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Review

Phase transitions in marine fish recruitment processes

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Abstract

There has been a recent resurgence of interest in fisheries recruitment as a dynamic and complex process that is integrated over several life stages, with a variety of factors acting across scales to initiate, modulate, and constrain population abundance and variability. In this paper, we review the theory of recruitment phase transitions using a marine fisheries perspective. We propose that transitions in recruitment are dependent upon the balance of activating and constraining processes of recruitment control, and we highlight fundamental differences in recruitment transitions precipitated by climate events, those related to community alterations, and those manifested by fishery practices (though each is not necessarily mutually exclusive). We maintain that the emergent properties of fisheries populations post-phase transition are contingent upon their histories, their differing initial states, the degree of food web complexity, interaction strengths among interspecifics, and contrasting external forcing, any or all of which may be dissimilar between one regime and another. We suggest that it may be challenging to forecast recruitment phase transitions, though we encourage efforts to determine whether there are unifying relationships that govern recruitment dynamics.

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Keywords: Recruitment; Phase transition; Regime shift; Fisheries; Climate

Contents

1. Introduction	206
2. Regime shifts, phase shifts, and phase transitions	207
2.1. Climate-induced transitions	208
2.2. Species interactions and demographic transitions	210

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2.3. Trophodynamic transitions	211
2.4. Spatially-dependent transitions	211
2.5. Fishery practices	212
3. Priorities for the future	213
Acknowledgements	115
References	215

1. Introduction

After nearly a century of study, the issues that surround the periodic and aperiodic fluctuations in marine fish population dynamics remain perplexing and indistinct. The inherent complexity of the recruitment process lies in the superimposed and non-linear interactions between stochastic, high-frequency external forcing events and more predictable, low-frequency, internal regulations (Bailey et al., 2003). To make the complex problem of recruitment more tractable, the historical approach has been reductionist, partitioning the process into three key avenues of research. First, many researchers focused on single species dynamics (as opposed to assemblage or multi-trophic level interactions), and much work was directed to understanding the irregularities in abundance of specific harvest species (cod, haddock, sardine, anchovy, etc.) (Gulland and Garcia, 1984; Garcia and de Leiva Moreno, 2003). Second, within the single-species framework, significant effort has focused on evaluating factors affecting just one phase of fish life history, the early life period. The idea that vulnerable larvae needed to survive a 'critical period' has been attractive, and the sheer numbers of larvae produced (10^9 – 10^{14}) make it theoretically possible to affect large changes in survival by managing only subtle abatements in mortality (Houde, 1987). Finally, much study has been directed to determine sources of year-to-year fluctuations in abundance (Sinclair, 1988; Bakun, 1996; Cushing, 1996), with comparatively less work on examining changes over longer time scales, or the overlapping relationship between the two. Research in the area of interannual variability has led to an enormous body of work on the contributions of advection, mesoscale oceanographic events (enrichment, retention, and concentration), predation, and food limitation to year-to-year mortality. Now that nearly 100 years of intense scientific scrutiny within these major recruitment subdisciplines are available

for reflection, what is our current understanding? Global fish stocks are in decline (Meyers and Worm, 2003), the cumulative effects of fishing and environmental variability on population abundance remain ill-defined, and the goal of reliably forecasting recruitment has been only modestly successful, at best. In the face of these tempering evidences, a groundswell of research interest has returned to a more holistic and integrated approach to recruitment dynamics (Miller, 2002; Cury et al., 2003). Whereas single species dynamics has been the norm, the current focus is on the interdependence of multi-species (and multi-cohort, Stenseth et al., 1999) interactions on recruitment variation (Hollowed et al., 2000; Carr et al., 2002). Additionally, it is increasingly being (re) recognized that recruitment in fishery populations is not exclusively linked to fluctuations within a single life history stage (Bradford, 1992; Bailey, 2000). Recruitment is now viewed as a dynamic and complex process that is integrated over several life stages, with a myriad of factors interacting at each stage and across scales to influence population abundance and variability (Rothschild, 2000). Finally, contemporary availability of longer time series data sets reveal decadal- and century-scale oscillations that are superimposed on interannual fluctuations in recruitment (e.g., Schwartzlose et al., 1999; Ravier and Fromentin, 2001; Finney et al., 2002). These low-frequency patterns demonstrate the presence of distinct, comparatively stable configurations ('mean density states'; May, 1986) in population abundance, community composition, and ecosystem structure that persist over long periods, with discontinuities that abruptly (1–3 years) shift the system to a new configuration with novel macroscopic properties.

In light of renewed interest in studying recruitment as a holistic complex, we review the theory of recruitment transitions from a marine fisheries perspective. We discuss how recruitment transitions are dependent upon the balance of activating (initiating)

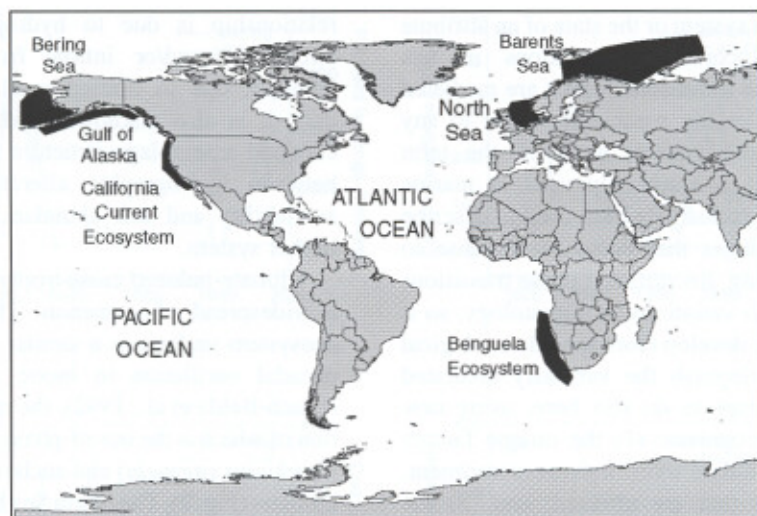


Fig. 1. Locations of systems discussed in this manuscript.

and constraining (modulating) processes of recruitment control, and we use case examples from the North Pacific, North Atlantic, and South Atlantic (Fig. 1) to highlight fundamental differences in recruitment transitions precipitated by climate events, those related to community alterations, and those manifested by fishery practices. Our objective is to offer a more complete characterization of the types of phase transitions in recruitment and their differing effects, as well as to set the stage for a new understanding of the biocomplexity that underlies marine fish population fluctuations (Bailey et al., 2003; Guichard et al., 2003).

2. Regime shifts, phase shifts, and phase transitions

Phase transitions are universal phenomena recognized in physics, chemistry, ecology, biology, and even social science (for examples of multidisciplinary research in complex adaptive systems see <http://resalliance.org>). A phase transition is a qualitative change in the state of a system under a continuous change in an external parameter (Li, 2002). The phenomena of phase transitions are interdisciplinary, but the terminology used to describe the process across disciplines is divergent and confusing. For example, the terms 'phase shift' and 'regime shift' have been

used synonymously (e.g., Folke et al., 2004), though we point out that they are not directly equivalent. 'Phase shift' has a distinct implication of regularly occurring, cyclical phenomena. For example, in physics the term 'phase shift' is used to describe a shift in the period of a waveform (Zheng et al., 2000), and in ecology as phase shift refers to a shift in the period so that two populations oscillate asynchronously (Henson et al., 1998; Stenseth et al., 1998; Turchin, 2003). An apparent phase transition observed under one cycle may ultimately be due to a phase shift. 'Regime shift' on the other hand, has been commonly used in the social sciences (politics, economics) to describe a rapid change in prevailing patterns. The term has caught on in climatology, ecology, and fisheries, though in these fields there are numerous slightly varying interpretations of a 'regime shift' (Steele, 1998; Beamish et al., 1999; Hare and Mantua, 2000; Scheffer et al., 2001; Collie et al., 2004; DeYoung et al., 2004). In order to be able to maintain constructive cross-disciplinary dialogue and conduct successful interdisciplinary research, it is critical that we achieve consensus on terminology (Li, 2002). We suggest that, at least from a fisheries perspective, 'regime shifts', 'phase shifts', and 'phase transitions' are fundamentally different, and that there is a hierarchical order between the phenomena. Regime shifts refer to changes in the parameters that force the system, while phase transitions describe changes in

either the state of the system or the state of an attribute of the system. Accordingly, variations in fish recruitment are phase transitions, which are mediated by regime shifts. 'Forcing parameters' refer to any factors that drive the system, however, the term 'regime shift', as it is commonly used in marine ecology, has almost exclusively been used to describe ecosystem-wide changes that occur in response to meteorological forcing. Recruitment phase transitions are not solely due to variations in climatology, so it seems appropriate to develop more specific ecological descriptors that distinguish the variously mediated transitions. We attempt to do this here, using new terminology that recognizes: (1) the unique factors that initiate and modulate transitions in recruitment, (2) the components that are affected, and (3) the ultimate nature of the new configuration. These clarifications offer a more complete characterization of the recruitment phase transitions in question, and provide a more widely applicable conceptual platform for the study of recruitment in marine systems.

2.1. Climate-induced transitions

Though the mechanisms that drive recruitment transitions in marine fishes are not well-understood, it is likely that at least some of these quasi-decadal alterations are initially activated by periodic variations in ocean circulation and atmospheric forcing (climate-induced transitions). One of the earliest characterizations of restructuring in a biological marine community due to alterations in climate was first described by Southward (1980) for the western English Channel (the Russell Cycle). In this system, variations in phosphate concentrations, alterations in the relative abundance of two chaetognath species (*Sagitta elegans* versus *S. setosa*), and profound fluctuations in herring (*Clupea harengus*) and pilchard (*Sardina pilchardus*) populations (Fig. 2) were noted. The mechanisms, which lead to the oscillations in the biotic components of this system, were heretofore unknown, though recent work by Beaugrand et al. (2002) offers a potential clue. These authors report on large-scale variations in copepod spatial distributions and assemblage structure in the North Atlantic, which they suggest are related to variations in the North Atlantic Oscillation (NAO) and to overall climatic warming. It remains unclear whether this potential

relationship is due to hydrographic variations in circulation and/or inflow from the Atlantic. In addition, due to limited availability of time-series data, it is also unknown whether these changes in copepod assemblage structure are cyclical, thus ties between hydrography, alterations in zooplankton availability and fish abundance remain postulatory in this system.

Climate-induced cross-trophic level restructuring is a widespread phenomenon. The California Current ecosystem undergoes a similar low-frequency, multi-decadal oscillation in biotic and abiotic structure (Lluch-Belda et al., 1992), the most visible manifestation of which is the out-of-phase relationship in sardine (*Sardinops caerulea*) and anchovy (*Engraulis mordax*) biomass (Fig. 2). The North Sea has experienced a well-characterized "gadoid outburst" (Cushing, 1980, 1984) (Fig. 2), and similar oscillations between gadids and forage fishes have been proposed for the Barents Sea. The North and Barents Sea cycles are likely forced by environmental conditions linked to the NAO, and a variety of hypotheses have been offered to explain the relationship. For example, climate-induced variations in transport (Planque and Taylor, 1998; Stephens et al., 1998), match-mismatches between zooplankton production and fish larvae (Cushing, 1980; Beaugrand et al., 2003), reduced predation on larvae and juveniles (Cushing, 1980), and differential growth (Loeng et al., 1995; Ottersen and Loeng, 2000) have all been cited as contributing agents, but the explicit mechanism underlying the biophysical coupling between climate and recruitment transitions remains unresolved. It should be noted that Atlantic cod populations in the North Sea are currently in sharp decline (Cook et al., 1997; ICES, 2002), and it may be that another climate-induced transition is underway, effectively reversing the famous "gadoid outburst" noted by Cushing (1980). Finally, the North Pacific ecosystem appears to have its own periodicity, marked by alterations in the Pacific Decadal Oscillation (PDO). PDO reversals have been linked to large-scale variations in phytoplankton (Polovina et al., 1995) and zooplankton abundances (Brodeur and Ware, 1992; Brodeur et al., 1999; Mackas et al., 2001; Peterson and Schwing, 2003), as well as to the decadal, out-of-phase recruitment patterns of forage and flatfishes (Anderson and Piatt, 1999; Hollowed et al., 2001) (Fig. 2). These examples point to the fundamental concept that ecosystem alterations can have profound

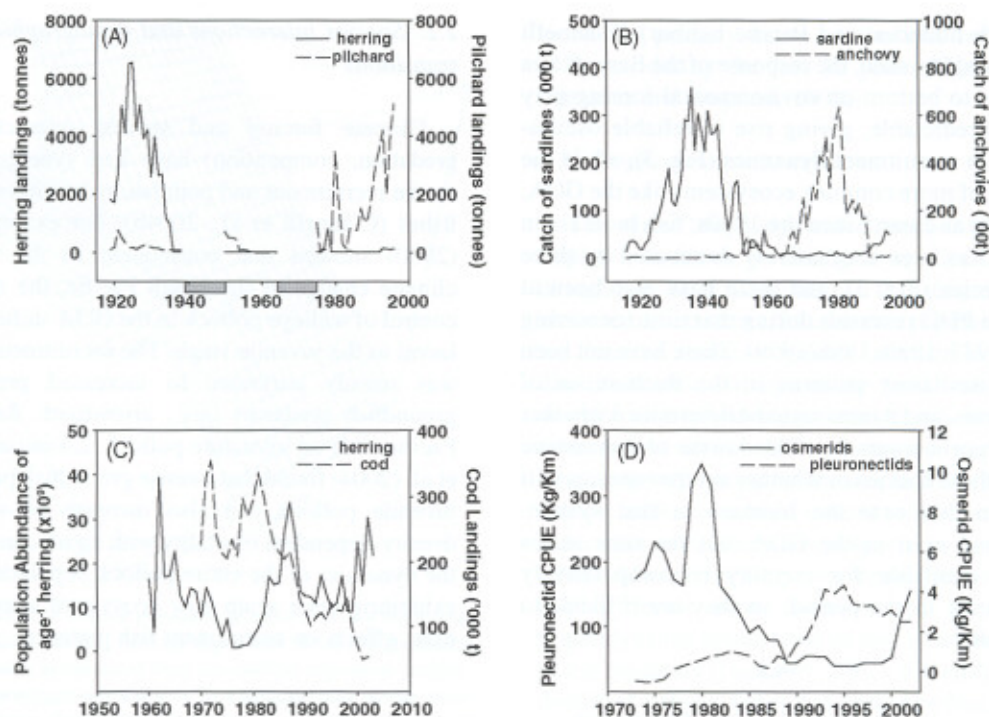


Fig. 2. Decadal, out-of-phase recruitment patterns of fishes in a variety of systems. (A) Plymouth, UK. Shaded areas indicate no data (adapted from Hawkins et al., 2003); (B) California Current ecosystem (adapted from Schwartzlose et al., 1999); (C) North Sea (data from ICES/CIEM); (D) Gulf of Alaska (adapted from Anderson, 2003).

impacts on fisheries recruitment, although, as seen below, recruitment itself can also exert impacts on ecosystem dynamics.

In any case, climate-induced transitions incite a chain of events provoked by bottom-up forcing and changes in ocean productivity (for example, changes in temperature, timing of the spring bloom, alterations in zooplankton production) which result in a novel trophic configuration. Recognized as such, recruitment phase transitions can be viewed as one manifestation of the overall trophic restructuring. Considering the transition in this light, as one part of a whole, may provide more insight into the sensitivities of certain species or communities to the effects of bottom-up forcing. For example, there are latitudinal dependencies that should be considered (Miller et al., 1991). Theoretically, in the North Pacific, recruitment of fishes at the cold end of their geographic range should improve during warm climatological periods (Wooster and Bailey, 1989), as these populations can now spawn earlier in the season and take advantage of

earlier spring blooms to provide their larvae with a selective advantage. Here we point out that recruitment transitions such as these can impact the ecosystem itself, as “warmer” species invade and colonize habitats previously too cool to occupy, potentially edging out later arriving competitors.

Another potential consideration in viewing recruitment phase transitions as one part of a whole is to be cognizant of the relative contributions of the number of major species that comprise the food web in various systems, as well as the strength of the interspecific interactions among the various food web constituents (Ciannelli et al., 2004a). For example, the food web in the Barents Sea is primarily influenced by a few species (Atlantic cod, capelin, and herring) that are highly abundant and demonstrate strong species-specific interactions (Hamre, 1994). The GOA ecosystem is considerably more biologically complex, possessing several key ecological species with weaker and more dynamic interspecific interactions (capelin, eulachon, walleye pollock, Pacific cod,

arrowtooth flounder, and Pacific halibut) (Ciannelli et al., 2004a). As such, the response of the Barents Sea ecosystem to bottom-up environmental forcing may be more predictable, giving rise to reliable oscillations in fish recruitment dynamics (Fig. 3), while the responses of more complex ecosystems like the GOA, may not be as clear. Since the 1960s, fish biomass in the GOA has been successively dominated by three major species (Fig. 3), and there have also been at least three PDO reversals during that time (occurring in 1976/1977; 1989; 1998/1999). There have not been obvious oscillatory patterns in the fluctuations of these species, and it remains to be determined whether the most recent reversal will lead to the re-dominance of one of these species or whether another species will emerge to dominate the biomass in that system. Cycles may exist in the GOA, but the time series currently available for scrutiny is comparatively short relative to the period, so they are difficult to distinguish.

2.2. Species interactions and demographic transitions

Climate forcing and species interactions (i.e., predation, competition) have had synergetic effects on the recruitment and population dynamics of marine fishes (Ciannelli et al., 2004b). For example, Bailey (2000) showed that consequent to the 1976/1977 climate change of the North Pacific, the recruitment control of walleye pollock in the GOA shifted from the larval to the juvenile stage. The recruitment transition was mainly attributed to increased predation by groundfish predators (e.g., arrowtooth flounder and Pacific cod) on immature pollock. Likewise, Ciannelli et al. (2004) found that intense groundfish predation on juvenile pollock can also increase pre-recruitment density-dependent mortality with significant effects on the dynamics of the entire pollock population (Fig. 4), exhibiting once again how ecosystem alterations can exert effects on recruitment fish patterns.

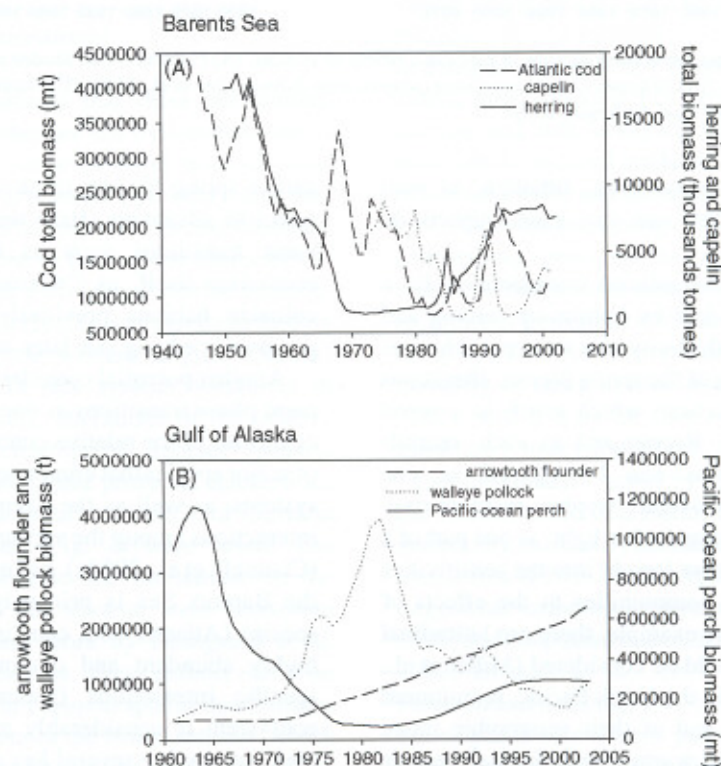


Fig. 3. Phase transitions in two different systems. (A) Oscillatory phase transitions in the Barents Sea (adapted from Ciannelli et al., 2004a) (B) Phase transitions in the Gulf of Alaska do not exhibit clear oscillatory patterns as yet (adapted from Dorn et al., 2003).

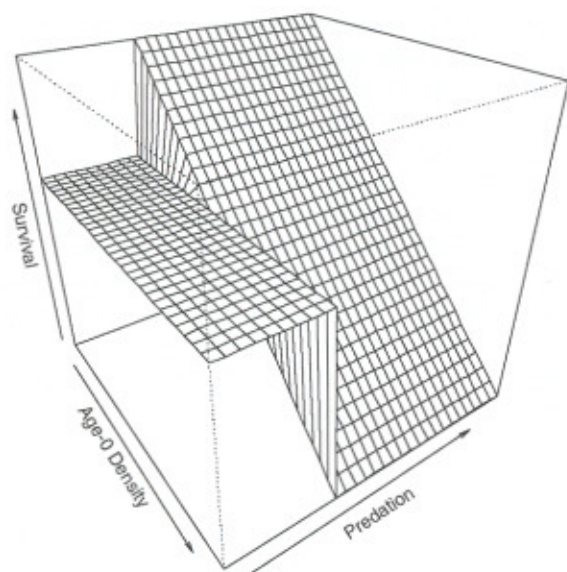


Fig. 4. Survival of walleye pollock from age-0 to -1 as a function of initial population density (density-dependent effect) and groundfish predation index as estimated from non-additive regression analysis. Density-dependence was found to be significant only during environmental phases characterized by high predation intensity and high water temperature (temperature effect not shown) (modified from Ciannelli et al., 2004b).

Similar species interaction effects on population abundance have also occurred in other marine systems. For example, in the Barents Sea, cod and herring recruitment are influenced by physical variables, such as sea surface temperature (SST), which is correlated with the NAO index. During years of low SST (low NAO), Atlantic cod and herring recruitment are always low, while during years of high SST cod and herring recruitment can be either high or low (Ottersen et al., 1994; Ottersen and Sundby, 1995). Capelin are the most important food item for cod from age three and up (Marshall et al., 1999; Dolgov, 2002), and juvenile herring can actively feed on larval capelin (Huse and Toresen, 2000). As a result of these species interactions, capelin abundance is expected to be drastically reduced during the years that follow high SST phases in the Barents Sea (Hamre, 2003). This pattern has been substantiated by Hjermmann et al. (2004), who have shown that capelin cohorts spawned 2 years after a warm year tend to have lowered recruitment success. Indeed, acute predation on capelin larvae by herring is suspected

to be the primary cause of the two major capelin collapses during the last 20 years (Gjøsæter, 1998; Gjøsæter and Bogstad, 1998).

2.3. Trophodynamic transitions

The term “trophodynamic transitions” inherently implies transitions pertaining to species interactions, though here we separate the two to distinguish between phase transitions that affect selected populations (which we describe above as species interactions) and those that reverberate throughout the food web (which we describe as trophodynamic transitions). Parallel long-term trends across different marine trophic levels, ranging from phytoplankton, zooplankton, herring, and marine birds, have been related to bottom-up control induced by environmental changes (e.g., Aebischer et al., 1990). Alternating long-term trends across successive trophic levels have been related to diminished trophodynamic interactions caused by overexploitation of top predators (Daskalov, 2002). Recently the role of dominant pelagic fishes has been emphasized as they might exert a major control on energy flows (wasp-waist control; Cury et al., 2000). In upwelling systems, few pelagic fish occupy the intermediate trophic level, which feed mostly on phytoplankton and/or zooplankton and are prey of numerous predators such as demersal and pelagic fishes, as well as marine birds, and mammals. These species can exhibit large biomasses, which vary radically in size according to fluctuation in recruitment strength, associated with mesoscale events (*sensu* Bakun, 1996). In the northern Benguela ecosystem, overexploitation of pelagic fish populations served to completely reorganize trophic flows towards lower trophic levels (e.g., jellyfish and gobies; Cury and Shannon, 2004). Meanwhile in the southern Benguela, despite alterations between sardines and anchovies, the overall functioning of the ecosystem has remained the same during the last two decades (Shannon et al., 2003). These examples show that changes in an important component of the ecosystem (pelagic species) can modify food-web structure in the long-term and induce changes system-wide.

2.4. Spatially-dependent transitions

Less recognized than temporal changes, recruitment phase transitions can be a function of variations

in spatial scale and habitat structure. Small-scale spatial heterogeneity has significant effects on intrinsic recruitment regulation. For example, Beverton's Concentration Hypothesis (1995) points out that if favorable habitat is limiting to new recruits, suboptimal habitat may be occupied and the population will be regulated through indirect, density-dependent mortality. Spatial variability in patch reef habitat quality influences the local density-dependent structure of reef fish, and could mask larger-scale patterns of density-dependence (Hixon and Carr, 1997; Shima and Osenberg, 2003). Variations in the extent of suitable habitat influence the production of successfully surviving larvae (Grimes and Kingsford, 1996; Lehodey et al., 2003) and juveniles (Rjinsdorp et al., 1992). Habitat extent for juveniles and habitat quality is especially critical for fishes whose juvenile stages have specific habitat requirements (for example, flatfishes; Gibson, 1999).

Decadal-scale variation in extrinsic factors, such as wind-driven transport of recruits to nursery areas (Wilderbuer et al., 2002; Bailey and Picquelle, 2002) or spatial redistribution of predators and competitors (Grosslein et al., 1980), influence recruitment through feedback regulations and inter-dependencies (Petraitis and Latham, 1999). In the first case, primary settlement by early pulses of propagules delivered to favorable nursery areas due to changes in circulation facilitate secondary colonization by successional conspecifics. In the latter, disturbances such as influxes of predators or competitors could cause sufficient mortality among existing residents to provide either an opportunity for new recruits of a different species to colonize the area (initiating a recruitment phase transition), or for remaining residents to re-invade the newly-available habitat (no phase transition) (Knowlton, 1992; Petraitis and Latham, 1999). Moreover, Petraitis and Latham (1999) point out that the initiation of a phase transition is inherently unpredictable, requiring: (1) a disturbance of sufficient scale to provide an opportunity for a transition, and (2) the chance delivery of a new species of recruits who can colonize the area. Effects on recruitment (and post-recruitment mortality) under these circumstances are likely to be spatially and temporally local, confined to a particular reef, bay, or mud flat, or within a given season.

Finally, spatial inconstancies in the interactions between larvae and local hydrographic features can

fundamentally affect the recruitment process, potentially generating population level phase transitions. For example, Lasker (1975, 1978) demonstrated that ocean conditions that disrupt stratified waters and interfere with feeding larval ability have significant effects on year-class success of northern anchovy. Bakun (1996, 1998) has suggested that a "triad" of oceanographic process (those affecting enrichment, concentration, and retention) need to be corroboratively in place to constitute favorable reproductive areas, although whether disruption to one or more of these factors negatively impacts recruitment success remains to be determined.

2.5. Fishery practices

The most obvious effects of fishing on phase transitions in marine populations is through the top-down effects of removing large predators from the ecosystem and the resulting trophic cascades (Pauly et al., 1998). In this case, the activating factor (fishing) may cause a trophic release from predation, especially among the juvenile stages of small pelagic fishes. Fishing out of replacement communities, those successive communities that take hold after higher trophic level communities have been depleted, lowers functional diversity and reduces overall stability and resilience to perturbation. There are also examples of the cascading effects of removing prey of large predators on the rest of the ecosystem (Jackson et al., 2001; Springer et al., 2003), and in this case, recruitment is less directly impacted.

Overexploitation of large fish predators that are targeted for their high economic value can cause complex changes in community dynamics by altering recruitment and survival patterns. Ecologists have long speculated how predatory fish species are able to achieve large body size, given that their juveniles must grow through a predation-competition phase involving the very species that will be their prey later in life. According to Walters and Kitchell (2001), large, dominant fish species that are the basis of many fisheries may be naturally so successful partly due to "cultivation effects," where adults crop down forage species that are potential predators/competitors on their own juveniles. For example, adult walleye pollock in the Bering Sea consume immature arrowtooth flounder (2–5 cm SL) and Pacific cod

(<13 cm SL) (Livingston and deReynier, 1996). In the adult stages, these two species are themselves major predators of juvenile walleye pollock. It should be noted that adult cannibalism of juvenile pollock is also high in the Bering Sea (Duffy-Anderson et al., 2003), which may serve to alleviate potential density-dependent mortality among immature stages (Laevastu et al., 1995). "Predator-prey role reversals" (Barkai and McQuaid, 1988), may also explain low recruitment success due to depensatory effects of some major stocks following severe declines.

Implications for ecosystem dynamics of fishing down the food web (Pauly et al., 1998) are two-fold: by depressing the abundance of large fish predators, fisheries release the top-down control of small fish. In doing so, they increase the risk of depensatory effects due to competition/predation between small fish, preventing the rebuilding of the stocks of larger fish species. For example, in the central Baltic, clupeid predation on cod eggs (Koester and Schnack, 1994) may result in the system being either cod-dominated or clupeid-dominated. In the northern Baltic, the increase in herring abundance in the late 1980s appeared to be the result of weakened top-down regulation due to the sharp decline by overfishing of its main predator, cod (Cushing, 1980). Herring were also affected by the availability of suitable-sized plankters, which was in turn, environmentally controlled (i.e., by salinity). A possible top-down effect of relaxed cod predation on herring as well as a bottom-up process mediated by changes in mesozooplankton species composition both seem to have contributed to the dynamics of herring populations in the Baltic, and a similar mechanism has been proposed for the Bering Sea (Oscillating Control Hypothesis; Hunt et al., 2002). Following the over-exploitation of sparid and serranid communities off North-West Africa in the 1960s, predation pressure on octopuses was released, which in turn became abundant in Morocco and Mauritania in the early 1960s and later in Senegal in the mid-1980s. Weakened top-down control by demersal fish species led to tight relationships between upwelling intensity and octopus recruitment patterns (Faure et al., 2000).

Other more subtle effects of fishing on phase transitions in populations include Allee effects (decreased reproduction at low population size due to physiological and behavioral factors; Frank and Brickman, 2001), reductions in intraspecific diversity

(Sinclair et al., 1985; Cury and Anneville, 1998), reduction in mean age (Longhurst, 2002), reductions in fishery yield due to size-selective harvest practices (Conover and Munch, 2002), and direct destruction of habitat (Kaiser et al., 2003).

3. Priorities for the future

Modern day concerns over the effects of greenhouse gas emissions and global warming on climate, the influence of phase transitions precipitated by climate change on ecosystem structure, functioning, and resilience, and declining pelagic and groundfish stocks have prompted a heightened sense of urgency in both the scientific and political arenas. In particular, there is a new emphasis on understanding the sources of climate variability and ecosystem fluctuations, and on knowing the harbingers of phase transitions with an ultimate goal of being able to predict transitions earlier to enhance societal preparedness. At this point, it is worth a note of caution that it is unwise to assume that fluctuations between two or more quasi-steady states implies a perfect return to pre-existing conditions. The marine community is at once dynamic and impressionable, and while its constituents may periodically self-organize into higher order stable states with overtly similar manifestations, it may be more appropriate to consider each state as a distinct reorganization rather than as an oscillation between one or more presupposed higher order complexes. This view recognizes that the emergent properties of the re-organized system are contingent upon the prior histories of the individual constituents, their differing initial states, the degree of food web complexity and interaction strengths among interspecifics in different systems, and contrasting external forcing, which may be fundamentally dissimilar between one ecosystem state and another. As such, it may be challenging to forecast recruitment phase transitions, though a fundamental historical awareness of the outcomes of past transitions can help to narrow the range of conceivable repercussions. Even a limited ability to predict phase transitions would be valuable, potentially serving to alert scientists and managers of a change in the status quo.

Pre-emptive strategies, such as long-term planning and flexible and responsive management practices,

remain advisable. The current emphasis of fisheries management is in the development of harvest strategies over short time frames, however in the presence of potential recruitment phases, it is unwise to fail to consider harvest guidelines on longer time scales that can accommodate the longer periodicity of climate and community oscillations. A typical example can be found in the inter-decadal oscillations of the North Pacific. During cold phases of the PDO, salmon productivity is higher along the western coast of the US than in Alaskan waters, while the pattern appears to be reversed during warm phases (Mantua et al., 1997). Although the mechanisms leading to the reversed pattern of salmon production in the North Pacific are not yet revealed (and current observations reveal increases in production in the California Current without the corresponding decline in Alaska), it is important to adapt harvest strategies over longer time scales to come into accordance with what is known about production regimes.

It is also necessary to consider synergic effects between climate forcing and species interactions. Most of the current management models assume that species dynamics are exclusively affected by internal mechanisms (i.e., density-dependence), though external factors (climate-linked variables) and species interactions can play a major role in affecting species dynamics. Internal and external variables can have non-additive effects on population dynamics, and as a result, the intensity of density-dependent control can change in relation to background external variables (Ciannelli et al., 2004b). In such a scenario, the mechanisms that control population dynamics are not bound to be the same over contrasting climate phases. Thus, we are left with the challenge of better incorporating species interactions in fisheries management models, and developing new analytical techniques to better capture the effects of non-additive and indirect climate forcing.

Also requiring additional work is the question of whether there are certain communities that may be more resilient (or susceptible) to the effects of transition events. Because of a more direct linkage with coupled atmosphere/ocean variability, pelagic communities may be more susceptible to climate variations, as pointed out by Paine (1986) and Bailey et al. (1995). Groundfish communities, on the other hand, may be susceptible to climate variability at

specific life stages, such as during their planktonic life or during the settlement process. After reductions in biomass due to overfishing, and perhaps declines related to climate-induced transitions as well, species like herring and other small pelagics that mature early in life may recover relatively quickly. Gadids and flatfishes may recover more slowly, showing little, if any, recovery up to 15 years later (Hutchings, 2000).

Community response may be predictable over the short-term, but long-range forecasts are likely dependent on predictability of climate systems. In the case of the North Pacific system, climate indicators are stochastic (Percival et al., 2001), and potential predictability is small (Bond et al., 2003). Whereas the primary climate indicator in the North Pacific, the PDO, signaled major changes in atmospheric, oceanographic, and ecological conditions in 1976/1977, it has not been as successful in recent years. The changes that occurred in 1989 and again in 1999 were either short-lived, did not reach the 'regime-shift' status that they appeared to forecast at the time, or their effects were limited in geographical extent (Bond et al., 2003). It is becoming increasingly recognized that single indices, such as the PDO, may not be adequate indicators of ecosystem status because of the non-linearities generated by intersecting processes reflected by, for example, the Arctic Oscillation (AO) and ENSO indices. To that extent, ecological forecasts will be made possible by better cumulative indicators of contemporary climate, and renewed attention should be given to examining the convergent affects of varying climatological oscillations.

Finally, the role of fishing should also be reconsidered in light of complexity in ecosystems. For example, does harvesting disturb the delicate balance of ecosystem stability sufficiently to cause trophic cascades? It is interesting to speculate that the massive overharvesting of Pacific Ocean perch in the GOA in the 1960s could have contributed to the dramatic increase in gadid populations in the 1970s and 1980s (Somerton, 1978). Likewise, fishing on gadids in the northwest Atlantic could have advanced the dramatic increase in the capelin population in that system (Carscadden et al., 2001), and the overharvesting of Atlantic cod in the North Sea could have expedited the rise in herring (Cushing, 1980, 1984).

We point out in this review that recruitment is a complex process involving a variety of factors that

initiate, modulate, and constrain population abundance and variability. We stress that it is critical to consider that the outcomes of recruitment phase transitions are contingent upon the system's history of ecological functioning. While these cautions make the concept of finding unifying relationships that govern recruitment dynamics daunting, it is not impossible. By adopting a global, comparative perspective, we may be able to discern whether there are broad-scale ecological patterns in recruitment fluctuations, and if so, determine whether these patterns point to basic mechanistic processes. Such common laws have been identified in biology (allometric scaling laws; West et al., 1997, but also see Makarieva et al., 2003; Li et al., 2004), ecology (Taylor's power law; Kilpatrick and Ives, 2003), and other fields (physics, chemistry), and we encourage new efforts to determine whether there are natural and universal laws that guide the dynamical behavior of recruitment.

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