitment decreases as steepness and/or σ_R increase, so an understanding of the levels of steepness and σ_R at which Spearman's correlation is able to detect an influence is important. The depletion of the stock (or the ratio of the current biomass to virgin biomass) also plays a role in the ability to detect an influence of spawning biomass on recruitment. Recruitment for a given steepness and σ_R (Beverton–Holt) were randomly generated from a range of spawning biomass sizes given a depletion level. For example, if depletion is 50%, stock sizes from 100% to 50% of virgin spawning biomass are sampled and recruitments are calculated from those biomasses given a steepness and σ_R. Spearman's correlation and a Beverton–Holt model were fit to the data (or calculated)

to explore the relative performance of each in identifying the influence of spawning biomass on recruitment.

Dome-shaped recruitment

Some relationships between recruitment and spawning biomass are hypothesized to be dome-shaped due to intensification of density-dependent effects at high spawning biomass and are not monotonic globally. If dome-shaped dynamics are present, Spearman's correlation will not be able to identify an influence of spawning biomass on recruitment. Beverton–Holt curves (Equation 1) and Ricker curves (Equation 2) were therefore fit to the data for each stock to identify dome-shaped recruitment dynamics, which were handled differently than stocks with no dome-shaped dynamics (e.g. Fig. 2).

$$\text{Beverton Holt:} \quad \text{Recruits (Spawners)} = \frac{a * \text{Spawners}}{1 + \frac{\alpha}{\beta}\text{Spawners}} \quad (1)$$

$$\text{Ricker:} \quad \text{Recruits (Spawners)} = \text{Spawners} * \exp(\alpha - \beta * \text{Spawners}) \quad (2)$$

The relative likelihood [or Akaike Information Criterion (AIC) weight] of each model was calculated as follows:

$$RelativeLikelihood\,(\text{Mod}_{min}) = \frac{1}{1 + \exp\left(\frac{\text{AIC(Mod}_{min}) - \text{AIC(Mod}_{max})}{2}\right)} \quad (3)$$

$$RelativeLikelihood\,(\text{Mod}_{max}) = \frac{\exp\left(\frac{\text{AIC(Mod}_{min}) - \text{AIC(Mod}_{max})}{2}\right)}{1 + \exp\left(\frac{\text{AIC(Mod}_{min}) - \text{AIC(Mod}_{max})}{2}\right)} \quad (4)$$

where Mod_{min} refers to the model with the lower value of the Akaike Information Criterion (AIC) and Mod_{max} refers to the model with the larger AIC.

Determining how much better a Ricker curve must fit the data to declare dome-shaped dynamics are present is difficult because a Ricker curve can mimic a Beverton–Holt curve, but a Beverton–Holt curve cannot mimic the dome-shape of a Ricker curve. Consequently, for stocks for which recruitment appears to be monotonically related to spawning biomass, the relative likelihoods of Beverton–Holt and Ricker curves are roughly the same (e.g. Fig. 2c,d). A relative likelihood for Ricker dynamics >0.75 was used as a cut-off for designating stocks with dome-shaped recruitment dynamics. Comparing the differences in fits of the curves for stocks with a relative likelihood just above the cut-off (e.g. Figures 65 and 68 in Appendix S1) to stocks just below the cut-off (e.g. Figures 178 and 180 in Appendix S1), lends support the selection of 0.75 for the cut-off.

The influence of spawning biomass on recruitment is tested for stocks with dome-shaped dynamics by removing the pairs of spawning biomass/recruitment observations in which spawning biomass is >50% of the maximum observed spawning biomass and recalculating the Spearman's correlation between spawning biomass and recruitment. If there is a significant positive relationship for observations of biomass which are <50% of the maximum observed biomass, the stock is designated spawning biomass driven over the range of observed biomasses. Ultimately, this method for addressing dome-shaped recruitment is acceptable for this analysis because management is concerned about recruitment decreasing as biomass decreases (which provides incentive to reducing fishing pressure when biomass is lower than the level corresponding the maximum of the stock–recruit curve), and less concerned with recruitment decreasing as biomass increases (which provides incentive to increase fishing pressure).

Changes in average recruitment

Changes in recruitment regime were identified using a variant of Rodionov's sequential *t*-test algorithm for regime shifts (STARS; Rodionov 2004). A minimum regime duration of 6 years was assumed for these analyses to allow sub-decadal variation to be captured, but the required significance for a shift was set relatively high ($P < 0.1$) to ensure shifts are substantial enough to be potentially relevant to management. The variation from Rodionov's original STARS is that the search for deviations from a regime average is started the year after the 'reference regime' rather

than in the second year of the reference regime. This modification allows outliers to be the start of a regime rather than ignoring outliers or assigning them as single-year regimes (which the original implementations of STARS do). Allowing outliers to signify a new regime is appropriate because changes in the environment may trigger an exceptional recruitment event which will then out-compete subsequent year classes through density-dependent effects. Ultimately, any method of identifying shifts in recruitment dynamics will have weaknesses. However, this algorithm serves the purpose of identifying the two 'important' events (from a management perspective) in the recruitment history of a fishery: (i) changes in average due to a persistent increase or decrease and (ii) changes in average due to an exceptional recruitment event.

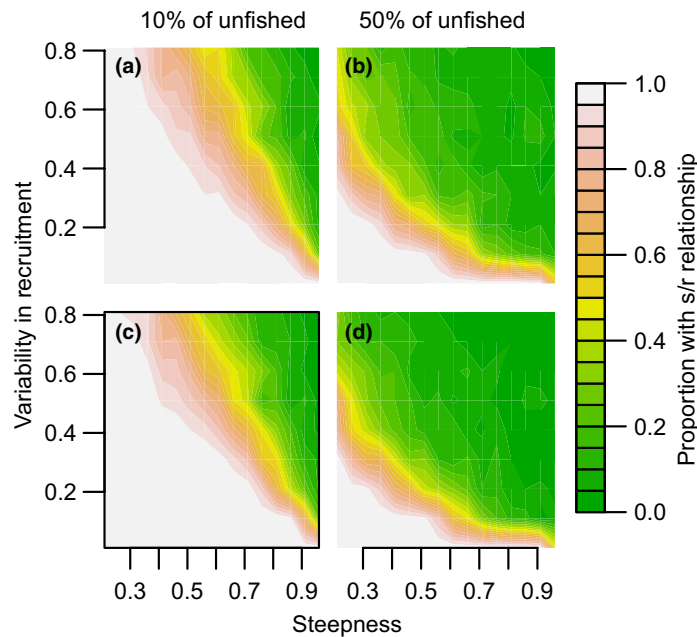### Significance of synchronous changes in average recruitment

The significance of synchronous changes in recruitment within an LME was assessed by generating random realizations of the timing of shifts in average recruitment for stocks within an LME

using a resampling method based on the number of observed shifts for a stock, the years during which the stock was observed and the assumed regime duration using the modified STARS algorithm. The number of stocks shifting in a random realization was summed in each year and the process was repeated 1000 times to construct a distribution for the expected number of shifts for a given year in a given LME. If observed synchronous shifts in a given year exceeded the number of shifts observed in 95% of the simulations in that year, synchrony in that year was denoted as 'significant'.

Results

Simulation results

Identifying a stock–recruit relationship is easier for a given σ_R and steepness when the stock is depleted to very low levels (compare columns of Fig. 4). As the lowest observed biomass increases, the influence of spawning biomass on recruitment becomes more difficult to identify even when steepness and σ_R are low. Consequently, the recruitment dynamics of a stock can be concluded to be

Figure 4 The proportion of simulated stocks with an underlying stock-recruit relationship for which spawning biomass was identified to influence recruitment for a given steepness, σ_R, depletion and detection method. A relationship between recruitment and spawning biomass was identified by selecting between a Beverton–Holt model and a 'random' model via AICc in the top row; the bottom row used Spearman's correlation.

driven by the environment over observed stock sizes (even though there may be an underlying influence of spawning biomass on recruitment) because the stock has not been depleted to low enough levels to observe an influence of spawning biomass. Spearman's correlation is as effective at identifying the influence of spawning biomass on recruitment as approaches based on fitting models (compare rows of Fig. 4).

Meta-analysis results

Overall trends

Dome-shaped dynamics were apparent in 38 stocks (17%), but only seven of these exhibited a positive relationship between recruitment and spawning biomass at stock sizes less than 50% of the observed maximum. Spawning biomass had no significant influence on 105 (47% of total) of the 186 stocks not exhibiting dome-shaped dynamics. Recruitment influenced spawning biomass more strongly than spawning biomass influenced recruitment in 52 of the 81 stocks that showed a significant positive influence of spawning biomass on recruitment. A strong influence of recruitment on spawning biomass can create a spuriously significant influence of spawning biomass on recruitment (Gilbert's thesis), particularly when average recruitment changes abruptly. Average recruitment changed in 160 of 188 stocks in which spawning biomass either could

not be shown to influence recruitment or recruitment had a larger influence on spawning biomass than spawning biomass did on recruitment. The overall mean regime length was 10.3 years with a standard deviation of 8.1 (Table 1). Repeating the analysis with only the stocks for which age-at-maturity are available did not change the relative proportions of drivers.

Among orders with more than 10 representative stocks, dome-shaped dynamics were most common in Perciformes (20%), strictly spawning biomass-driven dynamics were most common in Gadiformes (18%), and dynamics in which both recruitment significantly influenced spawning biomass and spawning biomass influenced recruitment were most often seen in Clupeiformes (43%). Only recruitment significantly influenced spawning biomass for a large fraction of Scorpaeniformes (65%). Longest average regimes were seen in Scorpaeniformes and Clupeiformes (both 11.0 years); average regimes were shortest for Pleuronectiformes (9.5 years).

Patterns in individual stocks

Four general patterns of significant cross-correlations between spawning biomass and recruitment were observed, illustrated in Fig. 2 by yellowtail rockfish (*Sebastes flavidus*, Sebastidae) in the Gulf of Alaska, haddock (*Melanogrammus aeglefinus*, Gadidae) on the Scotian Shelf, Atlantic cod (*Gadus morhua*, Gadidae) in the North Sea and Peruvian

Table 1 Summary of analysis of spawner and recruit data. Numbers under 'Dome-shaped' and 'Monotonic' represent the count of stocks falling in a given category of driver. 'Env', 'SpBio', and 'SpBio and/or Env' indicate recruitment dynamics that appear to be driven by the environment, spawning biomass and stocks for which it is difficult to distinguish between the two hypotheses respectively. The total sample size is 224 stocks. Mean length and standard deviation of recruitment regimes are given in years.

Drivers	Dome-shaped		Monotonic			Regimes		
	Env	SpBio	Env	SpBio	SpBio and/or Env	Stocks with/shifts in average	Mean length	SD
Totals	31	7	105	29	52	160	10.3	8.1
Clupeiformes	0	3	14	0	13	25	11.0	7.8
Pleuronectiformes	8	2	23	4	6	34	9.5	7.4
Scorpaeniformes	4	0	20	5	2	21	11.0	7.1
Gadiformes	5	1	25	10	15	39	10.4	8.4
Perciformes	10	1	19	5	14	32	10.7	9.3
Decapoda	1	0	0	4	1	2	7.1	6.1
Ophidiiformes	3	0	3	1	0	5	9.8	7.5
Osmeriformes	0	0	1	0	0	1	9.3	5.1
Tetraodontiformes	0	0	0	0	1	1	7.7	3.8

anchoveta (*Engraulis ringens*, Engraulidae) in the Humboldt current. A lack of any significant correlations between spawning biomass and recruitment suggests recruitment is environmentally driven over the range of observed data (e.g. yellowtail rockfish; Fig. 2a). Changes in average recruitment for yellowtail rockfish that are unrelated to changes in spawning biomass imply shifts in environmental drivers over time. Only recruitment influences spawning biomass (i.e. there is only a significant negatively lagged correlation) for haddock (Fig. 2b) and average recruitment shifts over time, both implying environmentally driven recruitment dynamics. A larger significant correlation at zero lag than at a negative lag suggests dynamics are driven by spawning biomass for the stock of Atlantic cod (Fig. 2c). This is intuitive, as its recruitment appears to follow spawning biomass, not the opposite. Spawning biomass of Peruvian anchoveta appears to influence recruitment, but recruitment influences spawning biomass more strongly (Fig. 2d). The perceived influence of spawning biomass for Peruvian anchoveta is likely a result of the relatively short generation time and shifts in average recruitment over time. This pattern

appears often in small pelagic fish and other species that mature shortly after recruitment and die rapidly.

Recruitment of Gulf of Alaska rock sole (*Lepidopsetta bilineata*, Pleuronectidae) appears to influence spawning biomass, but this species also displays dome-shaped recruitment dynamics (Fig. 5a). These dome-shaped dynamics are driven by 6 years of low recruitment at the end of the time series that follow 8 years of the highest recruitment for this stock. The influence of spawning biomass on recruitment for spawning biomasses less than 50% of the maximum observed spawning biomass is not significant ($P > 0.05$), and this suggests the environment drives recruitment at the lowest observed stock sizes for rock sole. Interpreting dome-shaped relationships when there are shifts in average recruitment and no influence of spawning biomass on recruitment at low stock sizes is difficult, because environmentally driven dynamics can easily generate these patterns in recruitment. For example, if recruitment is unrelated to biomass, and shifts from a high average to a low average, spawning biomass will not follow until the individuals from the high regime have left the population. This results in a high

Figure 5 Stocks demonstrating various patterns in cross-correlation. The top row displays regimes in spawning biomass and recruitment (coloured: recruitment; grey: spawning biomass) where box height represents the within-regime, among-year variance, length represents regime length, and the horizontal centre line is the average. Recruitment vs. spawning biomass (middle row) are coloured to match recruitment regime. AIC weights for Ricker and Beverton-Holt curves are given in the legend. Cross-correlation between spawning biomass and recruitment (bottom row) is significant when a vertical line exceeds the dashed horizontal lines; the value of most significant correlation at negative lag and zero lag are indicated above each position. Stocks for which age-at-maturity data are available have a box outlining the window of plausible lagged correlations to describe the influence of recruitment on spawning biomass.

spawning biomass when recruitment is very low (similar to rock sole). However, density-dependent effects at high spawning stock sizes could also be the cause of the dome-shape.

Pollock (*Pollachius virens,* Gadidae) on the Faroe Plateau (Fig. 5b) have no significant cross-correlation between spawning biomass and recruitment, but a Ricker curve fits the data decisively better than a Beverton–Holt curve (relatively likelihood: Ricker = 0.99 vs. Beverton Holt = 0.01). However, spawning biomass does not significantly ($P > 0.05$) influence recruitment at low biomass, so recruitment for this stock is likely driven by environment over the observed stock sizes relevant to management.

Spawning biomass influences recruitment but recruitment influences spawning biomass more strongly and shifts in recruitment occur over time for both of Pacific herring (*Clupea pallasii,* Clupeidae) in the Gulf of Alaska and Pacific sardine (*Sardinops sagax,* Clupeidae) in the California Current (Fig. 5c,d). Both stocks are examples of an apparent influence of spawning biomass on recruitment that is likely a result of short generation times and recruitment shifting between high and low regimes. A complete set of figures for the stocks included in the analysis are available in the supplementary materials.

Discussion

Comparison to previous meta-analyses

Myers and Barrowman (1996) concluded that 'when there is a sufficient range in spawner abundance' the highest recruitment occurs when spawning biomass is high and vice versa for 364 time series of spawner and recruit observations. Gilbert (1997) found that recruitment was related to spawning biomass for the salmonids according to his analysis, but not for marine spawning bony fishes. Our results lie somewhere in the middle of these two analyses. Some stocks clearly have a stock–recruit relationship. For example, stocks from the orders Gadiformes and Scorpaeniformes had the highest probability of exhibiting a stock recruit relationship, which is perhaps unsurprising given histories of high exploitation and relatively long lives respectively. However, recruitment dynamics for many stocks are not influenced by spawning biomass over the range of observed stock sizes.

Interpreting an absent influence of spawning biomass on recruitment

Stocks for which spawning biomass does not influence recruitment can be of two types: those for which recruitment does not depend on spawning biomass except for at very low spawning biomass sizes (i.e. steepness is very close to one) and those for which there is an underlying stock recruit relationship but the stock has not been depleted to levels where a decrease in recruitment is obvious (i.e. steepness is less than one, but spawning biomass is still relatively high). It is possible (even probable) that recruitment is influenced by spawning biomass at stock sizes lower than those observed for some of the stocks denoted as environmentally driven here. However, the stocks included in this analysis are actively managed and fisheries managers generally endeavour to maintain spawning biomass within the historically observed range. Given the desire to maintain stocks within this range, there would be little difference between the management decisions for the two types of environmentally driven stocks, so a distinction between the two types is not made here.

Target biomasses and environmentally driven recruitment dynamics

Several recent papers have assessed the status of world fish stocks by comparing current estimated biomass to a calculated target biomass (e.g. Branch *et al.* 2011; Worm *et al.* 2009). The target biomasses used in these papers assume a relationship between spawning biomass and recruitment, but this assumption is violated by environmentally driven recruitment. The spawning biomass-centric paradigm of recruitment dynamics is not restricted to these papers; it is a central tenet of much of fisheries management (e.g. Ricker 1954; Beverton and Holt 1957). Contrary to this paradigm, surplus production for many stocks has been recently suggested to be driven by factors other than spawning biomass (Vert-pre *et al.* 2013), but shifts in population dynamics should be searched for in recruitment (as done here) for two reasons. First, surplus production inherently has 'regimes' in it due to age-structure (e.g. Szuwalski 2013); recruitment does not. Second, surplus production integrates over many years of growth, natural mortality and selection in the fishery, whereas

recruitment occurs closest to the life history stage likely to be most strongly influenced by the environment (Dahlberg 1979). Consequently, linking changes in environment to changes in recruitment is more feasible than doing so for surplus production and is more directly relevant to fisheries management.
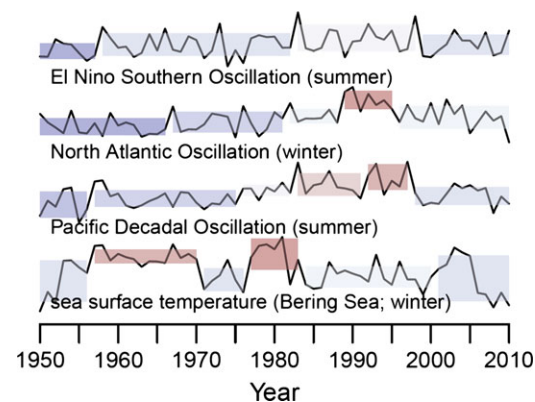
Although target biomasses calculated based on an assumed relationship between recruitment and spawning biomass are not supported by data for many stocks, there are still reasons to continue using target biomasses in management. Maintenance of trophic function, increased ecosystem resilience, the increase in catch per unit effort seen at higher biomasses and the asymmetric risk associated with incorrectly assuming the absence of a stock–recruit relationship are all important reasons for maintaining spawning biomass. Maintenance of genetic diversity and insurance against assessment and management errors are also persuasive reasons for maintaining relatively high spawning biomass. Recruitment dynamics for exploited fisheries are often more complex than assumed and, although an admission of this complexity will make setting hard and fast targets for biomass more difficult, it should encourage precaution in the face of uncertainty and discussion about how to calculate expectations for future recruitment in ways consistent with observations.

Methods used to calculate target biomasses for stocks with environmentally influenced recruitment should be carefully considered. Using long-term average recruitments in target biomasses (which is often done) may allow management to meet its goals, but only if the period of environmental forcing is shorter than the period of internal population dynamics, there are long time series available and there is no trend in the environmental forcing (Haltuch and Punt 2008). However, if the period of environmental forcing is longer than the period of a population's internal dynamics, there will be periods of time during which a stock is apparently 'overfished' when the stock is in a period of low productivity. Additionally, if environmental-forcing is non-stationary (e.g. increasing sea surface temperatures; Rayner *et al.* 2003), productivity inferred from data collected in the past may not be relevant today. Changing expectations for recruitment according to climate regime and then calculating regime-specific target biomasses can result in counter-intuitive management actions (Szuwalski and Punt
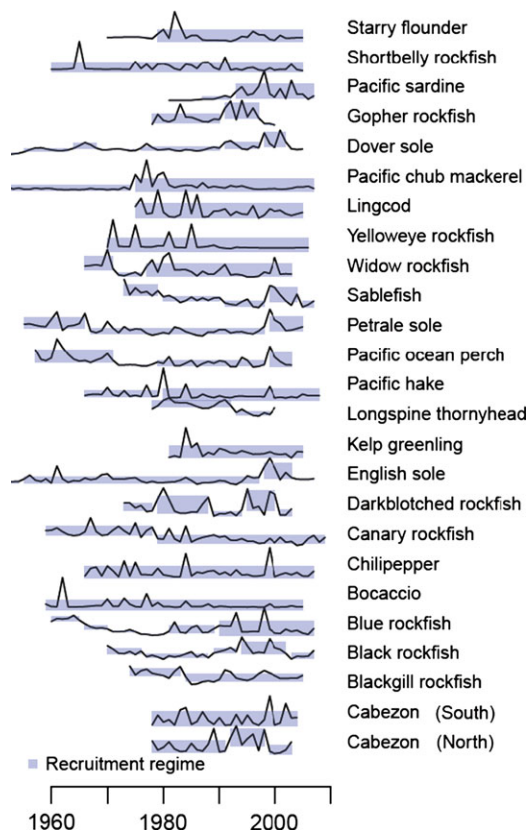
2012). For example, when productivity increases, a stock that was previously 'healthy' may be deemed overfished because the target biomass increases based on new expectations of recruitment, and catch limits may be subsequently decreased. Establishing target biomasses based on risk analyses that consider patterns in environmental influences on recruitment and the potential consequences of depleting a stock to low levels is a potential solution to these problems (e.g. Francis 1992; Francis and Shotton 1997; Lane and Stephenson 1998). Risk analyses can incorporate possible future scenarios to evaluate the risks and benefits of harvest strategies.

Identifying mechanistic drivers of recruitment dynamics

Identifying potential future recruitment scenarios can be aided by a mechanistic understanding of recruitment processes. A shift in average recruitment for a stock with recruitment dynamics unrelated to spawning biomass likely has some underlying environmental driver (e.g. Moran 1953; Ranta *et al.* 1997; Black 2009). Indices of environmental variation often exhibit shifts similar to recruitment (Fig. 6). Synchrony in shifts in recruitment between stocks in an LME in a given year may suggest a common environmental driver and represent 'low-hanging fruit' in the search for mechanistic explanation for changes in recruitment. For example, some synchronous shifts in the California Current (Figs 7 and 8c; 1977,

Figure 6 Regimes in time series of selected environmental indices. Box height represents the among-year variance within the regime, the length represents regime length, and the horizontal centre line is the average value.

Figure. 7 Shifts in recruitment from the California Current large marine ecosystem (1955–2006).
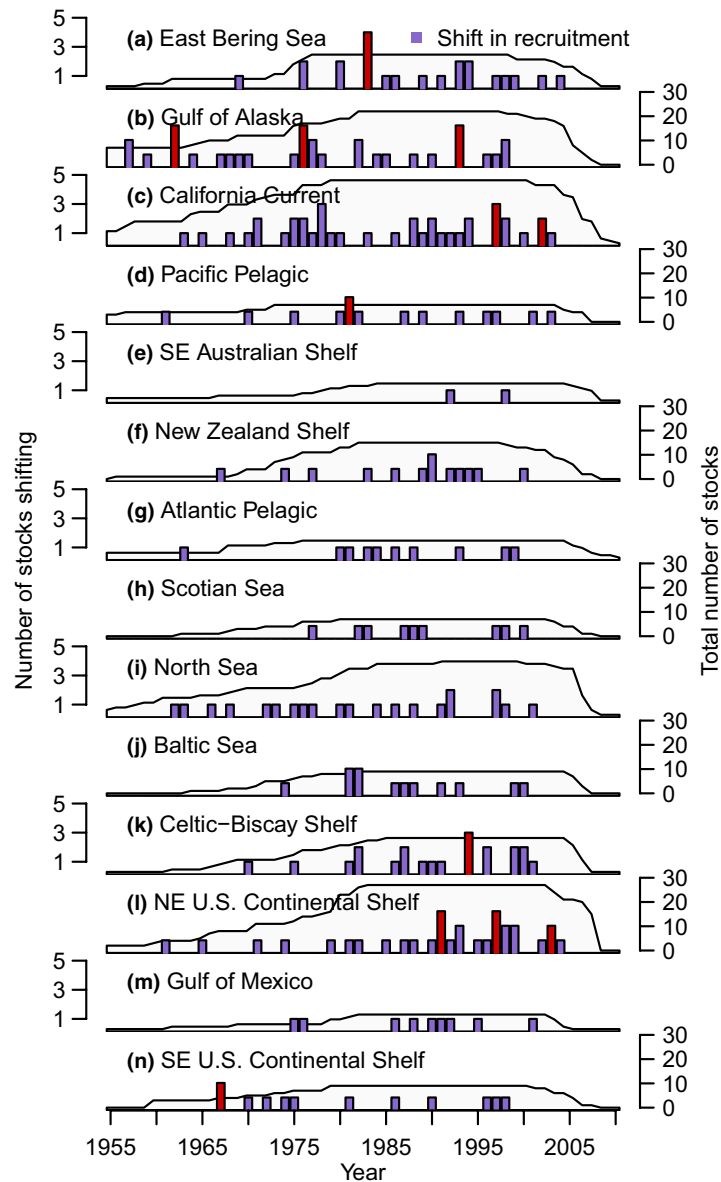
1998) and Gulf of Alaska (1976, 1977, 1998; Fig. 8b) mirrored climate shifts in the northern Pacific. Synchrony in changes in average recruitment also occurred in the eastern Bering Sea in 1983, which corresponds to a transition from a period of locally warm summer sea surface temperature (1978–1983) to a period of cooler temperatures (1984–2003) (NOAA 2013). Ten synchronous shifts in the California Current were observed, with eight of them coinciding with El Niño or La Nina years (Fig. 8c).

In the Atlantic, synchronous shifts in recruitment on the Celtic Biscay Shelf and in the Baltic Sea in 1981 and 1982 (Fig. 8j,k) roughly coincided with a shift in the average value of the winter North Atlantic Oscillation, NAO, in 1982 (Schwing *et al.* 2003). The Celtic Biscay Shelf had synchronous shifts in 1987, which roughly coincided with the reported ecosystem regime shifts in the North Atlantic forced by the NAO (Alheit *et al.* 2005). Average recruitment for many stocks in the Gulf of Alaska and the California Current

shifted in synchrony with stocks on the Northeast US Continental Shelf during 1997/1998 (Fig. 8l), potentially reflecting the observed similarities in climate indices over the Pacific and Atlantic oceans during strong El Nino events (Elliott *et al.* 2001). In total, synchrony in shifts in recruitment occurred 41 times in 10 of 14 LMEs. Some shifts in recruitment may be spurious given cyclical population dynamics; some synchronous shifts may be spurious given the number of observed shifts in an LME. Years in which recruitment for more stocks than expected shifted together (given a random sampling of the observed shifts; see methods) are denoted as 'significant' and occurred in 7 of 14 LMEs (Fig. 8).

Utility of environment/recruitment relationships

Synchronous shifts (regardless of their 'significance') are one logical entrance to the search for mechanistic explanations for shifts in recruitment given limited resources. However, relationships between recruitment and environment have long been hypothesized and searched for, with some successes (e.g. Bakun 1996; Cushing 1990; Wildebuer *et al.* 2013), but relationships discovered between recruitment and the environment are often not useful when providing tactical management advice for fisheries because of their instability [Myers 1998; a notable exception is the Pacific sardine, *Sardinops sagax*, Clupeidae, in the California Current (PFMC 1998)]. Identifying correlations between environmental indices and recruitment does not necessarily mean that an environmental index is driving recruitment (Granger 1969). Methods have been developed to attempt to determine causality of environmental forcing (Sugihara *et al.* 2012), but these methods have yet to be widely applied. In spite of these limitations, the character of the relationship between the environment and recruitment, can be useful in management strategy evaluations in which recruitment must be projected into the future (e.g. A'mar *et al.* 2009; Ianelli *et al.* 2011; Szuwalski and Punt 2012). Incorporating the potential periods, amplitudes and trends in environmental forcing into recruitment projections may drastically change the perceived trajectory of the 'future stock' and therefore management decisions in the present. However, a recent literature review by Punt *et al.* (2013) concluded that incorporating climate into management strategies only improves management

Figure 8 Number of stocks with changes in average recruitment by year within an large marine ecosystems (LME). Light grey polygon (background) is the total number of stocks for which there are recruitment estimates in a given year in an LME (axis on the right). Overlaid bar plots tally the numbers of shifts in average recruitment in a given year (axis on left; scale is different for 'total' stocks and 'shifting' stocks). Years for which the bar plot is red are 'significant' synchronies.

outcomes when the system is very well-known. This outcome is likely partly the result of the simulation studies included using stationary environmental forcing, rather than the non-stationary forcing that will likely be the reality of a future in which climate is changing. When projections incorporate non-stationary forcing (e.g. Ianelli *et al.* 2012), using more recent observations to

calculate targets can improve management outcomes.

Regime detection

Applying the variant of the STARS algorithm used here with a threshold of $P < 0.1$ may identify changes in average recruitment from time series

generated from white noise. This analysis was repeated with $P < 0.05$ to explore the sensitivity of our results to this assumption and the reduction in the total number of regimes was only 7 (from 160 to 153). The threshold determines how far from the mean an estimate of recruitment must be to initiate a regime. The mean of a time series may shift without observing a recruitment event outside of the confidence interval for the mean at a given threshold. Consequently, the cut-off of $P < 0.1$ was used a compromise between being unable to identify changes in average that may not be initiated by relatively extreme events and identifying too many regimes. Additionally, some have attributed long-term fluctuations in marine systems to red noise (Steele 1985) and have suggested that proclaiming sustained deviations from the mean value of a time series to be 'regimes' is improper. From the point of view of management, whether or not the underlying process is typified by white noise, red noise or true 'regime-like' behaviour is unimportant. A change in recruitment, regardless of its origin, will interfere with the ability of managers to achieve their stated goals and should therefore be identified and considered in management strategies.

The science behind the management of marine stocks is continually progressing, and data on stocks worldwide are increasing. Cross-correlation is a useful tool to help identify drivers of recruitment dynamics, provided dynamics do not appear to be dome-shaped. There are intrinsic statistical difficulties in analysis of the relationship between estimates of spawning biomass and recruitment derived from stock assessments (e.g. Dickey-Collas et al. 2014). Nevertheless, management advice relies on these estimates; therefore, management strategies should be consistent with these data. If recruitment is poorly related to spawning biomass, new measures for the health of stocks and management targets must be developed. Our results do not suggest that target biomasses should be abandoned, nor do we suggest targets should decrease or increase. Specific management actions will depend on the system in question. However, whatever those management actions are, they should be based on assumptions that are supported by data. The concept of the 'health' of a fishery can only have meaning within the context of the ecosystem in which it occurs. In the end, the ability to meet the world's growing protein needs through the harvest of marine resources may be different than projected if environment (and global climate change) influences the recruitment of marine species. Fisheries management must balance the risk of depleting stocks to low levels with the knowledge that productivity may change over time to effectively manage marine fisheries.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Figures 1 to 224.