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# ‘School-mix feedback’: a different way to think about low frequency variability in large mobile fish populations

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## Abstract

A conceptual perspective is introduced which appears to convey substantial explanatory power with respect to some prominent current issues in fisheries ecology, including evident regime shifts in resource productivity and/or in species dominance. Underpinning the proposed perspective are two key ideas. These are the ‘school trap’ concept and the notion of ‘affinities’ to specific ocean features or locations that may characterize individual fish. These two ideas lead to a mechanism, here termed ‘school-mix feedback’, by which mobile fish populations may automatically track low frequency environmental and ecosystem variability and make particularly rapid adaptive adjustments of behaviors and migratory tendencies to the associated changes in conditions. However the mechanism also appears to involve the possibility that a fish population could thereby fall into a short-period analog to an evolutionary feedback trap, from which it may not easily extricate itself without undergoing population collapse. Analogous adaptive responses to geographically-biased fishery exploitation may upset the integrity of naturally-evolved systems and potentially lead to chronic suppression of resource productivity. Possibilities for innovative adaptive management actions are suggested. Both heuristic and real explanatory examples are cited, in most cases dealing with pelagic fish stocks and upwelling ecosystems. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Fisheries science is currently confronted with a puzzling array of very strong signals, correspondences and recurring patterns in the population dynamics of the large fish populations on which large-scale fisheries depend. These are shaking our faith in some of the assumptions that have pervaded our science over the last century. What we have believed in before, seems to be becoming progressively more inadequate to explain the march of events satisfactorily. But the underlying connections and relationships continue to evade us. It seems that there must be some essential dynamics that are somehow escaping us.

For example, we are slowly realizing that not only are a large number of the world’s largest fish stocks varying radically on interdecadal time scales in ways that do not seem primarily explainable by fishery effects, but they are also doing so with a substantial degree of global-scale synchrony (Kawasaki, 1983; Lluch-Belda et al. 1989, 1992; Schwartzlose et al., 1999). Two logical implications of this synchrony seem to be firstly that the variability must be driven by global climatic teleconnections (Kawasaki & Omori, 1988; Kawasaki, Tanaka, Toba, & Taniguchi, 1991; Polovina et al., 1994) and secondly that the biological linkage mechanisms involved must be quite simple and direct (Bakun, 1996, 1998a,b). Thus the synchronizing signal from the global-scale climatic forcing cannot be reaching the fish species via propagation through a complex food web, otherwise nonlinear processes and associated chaotic local dynamics (e.g., May 1979) in the separate regional ecosystems would act to upset the coherence of the synchronous pattern. Rather the climatic effect must be acting directly on the fish species themselves, or if not, at least directly on their dominant food source.

Thus, we should be able to solve this problem. In fact, one may wonder why it has not already been solved. If the linkages between each separate stock to the climatic forcing are simple and direct, why has it proved so difficult to identify them clearly? One conclusion is that we have

been looking at the problem from the wrong point of view, i.e. that is to say that the basic conceptual framework conventionally used in fishery science to address such issues is either inadequate or inappropriate to resolve this particular problem.

I attempt to step back from the familiar, conventional ways of viewing fish stock variability in order to try to identify a new ‘angle of view’ that may have greater explanatory power in this respect. Confidence that one is on the right track (i.e., that the resulting arrangement of ideas might have a significant basis in actual fact) should be bolstered if the arguments seem also to shed some explanatory light on other conspicuous questions with respect to our current understanding of marine fish ecology. Among these are the following:

- (a) Why has the seemingly ‘primitive’ pelagic reproductive mode, where each fish may spawn many thousands of offspring, nearly all of which must die very early in life, been so successful in becoming the overwhelmingly dominant reproductive mode in modern marine fishes, having nearly totally supplanted more conservative modes (livebearing, brooding, parental care, clutches of few large eggs, etc.) that were more common among ancient marine fishes and continue to be quite common in modern freshwater and deepsea fishes?
- (b) Why, in pelagic ecosystems, where there is no place for prey to hide and where predators enjoy distinct size-related hydrodynamic advantages, do extinctions of prey species not occur more often (i.e. why do not the systems often collapse in the way demonstrated by simple nonlinear predator-prey models (e.g., May, 1979))?
- (c) Why, following an initial deep decline of a heavily exploited fish stock, does it sometimes seem nearly impossible, through fishery closures or other management actions, to return the stock to its former level of productivity?
- (d) Why do fish species with more terrestrial-type reproductive strategies (livebearing, or fewer more competent offspring, parental care, etc.) seem to be so much less resilient to fishery exploitation, even after making allowance for slower potential population responses?
- (e) Why do correlations between environmental variables and recruitment success tend to hold for a period of years but then abruptly ‘break down’ (i.e., no longer appear to hold at all)?
- (f) Why do habitual spawning locations often seem to be quite consistent from year to year but to drift radically from decade to decade in ways that are not simply explained by environmental properties such as temperature?
- (g) Why do large, mobile fish stocks tend to withdraw from the sites of major fisheries? And how do they manage to do it?

Underpinning the set of ideas introduced in this paper are two important ‘building block’ concepts. These are (1) the ‘school trap’ concept (Bakun & Cury, 1999), and (2) the idea of ‘affinities’ to particular geographic locations or ocean structures that may characterize individual fish. For the purposes of this discussion, the most relevant aspect of the school trap concept is that individual fish will not voluntarily leave a school and that in order to remain within a school, they must subordinate individual preferences, needs, and affinities to an overall composite volition, which reflects the relative frequencies of individual volitions contained within the school membership.

Clearly, most species of mobile schooling fishes do not seem to wander entirely aimlessly around the ocean, within the limits of their physiological tolerances. There is simply too much water volume to search, and size-dependent hydrodynamical advantages (Bakun, 1996) make rapid

growth far too important to survival, for access to favorable food concentrations to be left entirely to chance. Rather, fish seem to operate on some sort of ‘built-in plan’ that governs their migrational and locational tendencies (e.g., McCormick, Hansen, Quinn, & Saunders, 1998; Hansen & Quinn, 1998; many others). That is, they appear to possess some set of ‘affinities’ that guides them to particularly favorable areas or ocean conditions. The affinities possessed by individual fish may perhaps be inherent, or they could be the result of early life imprinting (Cury, 1994; Hansen & Quinn, 1998). It is also possible that where and when a particular individual has previously encountered a favorable location or set of conditions, the experience may be reflected in a degree of learned behavior.

## 2. ‘Red noise’ ocean variability and the pelagic reproductive strategy

Variability in the physical ocean system is characterized by a ‘red noise’ (Fig. 1) variance spectra (Steele, 1984). This means that the amplitudes of variations tend to grow larger as the time scale of variability increases (as opposed to ‘white noise’, which is often assumed in fishery models, in which the amplitudes remain relatively constant across the frequency spectrum). The very large heat storage capacity of water, as well as its mechanical inertia, results in organisms inhabiting oceanic ecosystems being relatively buffered against the intense variations in conditions experienced at seasonal and shorter time scales in terrestrial systems. On the other hand, the ever increasing magnitude of variability on longer and longer time scales must represent a potential disaster to populations of marine organisms that may be unable to track the changes and continue to adapt to them in one way or another. Such populations would eventually find themselves in an untenable position of being seriously maladapted to the ambient conditions.

The pelagic reproductive mode seems in some ways, to be a puzzling strategy for organisms needing to maintain population integrity in a dispersive media like the ocean (Sinclair, 1988;

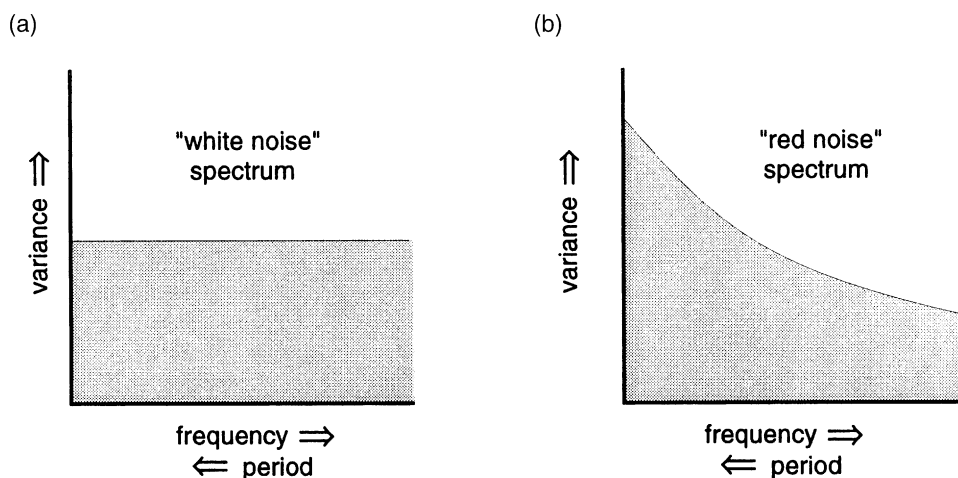


Fig. 1. (a) ‘White noise’ (random noise) variability spectrum, where variance tends to be spread equally over all frequency bands. (b) ‘Red noise’ spectrum where variance steadily increases toward lower frequencies (after Bakun, 1996).

Bakun, 1996), particularly in the vicinity of isolated islets and banks, and under the intensely dispersive conditions of upwelling systems, where wastage of eggs and larvae through their transportation away from their adapted neritic habitats is clearly enormous. However, it is undeniable that this reproductive mode is a successful one in modern bony marine fishes, and has nearly totally supplanted more conservative modes.

Here I will argue that one extraordinary advantage of this mode of reproduction is that it provides a means of automatically tracking and conforming to the longer-period components in the ocean's 'red noise' spectrum of variability. Frequent serial spawning of very large numbers of potential offspring by wide-ranging fish schools represents a continual exploration of the environment, which serves to adjust succeeding generations automatically to major environmental changes. Because so many potential offspring are produced at each 'test', a few 'correct' spawning trials might be so successful that the resulting progeny could be a significant component of the next generation's population structure. This massive degree of initial leverage may later be further multiplied by the response-rectifying effects of school behavior (which will be elaborated in the examples to follow). Thus the particularly successful affinities and behavioral traits may be effectively propagated and amplified in succeeding generations. In this way, the populations may effectively track the lower frequency components of variation, while avoiding fruitless belated adjustments to transitory higher frequency variability (for example, by allowing them to 'plow through' El Niño episodes, etc. effectively, without making any major adaptive adjustments that might leave them badly out-of-adjustment with events in the following year; see Discussion, Section 11).

Similarly, it will be argued that the pelagic reproductive strategy may allow the populations to react in a similarly automatic manner to changing patterns in either the predators they face or the prey upon which they themselves depend. In the pelagic environment, there are no refuges and gravity disappears as an effective constraint (Bakun, 1996). Because in a fluid environment size bestows distinct hydrodynamic advantages (Bakun, 1996), bigger fish generally have the capability to swim faster and more efficiently than smaller fish. Consequently, a larger predatory fish can ordinarily catch a smaller prey fish, if it is willing to expend the necessary energy to do so. The only advantage a prey species has over its predators in a pelagic situation is that its shorter generation time allows it to make correspondingly faster population responses. The examples and discussion to follow will attempt to make the case that (1) the pelagic reproductive mode automatically allows the prey species to employ this advantage to evade, and thereby interrupt, the growth of disastrous levels of predation, and that (2) a pelagic reproductive strategy could likewise serve the predator species by enabling it automatically, even if belatedly, to react to the pattern of variability presented to it by its more rapidly responding prey populations.

### **3. Example: hypothetical interaction of sardine and albacore tuna populations**

As an illustrative example, consider the following (deliberately oversimplified) 'cartoon' of an interaction between sardines and albacore tuna involving the major frontal interface (Figs. 2 and 3) that separates oceanic waters from upwelling influenced coastal waters off temperate eastern ocean coastal upwelling zones. The orientation of albacore tuna to such frontal interfaces is perhaps best documented off the west coast of USA (e.g., Laurs & Lynn, 1977), but similar behaviors undoubtedly occur in other temperate eastern ocean upwelling ecosystems (e.g., NW Spain,

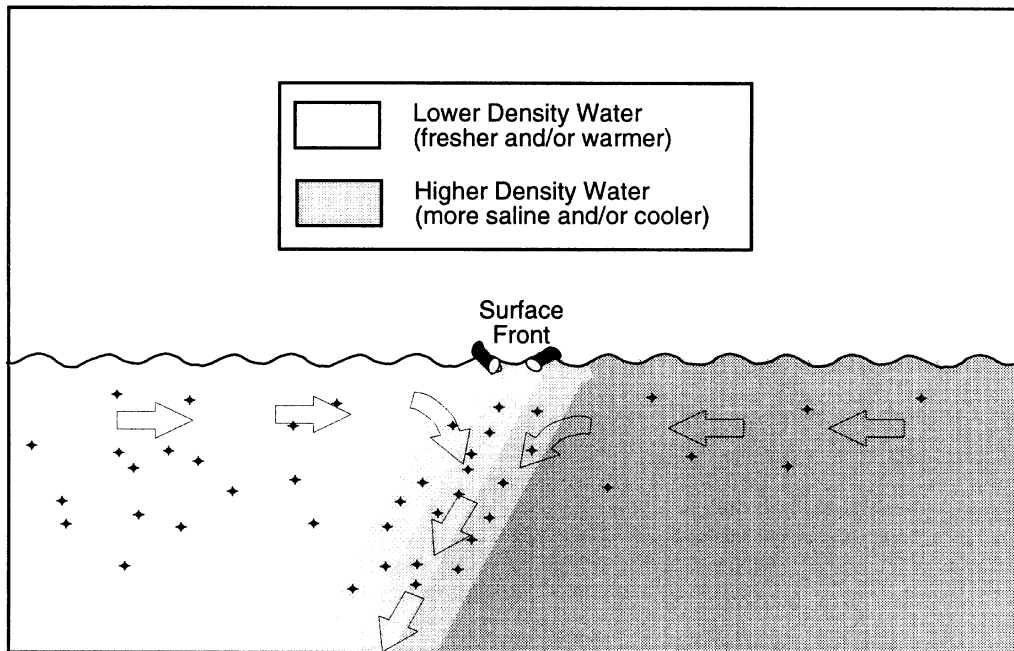


Fig. 2. Schematic diagram of a front between waters of differing density. Arrows indicate density driven flows associated with the formation of a mixed water mass at the frontal boundary, which sinks beneath the lighter surface water mass. 'Particle' symbols indicate planktonic organisms capable of resisting vertical displacement. Scales are distorted: vertical scale greatly expanded relative to horizontal scale; particles greatly magnified; surface waves not drawn to scale. Figure modified from Bakun (1996).

Canary Current, Benguela Current, Peru–Humboldt Current, etc.). During the periods of time when the annual visits of the albacore are neither lengthy nor intensive, some 'opportunistic' (Cury, 1994) schools of sardines may begin to stray away from their established zone of relative abundance near the coast (Fig. 3a) and 'discover' the region of enhanced food concentrations along the frontal region (Fig. 3b). Since they feed extremely well and are not being removed swiftly by predation, being serial spawners they will tend to spawn frequently. The resulting larvae and juveniles will also find conditions favorable for their survival and growth in the zone of enhanced concentrations of minute food organisms.

This will tend to result in the production of abundant offspring that have affinities with the frontal region. Let us suppose for the moment that this affinity may become imprinted early in life as proposed by Cury (1994). These offspring with imprinted 'offshore-frontal' affinities will mix with the rest of the population as they participate in the continual process of school fragmentation and formation, and they will exert a growing influence on the behavior of those schools in which they happen to be relatively abundant. For example, as they increase in their abundance and therefore in their representation in the 'mix' of affinities and tendencies within an individual school, more and more they will tend to impel the schools to expand their customary ambits to include the favorable feeding and reproductive conditions in the frontal region. The general expansion of the habitat and the access to particularly favorable conditions in the frontal zone would tend to support a general population increase. Moreover there will be a progressive relative

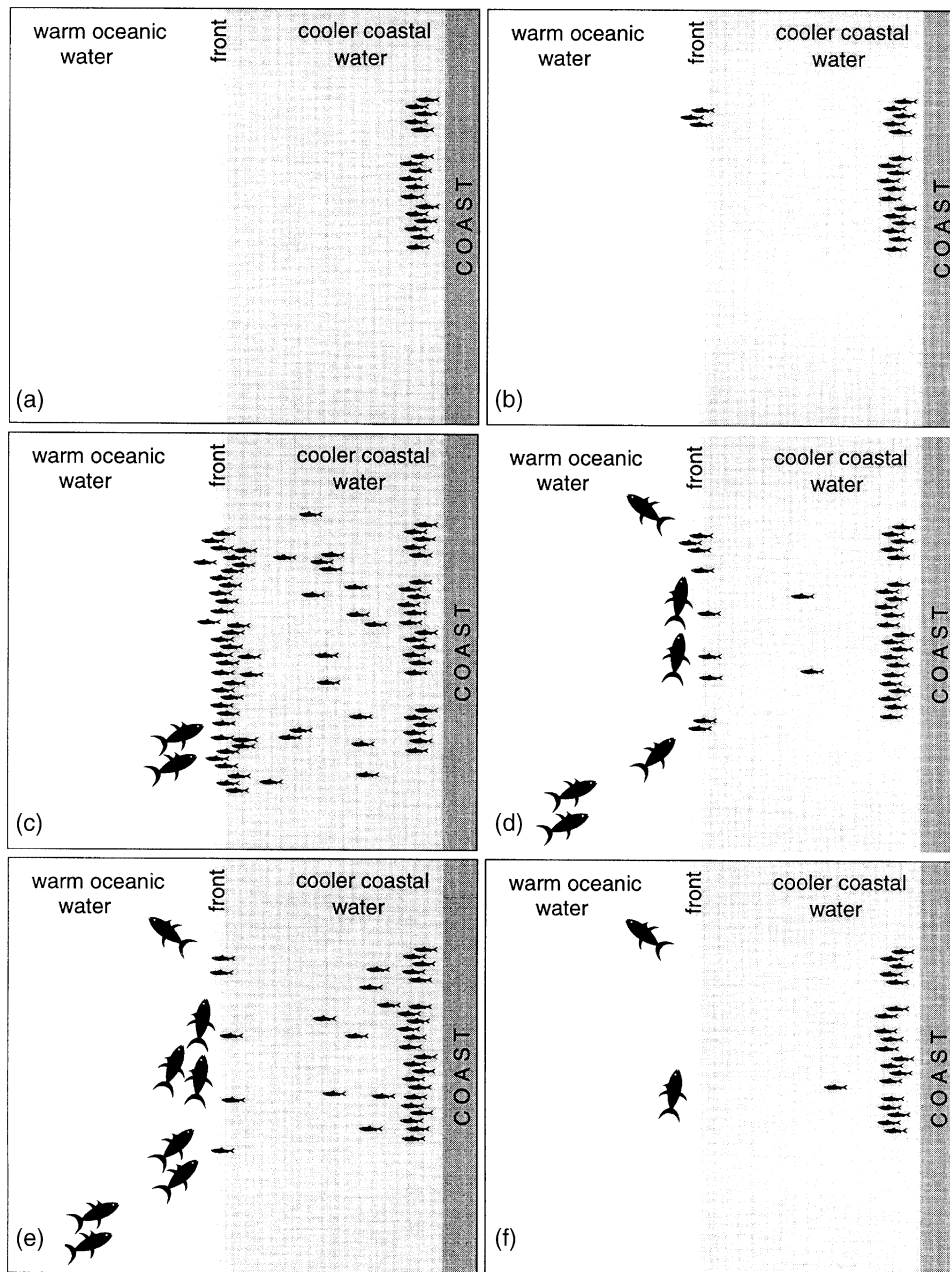


Fig. 3. Hypothetical multigenerational-scale sardine-albacore interaction in an oceanic front of the type generally found at the offshore limit of upwelling-conditioned waters in temperate eastern ocean boundary upwelling regions such as the California, Canary, Peru–Humboldt, and Benguela Current regions and off the coast of the Iberian Peninsula.

increase in individuals with affinities to the frontal zone and a corresponding greater influence of such individuals on school behavior and consequent ever greater affinity for the frontal zone of the population as a whole (Fig. 3c). Thus the sardine population may effectively spread out from its core distributional range in the upwelling-influenced coastal region to overlap the oceanic frontal interface. There they become susceptible to predation by the albacore tuna, which make feeding forays into the zone from the warm oceanic side, perhaps abetted by their well-known attraction to floating objects (Hunter & Mitchell, 1967) which accumulate in such convergent frontal structures (Bakun, 1996).

We can assume that eventually ‘opportunistic’ albacore schools (Fig. 3c) discover the newly highly favorable feeding opportunities that have developed in the frontal zone. They would have been in position to do so, because they contained a relatively high proportion of individuals with migratory affinities for the eastern extremity of their ocean basin-scale distributions. As the individuals in these schools feed efficiently and effectively in the favorable conditions, they will rapidly accumulate the energy stores they need to power them to the site of the next stage of their ocean basin-scale life cycle strategy and to support the rapid growth required by their particular wide-ranging high-energy strategy. Even though reproduction by these fish may be several years in the future, one may assume that these events must be important to their ultimate reproductive success. Otherwise, natural selection would not have mandated the very large energy expenditures involved in the associated migration. Success at this stage would thus contribute to their eventual reproductive success, to a resulting increase in relative frequency in the overall population of their eastern ocean migratory affinities, to a corresponding increasing frequency of individuals with such affinities within schools, and to a resulting increasing frequency of schools visiting the eastern ocean coastal frontal zone (Fig. 3d).

The consequent growth of predation pressure would soon act to reduce the concentration of sardines in the zone (Fig. 3d, e), and also to reduce the favorability of the frontal zone as a sardine reproductive habitat (as more and more adult sardines are consumed before having the opportunity to spawn) relative to the upwelling zone near the coast. This will lead to a decreasing frequency of frontal zone affinities in the sardine population, a corresponding decrease in the corporate attraction to the frontal zone acting within each school, and a resulting decrease in the number of schools visiting the frontal zone. Finally, a lack of sufficient numbers of individuals with frontal zone affinities within any schools may result in an effective cessation of use of the frontal zone by the sardine population (Fig. 3f).

This in turn puts the migrating albacore tuna population in a disadvantageous and perhaps even perilous situation. Having migrated a very long way through zones of more or less nonproductive waters to find the favorable feeding opportunity that has become ‘built in’ to the migratory behavior of their schools, they find themselves faced with a lack of prey with which to fuel the next leg of their long journey. It is quite possible that many schools might simply run out of energy and perish. Others may arrive in poor condition, with the energy stores needed to ensure growth and survival having been largely exhausted. The albacore population thus urgently needs a mechanism that enables it to withdraw from the disadvantageous situation before the situation becomes a crisis. Again, the pelagic reproductive mode may provide the mechanism that is needed, which may operate as follows to reverse the process that generated the situation.

Eventually the deteriorating reproductive success of fish returning from the eastern ocean migratory circuit would presumably act over time to lower the relative frequency of eastern ocean



migratory propensities within the overall albacore tuna population. This would lessen the strength of that tendency within the schools, resulting in a reduction in the magnitude of (Fig. 3f), and even eventually the complete interruption (Fig. 3a) of the migration to the eastern boundary oceanic front. This would reopen the opportunity for another re-colonization episode of the zone by the sardines, and a subsequent cycle of population expansion by the sardines would take place. This cycle would not have been possible had not the pelagic spawning strategy of the sardines being effective in orchestrating their withdrawal from the frontal zone, thereby forcing a longer-term withdrawal of the more slowly responding predator population.

Thus the two populations, the sardines and the albacore tuna, may both be preserved by their pelagic reproductive mode and their ‘school trap’ propensities from falling into a mutually-destructive ‘Robert May (1979)’-type tightly linked predator-prey feedback system (i.e. subject to chaotic system behavior and collapse).

Note that it is not a requirement that the sardine responses described above should necessarily be based on early life imprinting. They could also be the result of inherent tendencies acting in a similar way to those outlined for the albacore. That is, if the responses were based on inherent (genetic) tendencies, the initial sardine schools to visit the offshore front would tend to contain a relatively large number of individuals with inherent ‘offshore’ affinities. Good reproductive success in the frontal zone would increase these affinities in the population and consequently within the schools, poor reproductive success would decrease them, etc., leading to the same cycle of events as depicted in Fig. 3.

#### **4. Withdrawal of fish stocks away from established fisheries**

Following the discussion from the previous section, from the point of view of a fish population, a fishery represents nothing more or less than an additional massive source of predation pressure. Consequently, in the same automatic manner as the withdrawal from a damaging predator population illustrated in the hypothetical albacore–sardine example presented above, pelagic spawning fish populations may tend to withdraw automatically from established fisheries.

The experience of Morocco with its central subpopulation of sardine may be a case in point. There, a fishing industry developed in the adult feeding zone at the northern end of their migration route from their primary reproductive grounds to the south. Major fishing ports and extensive canning industries were established at ports such as Safi, Essaouira and Agadir. The fish have ceased to migrate to the north, and all that is left of the active fishery operates in the reproductive grounds to the south (near Tantan). Meanwhile, the biomass and productivity of this central stock seem to have been substantially depressed. As a result the Moroccan Government has been considering an enormously expensive and socially-disruptive move of a segment of industry and its associated population and infrastructure to a nearly uninhabited and infrastructure-bereft area on its Saharan coastline in order to gain access to the less impacted southern stock. (Do Chi & Kiefer, 1996).

Clearly, individual fish cannot simply move away from the danger represented by a fishery (even if a fish could become aware of such a danger, by the time it did so it would almost certainly be caught). But one explanation for such a population-level response is as follows. During the continuous process of school fragmentation, population mixing, and re-formation of

new schools, whichever school by chance happens to include a particularly high percentage of fishes with strong affinities to return to the good adult feeding area in the upwelling zone, will be the school most likely to migrate to that zone, i.e. to where the fishery is operating. Since the fishery thereupon takes out that school which contains higher than average content of individuals having a high degree of migratory affinity, it selectively removes the adults with a propensity to migrate from the system. In this way, the migratory affinity may be continually selected out of the population until insufficient individuals remain with the affinity to induce any schools to migrate to the fishery zone. Thus the migration essentially ceases, and the population has effectively removed itself from the situation where it had been available to the fishery.

Those familiar with the course that the Californian sardine followed in its famous demise (MacCall, 1986) may recognize distinct similarities to the Moroccan experience. Initially, the Canadian fishery at the extreme north of the adult migrational circuit collapsed. Then, as the migrational ambit progressively shrank away from exploitation at its northern end, the major fisheries of San Francisco, Monterey, and finally San Pedro which is within the primary reproductive area itself, successively collapsed from north to south. Finally, all that was left was a small, nearly unexploited, nearly non-migratory, remnant population situated off the Mexican coast of Baja California. Once the fishing stopped then the selective pressure against sardine migrations was removed, and as the ocean climate became favorable, the re-emergence of the migratory tendency began to be favored and sardine stocks have again re-appeared in Canadian waters (McFarlane & Beamish, 2001).

Another example is the Brazilian sardine (*Sardinella*) population, which is contained within the large coastal bight of southeastern Brazil between Cabo Frio in the north and Cabo de Santa Marta Grande in the south (Saccardo, 1983). At the onset of the industrial fishery, the population seems to have been concentrated at the northern end of the bight area and adult sardines apparently migrated northeastward out of the bight proper to feed in the upwelling zone off Cabo Frio (Bakun & Parrish, 1990). A very large fishing effort was developed rapidly near Rio de Janeiro in the northern zone. The response of the fish stock was to move southwards, away from the Rio de Janeiro fishery, which then collapsed. A replacement fishery then built up in the central part of the bight, opposite São Paulo. The fish population responded again by moving further south, inevitably resulting in the collapse of the local fishery. A third major fishery has been established even further south, at Santa Catarina at the southern extremity of the coastal bight (Sunye, 1999). At some point in the process, adults apparently ceased their habit of migrating to feed in the Cabo Frio upwelling zone. Concurrently with these shifts, the productivity of the stock has declined in a series of distinct steps. The fish population now appears to be responding to fishing pressure currently concentrated in the south off Santa Catarina by shifting back north again (Dr. Patricia Sunje, personal communication).

Readers may search their own knowledge and experience to find similar examples of evident withdrawal of mobile fish stocks from sites of major fishery exploitation. The important point to note is that, according to the hypothesis presented in this paper, this need represent no actual 'decision' or active evasive response by individuals. But it comes about through a purely automatic consequence of the pelagic reproductive strategy, acting through modification of the frequencies of individuals possessing particular migration-related affinities (i.e., through alteration of the 'school-mix'), which are then constrained to operate in concert by the school trap dynamics.

## 5. Illustrative example: an speculative interpretation of the Namibian sardine experience

The pattern of events that has occurred over the past few decades in sardine fishery off Namibia serves as an instructive illustration of some potential connotations of the speculative, conceptual viewpoint that I am exploring in this paper. It is in no way intended to be read as a comment on, or critique of, the management of the Namibian sardine resource, which is being managed according to currently accepted state-of-the-art scientific understanding and methodologies.

The Benguela Current system includes the strongest sustained locally wind-driven coastal upwelling of any of the eastern boundary coastal upwelling zones of the world ocean. For example, the annual volume of water per unit length of coastline upwelled at the upwelling centre near Lüderitz (Fig. 4a) is 250% that produced at the Cape Mendocino upwelling core of the California Current system. The upwelling core to the north in the vicinity of Cape Frio (Fig. 4a) is very nearly as intense. Because of this massive upwelling, the area is characterized by extremely high rates of primary productivity. However, the very strong offshore transport and high levels of wind-induced turbulence along much of the coastal ocean does not appear to provide ideal conditions for the fish either to feed or to reproduce (Bakun, 1996).

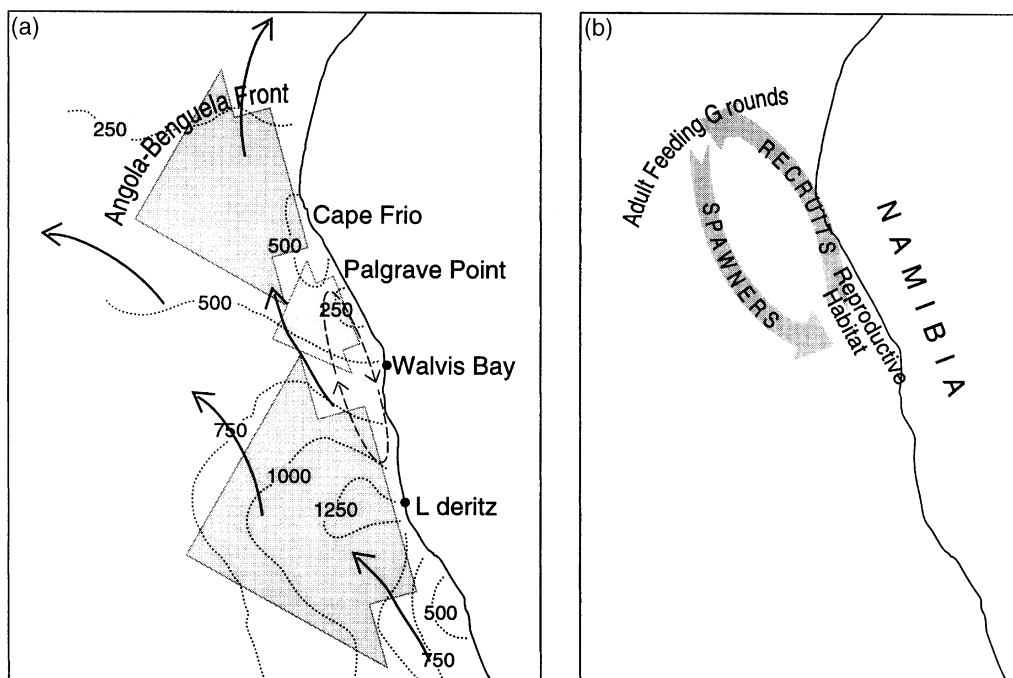


Fig. 4. (a) Diagram of characteristic summer flow features and wind-mixing index ( $\text{m}^3 \text{s}^{-3}$ , dotted contours). Broad, shaded arrows indicate surface Ekman transport (arrow symbols drawn so that linear dimensions are roughly proportional to transport magnitude). Solid arrows indicate the general trend of the underlying geostrophic current flow (no magnitude implied). The existence of a more or less enclosed gyral circulation south of Palgrave point is suggested by the dashed oval in that location. Figure modified from Bakun (1996). (b) Hypothesized original adaptive migration pattern that may have linked optimal adult feeding grounds to optimal reproductive habitat, thereby maximizing stock productivity.

In the mid-1960s, the pilchard (sardine) biomass in the northern Benguela was estimated to be about 10 million tonnes, and annual catches were about 1.5 million tonnes (Boyer, 1996). Since then, the biomass has consistently remained at about one million tonnes, a tenth of the earlier levels, while catches have remained in a range at 50,000–100,000 tonnes (Boyer, 1996). In the mid-1960s, most of the standing stock and the bulk of the reproductive output is believed to have been associated with the broad coastal embayment between Palgrave Point and Walvis Bay (Fig. 4) that is situated between the two intense upwelling centres near Cape Frio and Lüderitz. This area appears to be the best available local approximation to the ‘canonical type’ of preferred reproductive habitat for coastal pelagic fishes inhabiting eastern ocean boundary upwelling regions (Bakun, 1996, 1998b). The coastal configuration provides a habitat within the bight sheltered from the large-scale, alongshore wind stress and consequently

1. Turbulent mixing energy input drops to much lower values (seasonal mean ‘wind speed cubed’ mixing index values generally less than  $250 \text{ m}^3 \text{ s}^{-3}$ ) than along the exposed coastal segments to either side,
2. Offshore Ekman surface transport likewise falls to a local minimum,
3. A more or less enclosed gyral circulation pattern (Nelson & Hutchings, 1983; Gründlingh, 1999), which may help to retain larvae within the near-coastal zone, tends to form within the bight interior (Fig. 4a).

This constitutes an ‘ocean triad’ (Bakun, 1996, 1998b) where, not only is there an appropriate sequence of enrichment, concentration and retention yielding favorably high concentrations of food (zooplankton of all sizes appropriate for larval and juvenile feeding), but also the local gyre helps retain the larval and juvenile fishes within the favorable area.

Another widespread characteristic pattern (Parrish, Bakun, Husby, & Nelson, 1983; Bakun, 1996) of temperate eastern ocean coastal upwelling systems is that the adult sardines tend to migrate out of the principal reproductive habitat. Thereby they gain access to particularly favorable feeding grounds in areas of strong enrichment and concentration, but where the retention processes, the third element of an ‘ocean triad’, may be lacking. Here the ability of adult sardine to feed directly on phytoplankton is essential, because in the absence of any retention mechanism large localised concentrations of zooplankton may not have time to build up. The strong swimming ability of the adult sardine enables them to counter the tendency to be advected offshore out their favored coastal habitat. If the same pattern occurred in the northern Benguela region as elsewhere, during the high biomass years adults may have been migrating northwards from the main reproductive grounds to feed in the area of the Angola–Benguela Front (Fig. 4) where the wind-driven ocean surface transport tends to be directed strongly offshore (Parrish et al., 1983) and where frontal structures (Fig. 2) concentrate production resulting from recent upwelling, as the waters are being transported offshore out of the coastal zone. Boyer (1996) confirmed that in the northern Benguela, the juvenile sardine are particulate zooplankton feeders whereas the adults are filter feeders, feeding predominantly on chain-forming diatoms. In recent years, there has been no systematic adult migration, and the available evidence suggests that nearly all of the stock and essentially all of its reproductive is concentrated in the Angola–Benguela Frontal Zone.

Note that in the northern Benguela region, the build up of the massive fishery (largely composed of Soviet-bloc distant-water fleets) was established directly within the primary reproductive habitat

itself rather being focussed the migration route to adult feeding grounds as was the case in the Moroccan and Californian examples. The highly productive linked system (Fig. 4b) was thereby faced with the predation pressure of an extensive industrial fishery, positioned to sweep up the compact, migrating schools of large, reproductively-ready adults as they entered the reproductive area from the north. This suddenly inflated the ‘cost’ of the migrating strategy, and may well have been sufficient to shift the reproductive advantage toward individuals that did not undertake the migration but remained to complete their spawning in the Angola–Benguela Frontal zone. Fewer and fewer schools would then have contained large numbers of individuals with strong migrating tendencies (i.e. with strong affinities to the primary reproductive zone), and those schools that did would have tended to be rapidly removed by the fishery as they migrated into the zone of heavy fishing. The result may have been a steady preferential removal of individuals with strong migrating affinities from the population. As the affinities acting to bias the collective volition within the sardine schools towards migration would thus have progressively drained away, the cycle of adaptation for migration may have been broken in this population.

The destruction of the synergism represented by the migrationally-linked system may have adversely affected the productivity of both component areas with respect to sardine production. The southerly reproductive grounds would have been deprived of a massive influx of fat reserves accumulated by adults in the feeding grounds to the north, which could be converted to reproductive products, to be injected into the favorable reproductive habitat to the south. This reduced the reproductive potential in the extensively exploited zone, and may have made it even more difficult for the stocks to withstand the onslaught of the heavy fishery pressure. Conversely, the northern feeding zone would be deprived of the continual influx of new fish to compensate for the relatively poor local reproductive conditions. The result may have been the division of the stock into two ‘parts’ whose sum productivity is just a fraction of the original ‘whole’. This conforms to the observations that the stock has remained stuck in a low biomass and low productivity state for an unexpectedly long time after the implementation of modern and management practices.

## 6. A new ‘slant’ on ecosystem integrity

This suggests a new facet to the concept of ecosystem integrity. Generally, it has been noted (e.g., Beverton, 1990; Steele & Schumacher, 2000; Hutchings, 2000) that, inexplicably, long-exploited fish populations often seem to be less productive once they have suffered an initial fishery-related population collapse than they seemed to have been in their virgin state. Similarly, Pauly, Christensen, and Walters (2000) has found, in the behavior of their ‘FIB index’, a shortfall of expected return in terms of increases in total landings as global fishery exploitation progressively moves to lower trophic levels.

In the case of the northern Benguelan pilchard, according to my interpretation presented above, it may be impossible to restore the productivity of the resource to its former range without somehow being able to restore the integrity of the originally-evolved system, i.e., by restoring the migratory linkages that allow the opportunities afforded by different parts of the regional system to be exploited to the full by the population.

This may not be easy. Individuals, regardless of their individual tendencies and affinities,

perform their migratory behaviors within the context of the ‘school trap’. Thus, once the population has become dominated by a different mixture of tendencies, reversion to the former situation may be extremely slow or may never happen. If the schools no longer visit the more favorable reproductive habitat, there will be no reproduction from that area to provide a pool of individuals that will increase the frequency of affinities to that area within the composition of the schools to migrate to that area. The situation may be analogous to a classical evolutionary feedback trap (although of course acting on much shorter time scales). Once integrated migrational tendency within the schools falls below a critical threshold, the frequency of migrations to the favorable reproductive grounds will rapidly diminish. There will also be a progressive diminution in the production of individuals with the appropriate migration affinities, as well as a lowering in the productivity of the stock.

A surprising implication of this line of thought is that such a negative trend may actually be enhanced and maintained by the conventional management procedures aimed at conservation, which may set small total allowable catches (TACs) that are only a minor fraction of the total estimated biomass. However, because the fishing ports, marketing facilities, consumer demand, and the fishermen themselves tend to be concentrated near the site of the formerly productive fishery, that minor fraction tends to be taken in that same location. Since the TAC is set at a low level, there is little incentive to expend resources searching further afield for better catch rates. The result is that whenever stochastic variability in composition of small schools may even temporarily allow an opportunist migrating volition to dominate the behavior of a small percentage of schools, so they might return to the formerly favored spawning grounds, a fishery is already there to remove them before they can spawn and thereby begin to restore of the migrational affinities within the population as a whole. Thus, the conventional management methods, rather than serving to allow the stock to rebuild to its former productivity, may established a ‘conduit’ for continually draining away of the very affinities and tendencies that could eventually allow the former ‘system integrity’ to be re-established. Consequently the stock may be inhibited from rebuilding to its former level of productivity and biomass.

## **7. Generalization: the school as an adaptive structure**

Intriguingly, this line of argument projects the school itself into the role of an adaptive entity that would be able to change its established habits and behaviors rapidly in response to changes in the frequency of individuals with given traits and affinities. Note that it is not necessary for any such school to have a longstanding identity or autonomy. It is well known that schools of small pelagic fish species frequently split up and reform in new combinations, often with a large component of diurnal rhythm. The only requirement is that, when new schools form, they constitute a sample of the ambient background distribution of traits and affinities. An evolving process proceeds as these altered frequencies of traits and affinities operate to change the behavior of the schools in a manner that further alters the background distributions of traits and affinities. The potential for extremely rapid responses exists because of the very large numbers of offspring, and the very large average mortality rates of potential offspring, which are ‘sacrificed’ to the selection process during each spawning trial. That is to say, even if only a few schools get it exactly right, they have the potential to shift significantly the background frequency distribution of tendencies

and affinities within the overall population from which the membership of newly-formed schools will be continually drawn, toward the distribution in those few currently successful schools. The shift is then rectified by the ‘school trap’ behavioral responses that drives a shift in the effective affinities and propensities not just of these offspring, but of the entire inter-schooling population.

Thus we have a process that acts somewhat like biological evolution, involving selection of currently desirable traits to yield a more advantageous response to current conditions. But this school-mediated ‘school-feedback’ adaptive process can probably occur very much more rapidly than biological (genetically-mediated) evolution ever can.

Moreover, the background frequency distributions of individual traits and affinities, and the consequent school behavioral and migrational propensities, would obviously have the potential to evolve more rapidly in species with shorter life cycles. Thus, the ‘school-mix’ structure of a prey species gives it the capacity to adapt to fluctuating environmental conditions faster than its predators. This allows both predator and prey continually to evade being caught in a mutually-destructive, tightly-linked predator–prey loop (see the heuristic example of Section 3).

When a population becomes fragmented into disjointed subgroups, as often occurs when total population biomass happens to be low, there may be separately evolving school-mix structures, each confined to a relatively isolated segment of the total population. When the population biomass is high, the fishes tend to expand their distribution to occupy their entire regional habitat (Lluch-Belda et al., 1989; MacCall, 1990). All segments tend to interact, and schools frequently meet and exchange membership throughout the total population range. The trend would then be towards a single school-mix structure that may adapt toward greater and greater specificity in a period when environmental and ecosystem trends can be effectively tracked by the school-mix feedback mechanism. As long as this increasingly specific solution tends more and more toward a currently ‘correct’ mode, the population may continue to grow, leading to ever more frequent mixing of the schools and greater homogenization of school membership demographics and corresponding behavioral propensities. However, this increasing specificity may place the population in jeopardy of falling into a feedback trap from which, when conditions change radically or abruptly, the tracking mechanisms may fail to extricate the population without it suffering a collapse.

## **8. Heuristic example: hypothetical interpretation of some elements of the Japanese sardine experience**

To illustrate some additional connotations of the school-mix feedback mechanism, we now construct a speculative rationalization of information on the Japanese sardine presented by Hiramoto (1991). In the period of low abundance that preceded the massive population expansion that occurred in the 1970s, Hiramoto postulated there were two groups of sardines inhabiting Japanese waters. One was a coastal group living mostly in bays and other near-coastal waters, which was fast growing and spawned at one year of age, but undertook limited, if any migration. The other was an oceanic group, which migrated over a large area, but grew slowly and only spawned in their second or third year. As the population started to expand in the mid-1970s, the migratory group seems to have become explosively dominant; by the early to mid-1980s, concentrations of migratory sardines extended eastward, half way across the North Pacific to beyond the

International Date Line (Wada & Kashiwai, 1991), and also colonized the Sea of Japan and the coastal waters of Korea and the former Soviet Union. Hiramoto concluded that the non-migratory group may have lost its autonomy during this expansion, and after 1980 the two stocks merged. The former spawning ground of the coastal group off western Honshu appeared to have been abandoned (e.g., see Fig. 4, in Wada & Oozeki, 1999). Later, after the mid-1980s the sardine population began an unexplained progressive multi-year collapse.

Logically, some environmental change or trend commencing in the early to mid-1970s must suddenly have strongly favored the migratory strategy of the oceanic stock in which the apparent disadvantages of slower growth rates and later maturation must have been more than offset, perhaps by reduction of intense predation or some other factor reducing mortality at one or more life stages.

As the migratory group grew in abundance, it essentially filled the entire regional habitat, so that it impinged upon and circulated throughout the coastal areas occupied by the non-migratory group. The members of the non-migratory would have tended to become entrained in 'school traps' (Bakun & Cury, 1999), and so become dominated by the more abundant migratory group. Individuals of the non-migratory group would have found themselves having to take up the life style of the migratory group, to which their particular traits would be unsuited. This would have favored a progressive decline in their relative numbers. In addition because the non-migratory group inhabited waters close to the major fishing ports, they may have been exposed to disproportionately heavy fishing pressure as the overall population increased. At some point the continual interchange between the abundant schools that now freely traversed the entire range of distribution probably resulted in the mixing and homogenization of the distribution of migrational tendencies and affinities within the schools. The result would be the amalgamation of the population in a single regional-scale school-mix structure where formerly there had been at least two if not more. While this single school-mix structure continues to be able track and adapt to the environmental oscillations the population will retain a unified, regionally-coherent structure. Consequently, the population may continue to grow rapidly, intensifying the tendency for homogenization of school composition and behavioral propensities. For example, the schools may take on a more and more 'super migratory' character.

However, once the external trend is broken the single school-mix structure which may have become quite specifically-adapted, may lose its ability to track the trends and find itself in a 'feedback trap'. The loss of diversity of available school behavioral responses will then handicap the location of a viable strategy to cope with the new conditions. For example, if the advantage of the highly migratory strategy were to be lost through a regime shift, whatever progeny of the former non-migratory group that remain would continue to be submerged within schools operating as 'super migratory' school-mix structures. Thus, even if significant numbers with non-migratory adaptations had managed to survive the adverse selection process in these schools, they would be unable to break free from the 'super migratory school traps' to reestablish the formerly successful lower-biomass non-migratory strategy. This could only re-occur after the population had collapsed sufficiently so that much smaller schools of random combinations of individuals could remain autonomous (not meet and consequently become incorporated and mixed within larger school groups) long enough to initiate a new, fresh process of school-mix feedback to begin to track and adapt behavior and geographic affinities to the new conditions.



## 9. Species alternations (anchovies versus sardines, etc.)

Over the history of fishery exploitation, for which we have direct evidence of the population fluctuations, sardines and anchovy populations have almost never coincided at high abundances in the same region. The alternation between these two species groups between exclusive high biomass periods has been one of the most striking features of the recently recognised ‘regime change’ phenomena in marine ecosystems (Kawasaki, 1983; Lluch-Belda et al. 1989, 1992; Kuroda, 1991; Bakun, 1996, 1998b; Schwartzlose et al., 1999). The consistent pattern of out-of phase alternation is remarkable, since it has been extremely difficult to identify any mode of substantial adverse population interaction between the two species such as competition for food, preferential predation by adults of one species on the larvae of the other.

Bakun and Cury (1999) have suggested the ‘school trap’ mechanism as a potential factor contributing to the missing adverse interaction between the two species. Since the less abundant of the two species is evidently driven by its schooling imperative to school with the more abundant species, it may suffer similar adverse effects as described for the within-species interaction discussed in the previous section (but probably much more intense since anchovies and sardines probably differ more extensively in their needs and capabilities, than do more migratory and less migratory groups of the same sardine species). The result is that once a species’s abundance declines, the ‘school trap’ mechanism may tend to impose a burden on its productivity driving it to even lower abundance. But while that may supply the ‘feedback instability’ mechanism needed to explain the tendency for opposite extreme states of overwhelming dominance by one or the other of the species pair, rather than deviations about some mean ‘ideal’ ratio between the species’ abundances, it does not explain how the observed shifts from one extreme state to the other may be initiated. For this we need to rejoin the argument of the previous two sections, where we left the dominant species in a process of population collapse because of its inability to ‘back out’ of its overly-specific set of adaptive responses, in the face of a major change in conditions.

While such a collapse is occurring, the formerly suppressed population may already be primed to react. Having fragmented during its low population state into small disjunct locally-resident subgroups (Lluch-Belda et al., 1989), some of these subgroups may already possess the suite of adaptive solutions to emerging environmental conditions. If one or more of these represents a fairly suitable initial fit to the new circumstances, the species would have the crucial ‘head start’ in the race for dominance. This race begins as the population collapse of the formerly dominant species relaxes the suppressive adverse school-trap effects (Bakun & Cury, 1999). It is interesting in this context that anchovy populations have been found to exhibit much larger genetic diversity than sardine populations (Hedgecock, 1991), perhaps reflecting a tendency for it to maintain a more permanent variety of inherent affinities and tendencies within a population. Conversely sardines, which are naturally the more migratory, may rely to a greater degree on the broad-scale exploration and rapid school-mix feedback mechanism we have proposed here to develop a better adaptive response to changed conditions.

In any case, the species that manages to win the race to the point of numerical dominance where it can begin, via the ‘school trap’ mechanisms or other means, to suppress the other species, will be the one that dominates the next multi-year interlude. Should this be the species that had been formerly dominant, the result is an episode of major fish population variation, which may be correlated with a combination of local and/or global environmental variables. If, however, it

is the species that was formerly suppressed that manages to use its greater diversity of responses to win the dominant position, the result is a ‘regime change’ in species dominance.

## **10. Locking onto and growing with a climatic trend**

Now we arrive at a key question. How do we link the rapid adaptive process that we have called ‘school-mix feedback’ to synchronized population variability in many of the world’s largest fish populations, as was manifested rather convincingly particularly during through the early 1970s into the mid-1980s? During this period, sardine populations in widely separated corners of the Pacific expanded explosively (Kawasaki, 1983), while the anchovy populations declined (Lluch-Belda et al. 1989, 1992), led by the famous collapse of the Peruvian anchoveta, which had previously supported the largest fishery that has ever existed on earth. Various other large populations of small pelagic fishes around the world, as well as major groundfish and salmon stocks of the subarctic Pacific, followed similar patterns of expansion or decline during the same period (Bakun, 1998b; Schwartzlose et al., 1999). Then, during the mid-1980s these trends generally abruptly reversed (or at least were temporarily interrupted, as for example in the case of the northeastern Pacific sockeye salmon).

As indicated in the Introduction, there seems to be no other way to explain the synchronization of these population variations other than as a consequence of global climatic teleconnections. However, no single climatic or environmental property, such as temperature has been found to have varied in the same sense in all the various regions where either simultaneous growth or declines of similar species groups had occurred. Logically, one would expect that any climatic/environmental effects must have acted in some way to interfere with established biological population-control mechanisms thereby initiating the synchronized, explosive population expansions.

One thing one notices when examining environmental characteristics during this period early 1970s to the mid-1980s is the presence of particularly strong monotonic decadal-scale (low-passed) trends. For example, it was pointed out early on (Kawasaki & Omori, 1988) that this period corresponded to when there was a particularly rapid increase in global mean temperatures. But of course this can only suggest some global climatic effect, since no fish has the ability to sense a global mean temperature, and regionally the temperature trends differed widely. For example, the western and eastern Pacific regions are generally out-of-phase with respect to temperature (Uda, 1962). More particularly, this period was marked by a deep decadal-scale decline in a low-passed version of the Southern Oscillation Index (SOI), indicating a tendency for progressive relaxation of the ocean-atmosphere system of the tropical Pacific; a sort of decadal-scale analog to an El Niño episode (Bakun, 1996). This relaxation appears to have been countered by intensified dynamics in many of the peripheral regions of the world’s ocean. For example, this mid-1970s to mid-1980s period was characterized by general intensification of the Aleutian Low pressure system (Norton, McLain, Brainard, & Husby, 1985; Wooster & Hollowed, 1995). This affected the entire subarctic Pacific region, including the habitat of the Japanese sardine. Parrish, Schwing, and Mendelssohn (1999) indicate that during the decade after the 1976 winter, eastward wind stress, as inferred from marine weather reports, doubled over a broad area in the central North Pacific and that the line of wintertime zero wind stress curl was displaced about 6° south-

ward. These trends in the North Pacific are well represented in the Pacific Decadal Oscillation (PDO) time series (Mantua, Hare, Zhang, Wallace, & Francis, 1997) in which this period showed the strongest increasing trend of the PDO since 1900. In addition, wind-generated ocean processes (turbulence, offshore-directed Ekman transport, etc.) appear to have increased strongly off Peru. There was also a pattern of apparent rises to a higher general level of intensity of upwelling-favorable winds during the spring-summer upwelling seasons off California, northern Chile, north-western Africa, and the Iberian Peninsula during this period (Bakun 1990, 1992; Roy, 1990; Yáñez, 1991). Off central Chile the mean upwelling rate apparently did not intensify, but the wind-induced turbulent mixing increased dramatically during this period, whereas off south-central Chile, the upwelling-favorable wind stress underwent an opposite sharp long-term relaxation (Yáñez, Barbieri, & Santillán, 1992).

This general prevalence of strong environmental trends during the period makes it tempting to try and identify a simple rationale by which the existence of a strong trend itself might interact with biological control mechanisms in a way that would promote population growth. Such a rationale can be constructed on the basis of the school-mix feedback mechanism being explored in this paper.

For example, suppose that a new opportunity such as the development of a particularly favorable oceanic structure (for example, a front such as illustrated Fig. 3 developing in a new location) suddenly opens up because of a climatic or other ecosystem change. If, as argued above, a population of small pelagic fish could adapt their school affinities faster than their predators could, it would tend to enjoy a temporal ‘window of advantage’. This would enable its population to increase dramatically before the predators would be able to respond (e.g. Fig. 3a–c). However, if the feature is persistent and stable, the predators may soon catch up (e.g., Fig. 3d), thereby canceling the temporary advantage enjoyed by the small pelagic species (e.g. Fig. 3d–f).

However, if the feature were to move continually, but in a sufficiently regular fashion that it could be tracked by the automatic mechanisms of school-mix feedback, the prey population might then be able to stay ahead of its more slowly adapting predators and thereby extend its ‘window of advantage’ and continue to grow in abundance.

Having used the example of Fig. 3 to make the general point, it must be said that major frontal interfaces separating oceanic waters and upwelling-influenced coastal waters are unlikely to undergo radical shifts in position in response to decadal-scale climatic trends (although in a real situation an intricate shifting complex of frontal filaments may develop, rather than a single linear front in the idealized example; the mean strengths and positions of the various frontal segments may shift significantly in time along with a climatic trend). The types of variable ocean features that are more likely to support the ‘growing along a trend’ process being suggested here, might be shifts in favorability among the various available ‘ocean triad’ structures (Bakun, 1996; Bakun, 1998b) perhaps interacting with shifts in location of wind-controlled ‘optimal environmental windows’ (Cury & Roy, 1989; Durand et al., 1998).

This elementary mechanism must represent a highly simplified cartoon of processes that will be more complex in real marine ecosystems. However, it may serve to suggest the manner in which a strong multi-year climatic trend may open a series of ‘loopholes’ in the established pattern of biological controls, which a nimble rapidly-responding low trophic level fish population might exploit, thereby initiating a sequence of favorable opportunities for the trophic levels above it. This process could accrue up to the point that biological controls are re-established and impose limits on the productivities of the populations involved.

It is not necessary for the climatic trend to be completely monotonic. Since there are multiple age classes in a population and also a tendency for the older age classes to be relatively much more fecund (Parrish, Mallicoate, & Klingbeil, 1986; Beckley & van der Lingen, 1999), the school-mix feedback mechanisms may act as a low-pass filter of interannual variability. For example, the shift in composite school tendencies and affinities caused by a one-year event, even one as intense as a strong El Niño episode, would be limited to a single year class (or two year classes in cases of the longest lasting El Niño episodes). This year class would have restricted fecundity in the following year, when its El Niño-altered distribution of imprinted or inherent affinities would be maladapted for the prevailing non-El Niño conditions, and this poor reproductive success would rapidly weed out the inappropriate traits. Meanwhile the older, relatively much more fecund year classes, having had their composite affinities and propensities determined pre-El Niño, now once again have affinities to adapted to the prevailing non-El Niño conditions. Thus the population is able to ‘plow through’ the perturbation imposed by the short-term climatic event. Thus, depending on the number and relative reproductive effect of the age classes in the population, a climatic trend may be tracked by these automatic processes, even if the trend may contain intermittent reversals of a year or more. This is the reason that we cited ‘low-passed’ environmental trends in this context above.

This leads to yet another potential class of fishery effects that need to be considered. The multiple age classes that existed in many virgin sardine stocks would have generated a much more effective low-pass filter for shorter-scale variability than stocks in which a fishery has effectively reduced the age structure to just one or two age classes. Consequently, another way fishing pressure may introduce durable impacts on the potential productivity of a resource stock is by reducing its ability to track the longer term components of ‘red noise’ environmental variability and avoid being deflected into fruitless responses to more transient events. It may also reduce the stock’s ability to take advantage of the windows of opportunity to expand their population ‘along a trend’, through the process we have hypothesized in this section.

## **11. Discussion: expanded opportunities and scope for adaptive management interventions**

I have argued here that ‘the school-mix structure of a prey species may possess the capacity to respond faster than that of its predator, allowing both species continually to evade being caught in a mutually-destructive tightly-linked predator-prey system’. The interaction with a major fishery presents an obvious analogy. If a fishery is quite localized and geographically static (i.e. responding more slowly than counteracting school-mix feedback processes acting within the targeted stock), it would indeed appear possible for the targeted population to be able to automatically act, through the mechanisms outlined above, to deprive the fishery of the ability to destroy it totally. Indeed this may be an additional reason, in addition to the commonly cited slow rates of population growth, as to why sharks, marine mammals and marine turtles, which largely lack this interacting set of automatic rapid exploration and adaptive response mechanisms, tend to be driven to near extinction when targeted by fisheries.

As argued in my speculative discussion of the Namibian sardine experience (Section 5, above), the automatic adaptive response to cope with the growth of intolerable predatory (or exploitive) pressure might be at the expense of the overall productivity of the stock. This may lead to another

type of biological regime change, which one might call ‘stock productivity regime change’ or, in words employed in Section 5, a durable disruption of evolved ‘system integrity’.

This line of reasoning opens new perspectives for consideration of adaptive management options. To the extent to which a fishery is able to adapt its exploitation faster than its targeted resource population is able to respond, it may destroy the resource. More optimistically if ecological understanding is improved, a fishery could be managed such that the stock is preserved or even encouraged to increase (i.e. to reverse an earlier disruption of system integrity which had led to a lower productivity regime).

In the Namibian sardine example, if the authorities were to find the speculative arguments presented here compelling, an improved management approach might include specific regulation of the geographic pattern of the exploitation. This would not require abandoning the conventional management techniques, but could merely be superimposed on them; the same total allowable catch (TAC) could continue to be allocated using standard state-of-the-art methodologies. If the aim were to shut down the potential ‘conduit’ (see Section 5) that might be draining away the affinities and tendencies that maintain ‘system integrity’, the short-term economic costs might be tolerable. The longer-term benefits might be substantial, particularly if the former ‘system integrity’ were to be re-established and the stock recovers its former levels of productivity and biomass. For example, by preventing any of the current TAC from being taken within the traditional fishing grounds in the area from Palgrave Point to Walvis Bay, the fishing pressure might be shifted to the zone near the Angola–Benguela Front, thereby imposing a relative biological ‘cost’ on purely local spawning behavior in that area. This alteration of relative cost might then begin to change the relative frequencies of affinities and migratory tendencies within the schools. If the conceptual framework proposed here is correct, then it is feasible that the population might even be ‘nudged’ back towards the re-establishment of the integrity of its former migration-linked adapted system, and back towards re-establishing the earlier more productive ‘regime’.

## 12. Concluding remarks

To recapitulate, if the apparent global synchrony in population fluctuations of large, mobile fish populations is real, and reflects a direct mechanistic linkage rather than is a serendipitous juxtaposition in time series, which are too short relative to the time-scales of the dominant variability, it may be a ‘gift’ to fisheries science (Bakun, 1996, 1998a,b). The value of this gift does not necessarily lie just in future utility of the synchrony itself. We can not know whether the specific conditions that led to the patterns of the 1970s and 1980s will again be manifested with such strong global-scale consistency as to yield effects which will be large enough to be evident through the regional-scale ‘noise’. Rather, this remarkable period has yielded unique insight as to how these systems must operate. The biological mechanisms involved must be simple. Consequently, we should be able to find the solution to the scientific problem of understanding this particular aspect of variability in the abundance and productivity of large exploited fish populations.

To over-generalize in order to make a point, traditionally there have been two main groups of fishery scientists attempting to deal with natural variability in fish stocks. One group of fishery oceanographers has generally assumed that the basic ‘biology’ of a species is static within the

time scales they operate, so that variations in stock productivity and abundance are controlled by environmental or ecosystem variability, and by fishery exploitation. The other group of applied mathematicians and ‘mainstream’ fishery biologists has also customarily assumed that nearly everything is static and hence potentially predictable, apart from exploitation rates, but superimposed on this underlying stasis is a very large component of quasi-random noise that renders the observational data used for estimation very uncertain so that net ecological results (e.g., recruitment) are only known after the event. Fishery oceanographers have sometimes discovered interesting correlations that appear promising for a group of years, but then abruptly ‘go away’, often immediately upon publication, which tends to discredit the group’s efforts. The second group tends to blame its failures either on poor execution or non-compliance with their recommendations, or on inadequate data (sampling error), or on bad luck (a series of poor annual recruitments happening by unfortunate chance to follow one upon the other), or unfathomable long-period changes in stock productivity.

Both groups tend to make the tacit assumption the basic biology of the populations remains invariant, although they all through the scientific literature must be very well aware that average values of basic measured biological parameters (growth rate, age of maturity, fecundity) are far from being unchanging, but fluctuate on the multi-year time scales that are crucial for sustainable management. In summary, if

1. The evident global synchrony implies that the linkages between the climatic forcing signal and the fish stocks must be simple and direct, yet so far we have missed seeing the connection.
2. The customary way of investigating such linkages is to assume the ‘biology’ is effectively stationary.
3. We are well aware that biological parameters vary markedly on time scales similar to those exhibited by the radical population variability.

A reasonable conclusion might be to ask whether explanatory power might ensue from relaxing the tacit assumption of biological stationarity.

But how is this to be done properly? The problem of spurious empirical results is already so serious in fishery-environmental science (Bakun, 1996, 1998a) that such results are seldom afforded serious operational credibility by fishery managers (with the exception of El Niño effects on the fisheries off western seaboard of South America, which are so pronounced that they cannot be ignored). Relaxation of any constraining assumption on potential empirical fits to available data would tend to exacerbate this problem of spurious relationships.

Key questions are how much of this apparent biological invariance results from straight-forward phenotypic plasticity (e.g., Warner, 1997), and how much is the result of the rapid process of school-mix feedback as suggested above. It does make a difference. In the former case, there must be inherent ‘rules’ for the phenotypic transitions that have been evolved over the very long time scales at which genetic evolution operates; otherwise, how could the selective process that produced the plasticity have been driven? These rules would seem to be amenable to experimental testing. Presumably this has been tried, and if not, it certainly should be. It would a reasonable way to proceed on this general problem. However, if it has been tried, it has not solved our problem.

On the other hand, if the biological non-stationarity were the result of the proposed school-mix feedback process, this is a process that should be amenable to understanding and interpretation

on a purely logical basis. Some outcomes, such as the potential effects of geographically-biased fishing effort (see discussions in Sections 4, 5, 6 and 8) should on an a priori basis be predictable, perhaps not as a precise quantitative forecast, but at least in terms of a trends which management actions might tend to ‘push’ the current circumstances. Once a hypothetical framework for interpretation is available, it might be possible to track major changes in spawning habitat selection, using tools such as the continuous underway fish egg sampler (Checkley, Ortner, Settle, & Cummings, 1997; Checkley, Hunter, Motos, & van der Lingen, 2000), and continuously to interpret and to forecast potential consequences.

We search for a conceptual model that has the most explanatory power with respect to observational data that are poorly explained by conventional models. The attraction of the mechanisms involved in the school-mix feedback idea is the apparent breadth of their explanatory power. They appear to shed light on a number of issues discussed above (see Section 1 (a)–(g)), and a group of phenomena, which may not generally be considered in conventional treatments of fishery science, but which will probably resonate with the experience of most readers with a reasonably broad background in fisheries issues. These include the ‘species regime’ change and ‘stock productivity regime’ change phenomena, and the apparent tendency for fish stocks to withdraw away from established fisheries.

It is often said that that function of science is to predict. The conventional paradigm in fishery science is for managers and scientists to regard the value of fish ecology and oceanography merely in terms of their potential value in providing quantitative forecasts (e.g., how much recruitment to expect). But, in my speculative discussion of the Namibian sardine experience (Sections 5 and 8) and in the decisions currently facing the Moroccan Government (Section 4), perhaps the more important question is ‘what is really going on?’ Managers really need to understand the real nature of what may be happening — and why it is happening. Predictive forecasts to feed conventional procedures may be entirely secondary to this.

To underscore the value of understanding, consider the example of the Darwinian theory of evolution. It offers little in terms of operational predictive capability, but is perhaps our most valuable tool for understanding and interpreting the world around us, and maybe also the society in which we live. Another good example is our current understanding of the ENSO mechanism. We are poor at predicting El Niño. The massive 1997–98 El Niño was not generally anticipated even as late as February 1997 (e.g., Anon., 1997). But anyone reasonably familiar with the ENSO mechanism could in April 1997 have consulted one of the sites on the internet displaying ocean surface temperatures in the Pacific and recognize that an major El Niño was underway. Just that single image should have alerted people that for example it was a very bad idea to start burning fields in Indonesia in the expectation that monsoon rains would arrive on schedule to control the fires, or that it might be a profitable move to call one’s broker to selling any disaster insurance stocks in one’s portfolio, but to buy fishmeal futures.

The nature of the results needed from fisheries science is changing inexorably. Experiences of drastic regime changes in both species dominance and stock productivity are accumulating. Some national governments are even now evaluating extremely expensive and socially disruptive remedial actions. The general public, through efforts of organizations such as the Marine Stewardship Council (Sutton, 1998), is increasingly intervening in decision-making processes. Whatever one’s viewpoint on these interventions, few would wish them to be based on an inadequate level of understanding or a superficial interpretation of information. But this will happen if mainstream

fishery science does not become engaged in a constructive and credible manner. Meanwhile, the failures of conventional methodologies are increasing reliance on experimental adaptive management. Global climate change and other progressing environmental changes are necessitating the extrapolation of results well beyond the range of available historical data. If it is to respond in an effective manner, fisheries science needs to address processes and mechanisms, not merely strive to fit a scatter of data points to idealized simplistic mathematical functions.

In summary, fishery science can not afford to remain constrained by the somewhat deliberate limitation (Bakun, 1996) of admissible information and understanding that has been a hallmark of many of the conventional methodologies. Breaking free of these constraints will require the elaboration of some well-founded conceptual frameworks upon which to array the available information and experience in order to reveal configurations capable of distinguishing informative patterns of cause and effect. Whether the proposed line of reasoning outlined here, involving the ‘school trap’ mechanism, the notion of specific affinities and tendencies affixed to individual fish, and the associated process that has been here called ‘school-mix feedback’, will provide fisheries ecology with the essential missing dynamics, or even stand the test of time and observation to become a useful and accepted logical element of our science remains to be seen. Nevertheless at this point in time, it does seem to provide a substantial measure of explanatory power with respect to several very important unresolved issues.

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