ELSEVIER

Review

Recruitment of walleye pollock in a physically and biologically complex ecosystem: A new perspective

Kevin M. Bailey [a,*], Lorenzo Ciannelli [b], Nicholas A. Bond [c], Andrea Belgrano [d], Nils Chr. Stenseth [b]

[a] *Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA*
[b] *Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, PO Box 1050 Blindern, N-0316 Oslo, Norway*
[c] *Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA*
[d] *NCGR - National Center for Genome Resources, 2935 Rodeo Park Dr. E Santa Fe, NM 87505, USA*

Abstract

Walleye pollock (*Theragra chalcogramma*) is a commercially important marine fish in the Gulf of Alaska that has provided a natural experimental system to study many features of the recruitment process. We review recruitment of pollock in the Gulf of Alaska in the conceptual framework of a complex system. In this perspective, high frequency, or activating, events during egg and larval life introduce variability to the dynamics of the population, whereas lower frequency constraining processes tend to promote broader patterns. This view is supported by both simple population and complex statistical models that capture the trends and general patterns in the time series of recruitment. Consequences of this view of recruitment are discussed in terms of forecasting strategies.
Published by Elsevier Ltd.

Keywords: Theragra chalcogramma; Complex systems; Recruitment prediction; Forecasting; Gulf of Alaska

Contents

* Corresponding author. Tel.: +1 206 526 4243; fax: +1 206 526 6723.
 E-mail address: kevin.bailey@noaa.gov (K.M. Bailey).

1. Introduction

The highly variable and sometimes cyclic nature of marine fish recruitment is influenced by many processes operating at varying scales. For example, critical periods of mortality may occur at different life stages and are influenced by the interactions of biological and physical processes at spatial scales ranging from the perceptual distance of larvae (several mm) to climatic events such as El Niño (entire ocean basins), and time scales spanning from days (the period of episodic larval mortality) to decades (environmental regime shifts). It is recognized that ecological patterns occurring at one scale of observation are the result of processes operating at other scales (Brown, Whitham, Morgan, & Gehring, 2001; Levin & Pacala, 1997). How these patterns emerge is part of the concept of complexity. By complex, we mean not just complicated or made of many parts, but a form where the parts are interconnected. Complex ecological processes, such as the dynamics of populations, are affected by a multitude of inter-connected factors, whose effects are often non-linear (Bjørnstad & Grenfell, 2001; Dixon, Milicich, & Sugihara, 1999; Rothschild, 2000) and perhaps non-additive (Stenseth, Chan, Framstad, & Tong, 1998). Although complexity has become a familiar term in ecology (Brown et al., 2002; Pascual, Roy, & Franc, 2002), in our opinion it has not received enough attention in the study of fisheries population dynamics.

Progress in understanding the complexity of recruitment, will come from understanding how the component processes (spawning, feeding, predation, etc.) interact to make the observed patterns, and how such patterns are affected by changes in larger-scale systems, such as climate regimes or ecosystems. Sometimes a macro-ecological perspective can reveal recurrent patterns in natural processes; that is, order in the system can be distinguished at a sufficiently large scale of observation (Maurer, 1999). Thus, there may be high variability on small scales, such as in the local dynamics of recruitment, but regular patterns can be observed when viewed macroscopically. If ecological patterns, at any given scale, arise from the interaction of various factors, each in turn operating at different spatial and temporal scales (Levin, 1992), then a challenge for ecologists studying recruitment is to understand how a pattern that is manifested at a certain scale may be induced by factors operating at other scales. For example, how do 3–5 year cycles in recruitment that have been observed for pollock and hake arise (Bailey, Ciannelli, & Agostini, 2003)? What causes similarly large-scale regional patterns in the response of different marine fish populations to environmental conditions (Anderson & Piatt, 1999; Beamish, 1994; Hollowed, Hare, & Wooster, 2001; Southward, Boalch, & Maddock, 1988)? What underlies similar patterns in the cycles of marine fish populations on a global scale (Omori & Kawasaki, 1995; Schwartzlose et al., 1999)?

In this synthesis we suggest that the process of recruitment at the population level falls between the complexity of small-scale processes and the more predictable order of the macroscale; that is, recruitment at this scale is governed by the dynamic tension between small-scale activating and large-scale constraining events

(Bjørnstad & Grenfell, 2001; Fromentin, Gjoesaeter, Bjørnstad, & Stenseth, 2000; Levin & Pacala, 1997; Stenseth et al., 1999; Stenseth et al., 2002). By constraining factors, we mean those factors that confine the extent of change within limits (i.e., the constraining envelope) and tend to promote stability, while activating factors promote variability within the constraining envelope. We define activating and constraining factors primarily based on the scale of observation, and their variability relative to the variability of the process being affected. Thus, activating factors are those which tend to change (over time or space) more frequently than the process being affected, while the reverse applies for constraining factors. Similar terminology (stimulating and constraining factors, disruptive and regulative factors) has been used in ecology (Levin & Pacala, 1997) and oceanography before to describe processes as diverse as control of the vertical migration process (Longhurst, 1976) and the dynamics of marine fish populations (Stenseth et al., 1999).

To construct this perspective of recruitment as a push–pull relationship between small-scale activating and larger-scale constraining factors, we synthesize information on recruitment of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska (GOA); this population is a good model for presenting a conceptual view of recruitment as a complex process. In this sense, we review the recruitment process of pollock, usually an oceanographic topic, in the context of a theoretical ecological framework. We then review activating and constraining processes influencing recruitment of pollock. The conceptual model proposed here is compared to other models, and finally we discuss how these views may influence a strategy to forecast recruitment.

2. Background

2.1. The physical setting

The oceanographic setting of the Gulf of Alaska has been described in several review articles (Musgrave, Weingartner, & Royer, 1992; Reed & Schumacher, 1987; Royer, 1998; Stabeno, Bond, Herman, Mordy, & Overland, 2004), so only pertinent details will be summarized here. Currents in the Gulf of Alaska are dominated by atmospheric and topographic forcing and freshwater runoff (Royer, 1981). This flow is impacted by bathymetry along a shelf of varying width that is penetrated by numerous canyons and troughs. Variability in transport is largely dominated by variability in winds. The wind variability itself is closely tied to the passage of cyclonic storm systems, especially during the winter. Because of the prominent coastal orography encircling the Gulf of Alaska, the coastal winds are sensitive to interactions between the effects of the local terrain and basin-scale pressure gradients (e.g., Wilson & Overland, 1986). Precipitation accumulates as snow on the coastal landmass during winter, then melts with seasonal warming, resulting in strong seasonality of freshwater runoff.

The main currents over the shelf are the Alaska Coastal Current (ACC) nearshore and the Alaskan Stream (AS) over the outer shelf and slope (Fig. 1). The ACC is one of the most dynamic coastal currents in the world, with speeds of 25–100 cm s^{-1} (Stabeno, Reed, & Schumacher, 1996). It flows westward along the Kenai Peninsula and down Shelikof Strait. About half of the transport joins the Alaskan Stream, and the remainder flows along the Alaska Peninsula over the shelf (Schumacher, Stabeno, & Roach, 1989) with speed slowing to about 10 cm s^{-1}. The ACC often includes both a barotropic component due to the typically downwelling favorable winds along the coast, and a baroclinic component due to the copious discharge of freshwater from the numerous rivers along the coast (Royer, 1981). It appears that the barotropic component dominates the net transport of the ACC, while the baroclinic component is responsible for considerable vertical shear and eddy development. The AS is also a relatively strong flow, with speeds of 50–100 cm s^{-1}. Large eddies in the AS form routinely in the eastern part of the Gulf. These eddies may impinge onto the shelf, advecting nutrient-laden deep water and offshore plankton species assemblages.
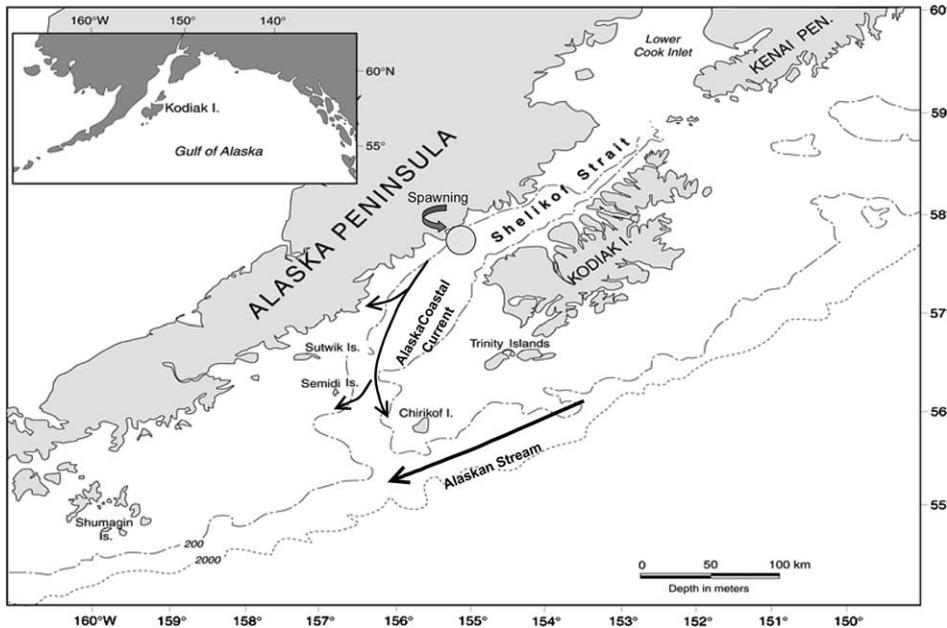
Fig. 1. Geographical setting and major currents in the northern Gulf of Alaska. Also shown is the location of pollock spawning in Shelikof Strait.

Our main interest in this review is the spawning center and main nursery region of walleye pollock in Shelikof Strait and the sea valley and shelf region downstream of it. In this portion of the ACC, complexity of flow is accentuated by upwelling, eddies, meanders, episodes of flow reversal, and cross-shelf flow. Eddies over the Shelikof sea valley are 20–30 km across, extend to depths of 200 m and can endure for several weeks (Bograd, Stabeno, & Schumacher, 1994; Schumacher, Stabeno, & Bograd, 1993). There is estuarine-like circulation in the Shelikof sea valley, with surface flow down the valley countered by deeper currents flowing up it, especially along the Kodiak Island side.

An intense phytoplankton bloom occurs in the ACC in late spring and early summer (Napp, Incze, Ortner, Siefert, & Britt, 1996). This bloom is often patchy and appears to be prolonged around Kodiak Island and in Shelikof Strait. Phytoplankton concentrations tend to be high in frontal regions. The springtime bloom supports local production of copepod nauplii and other microzooplanktonic prey of early feeding walleye pollock larvae.

2.2. Biology of walleye pollock

Walleye pollock is a key species in northern North Pacific ecosystems that has important predator–prey interactions with trophic levels above and below it. Pollock are opportunistic, thriving in temperatures from about 1 to 10 °C and in habitats ranging from eelgrass beds in Puget Sound to the open oceanic waters of the Aleutian basin. Pollock feed on a variety of prey from planktonic and benthic crustaceans to pelagic fishes, often including their own young. Declines of pollock have been implicated in collapses of Steller sea lion (Merrick, Chumbley, & Byrd, 1997) and bird populations (Springer, 1992), and have been linked to broader and more complex changes in ecosystem structure (Estes, Tinker, Williams, & Doak, 1998). As a predaceous species with a biomass averaging about 1 million tons in the Gulf of Alaska, pollock can remove a lot of prey from the system. They may compete with humans for resources such as shrimp and with salmonids and other important commercial species for zooplankton.

Individual pollock females spawn millions of eggs each year after maturing at 3–4 years of age. In the Gulf of Alaska the main historical spawning location has been Shelikof Strait. Spawning occurs in late March and early April. The Shelikof Strait spawning area is noted for the mixing of coastal and nutrient-rich oceanic waters, which leads to phytoplankton blooms. Eggs take about 2 weeks to hatch at 6 °C, and larvae are supplied with yolk to survive a few days before feeding is initiated. Larvae feed on microzooplankton and naupliar stages of zooplankton. Larvae drift with currents for several months to reach their primary nursery area over the shelf between the Semidi and Shumagin Islands and may also be found in eddies (Napp, Kendall, & Schumacher, 2000; Schumacher et al., 1993). Pollock begin to recruit to the harvested population at age-2 and are fully recruited by age-4 or -5. The number of 2 year olds in the population estimated from catch-at-age models ranges from about 0.1 to 5 billion individuals.

Stock structure of pollock in the North Pacific is unresolved after many years of study. Although historically the main spawning area has been Shelikof Strait (Kendall & Picquelle, 1990), in recent years other spawning aggregations appear to have increased in importance, most notably in the Shumagin Island region. The migration of animals among populations is unresolved and controversial (Bailey, Quinn, Bentzen, & Grant, 1999). Over the years we include in our analysis (1975–1996), these other spawning groups appear to have been of minor significance, although in more recent years the Shelikof population has declined, and the relative representation of individuals from other spawning areas in the Gulf of Alaska system has likely increased.

3. Scale considerations

Population dynamics may be studied on different time and space scales, with different scale-dependent patterns emerging (e.g., Botsford, 2001); that is, the amount of variability in population abundance may depend on the scale of observation. The spatial scale of interest for recruitment studies of commercial fishes is at the level of stock management, where a stock is a group of individuals that are for the most part demographically independent (Bailey et al., 1999). This is at a higher level of organization, for example, than localized studies of recruitment of larvae to individual reef structures (Dixon et al., 1999). At the same time it is a lower level of organization than studies of broad changes in fish recruitment; for example, recruitment of fishes to global populations comprised of many different stocks (Omori & Kawasaki, 1995). Time scales of recruitment can also vary dramatically from post-settlement abundance of reef fishes established at ages of a few months (Hixon, 1998) to the age-at-recruitment of Pacific halibut of 8 years (Clark, Hare, Parma, Sullivan, & Trumble, 1999).

Processes affecting recruitment of different life stages of pollock have been examined at spatial and temporal scales ranging from patches that may last for days (Incze, Ortner, & Schumacher, 1990) to large basin populations varying over decades and probably aggregating multiple stocks (Hollowed et al., 2001). In the following paragraphs the degree of interannual variability in abundance is compared to the spatial scale of observation for different life stages of pollock.

The interannual variability in larval abundance at a fixed location (a small spatial scale) within the main area of larval distribution is high (Fig. 2(a)). Total larval abundance is dominated by the numbers of small larvae that have not yet been decimated by high and variable mortality rates. On this small scale, spatial patchiness (Stabeno, Schumacher, Bailey, Brodeur, & Cokelet, 1996), natural variations in abundance due to changing demographic rates (Bailey, Picquelle, & Spring, 1996), timing of spawning, and variations in the physical environment, such as advection (Bailey & Macklin, 1994), contribute to the high variability. These factors are discussed in more detail below. On a larger scale of spatial aggregation, interannual variability in larval abundance in surveys of the western Gulf of Alaska is also high, again due to the factors mentioned above, but somewhat decreased from the single station variability due to the effect of averaging over stations (Fig. 2(b)).
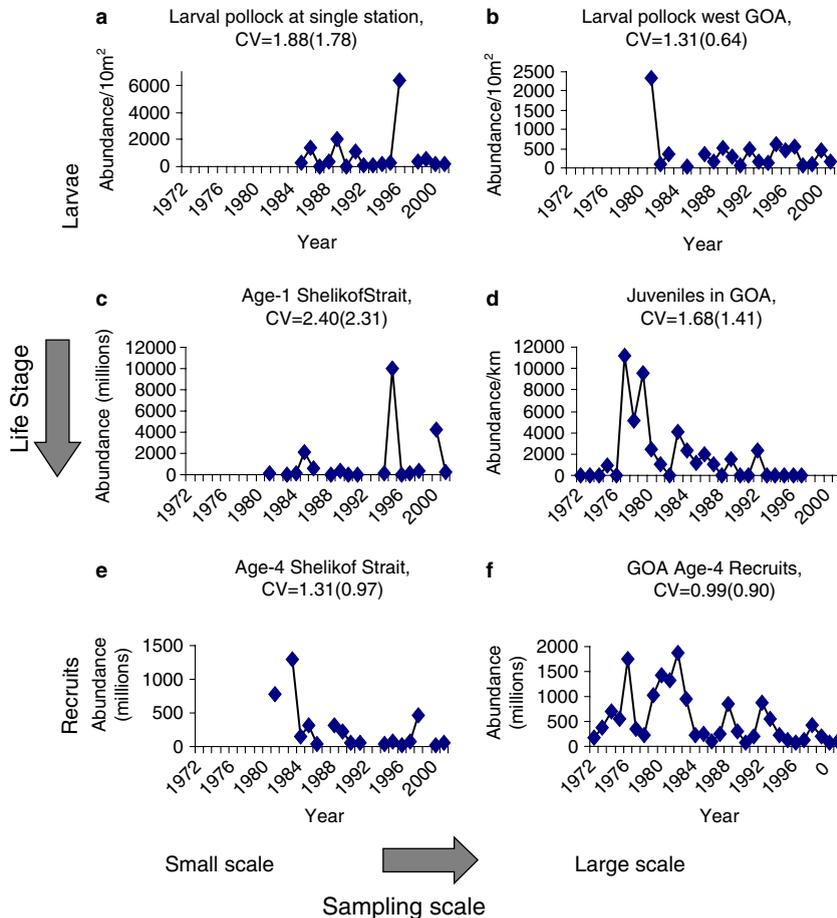
Fig. 2. Interannual variation in pollock abundance indices at different spatial scales and life history stages. CV is the coefficient of variation for the whole time series shown, the number is parentheses is the CV for the years-in-common data set, 1985–1997. (a) Abundance of pollock larvae (per 10 m^2) caught with 60 cm bongo tows with 0.333 mm mesh netting in May in the vicinity of a single station location in Shelikof Strait. (b) Abundance estimate of larval pollock caught in plankton surveys (using bongo tows) in late May in the western Gulf of Alaska (estimates provided by S. Picquelle, pers. comm., Alaska Fisheries Science Center). The estimate is the average catch of larvae (per 10 m^2) within a standardized area over the continental shelf between Shelikof Strait and the Shumagin Islands. (c) Abundance of age-1 juvenile pollock in the Shelikof Strait region during late March (acoustic estimates, data from Dorn et al., 2003). (d) Average abundance of juvenile walleye pollock (in numbers per km) in the western Gulf of Alaska from small mesh trawl surveys (data provided by P. Anderson, Alaska Fisheries Science Center, from Anderson and Piatt, 1999). Only the total weight by species was reported for each catch. To convert biomass to numbers we assumed that all pollock in catches were juveniles with an average weight of 2.5 g. (e) Abundance of age-4 recruit pollock in the Shelikof Strait region during late March (acoustic estimates, data from Dorn et al., 2003). (f) Abundance of age-4 recruit pollock in the western Gulf of Alaska (from age-structured population models, data from Dorn et al., 2003).

Increased variability in abundance at the juvenile stage results from several biological and sampling issues. First, each cohort's history of highly variable larval and early juvenile mortality leaves behind a variable number of juveniles. Second, there is increased patchiness at the juvenile stage due to schooling behavior, making them hard to sample; and finally, as they get older and more agile, it is difficult to sample the evasive juveniles with nets. (Fig. 2(c)). Variability is decreased over a larger scale, again due to spatial averaging effect (Fig. 2(d)). At age-4 approaching full recruitment to the population, variability in abundance decreases on both the small and large spatial scales (Figs. 2(e) and (f)).

For walleye pollock, as evidenced above, the degree and pattern of variability depend on the observational scale of recruitment studies, the life history stage observed, and the gear used to study them. The choice of the observational scale is important because changes at one extreme of scale may not be indicative of changes at the other extreme. For example, recruitment dynamics at local scales are not necessarily reflected at broader scales, and vice versa. Furthermore, the patterns might change across scale, and the agents causing variability can shift in dominance as well.

4. The process of recruitment

4.1. Recruitment analyses

The effects of environmental conditions on pollock recruitment have been simulated using a variety of statistical and mechanistic models. Using multiple linear regression models Megrey et al. (1995) and Quinn and Niebauer (1995) tested the effect of many abiotic environmental variables in the Gulf of Alaska and eastern Bering Sea, respectively. Key variables were precipitation and wind mixing in the Gulf of Alaska and air temperature and ice cover in the Bering Sea. However, due to the indirect link between the variables and recruitment, these models provide little mechanistic explanatory power. Similarly, Megrey, Hollowed, Hare, Macklin, and Stabeno (1996) used a non-linear transfer function model to examine correlations of an index of atmospheric pressure in June and Kodiak rainfall in January and February with pollock recruitment in the Gulf of Alaska. Using these indirectly linked variables, the model explained 69% of variability in pollock recruitment.

The inclusion of non-additive and non-linear effects of environmental variables in a non-parametric statistical recruitment model (i.e., a generalized additive model, GAM) gave significantly improved fit compared to models with only linear variables (Fig. 3; Ciannelli, Chan, Bailey, & Stenseth, 2004). Stage-specific mortality models showed that springtime temperature and wind mixing were important in egg to age-0 survival, and fall temperatures and predatory fish abundance were important in survival from age-0 to age-1. Moreover, it was shown that environmental effects can change the degree of density- dependent mortality (a non-additive effect) in the pollock population. In particular, it was found that high groundfish predation and high water temperature induced a higher intensity of negative density-dependent mortality during juvenile stages, while high wind speed induced higher density-dependent mortality during the larval stages. These changes of density dependence can also result in a phase transition of recruitment metrics
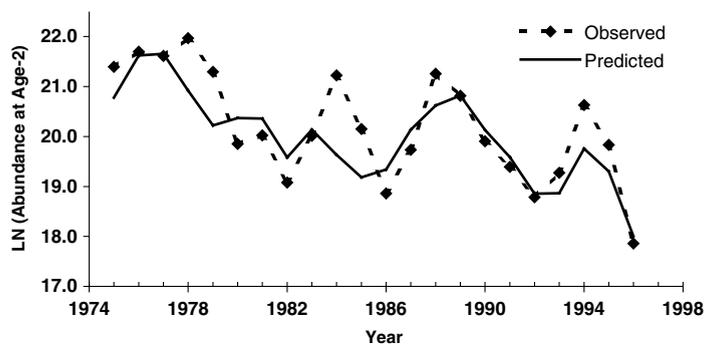
Fig. 3. Observed versus predicted Gulf of Alaska pollock recruitment. In this case predicted values of pollock recruitment were estimated from a non-linear model (Ciannelli et al., 2004), which included non-additive effects of environmental variables on pollock pre-recruitment survival.
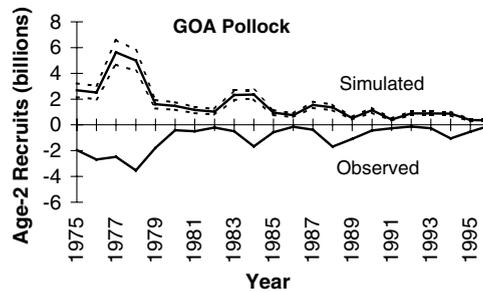
Fig. 4. Mirror-image comparison of observed recruitment (below axis line) to simulated recruitment of Gulf of Alaska pollock *Theragra chalcogramma* from a hybrid model. The dotted lines represent ±1 sd from 200 simulations (from Bailey et al., 2003).

(Ciannelli, Bailey, Belgrano, & Stenseth, in press). Specifically, during climate regimes characterized by high water temperature and high piscivorous biomass (i.e., the post-1976 climate and biological regime of the North Pacific) pollock recruitment was estimated to be lower in magnitude and variability, and the stage of recruitment control was delayed until the second half of the first (age-0) or the second (age-1) year of life. During opposite climate regimes (i.e., pre-1976) recruitment was estimated to be higher in magnitude and in variability, and recruitment control was set within the first half year of the cohort life, at the late-larval stage.

A hybrid model representing walleye pollock recruitment as a hierarchical process affected by factors promoting contrasting levels of stochastic (activating) or deterministic (constraining) dynamics captured both the patterns and trends in the time series of pollock recruitment (Fig. 4; Bailey et al., 2003). In this model, early mortality rates were stochastically generated, but the levels were dependent upon environmental conditions, such that low SST and high winds tend to result in high larval mortality. Mortality of later juvenile stages was derived from deterministic models of intra-cohort density dependence or of consumption of juveniles by groundfish. The similarity in pattern and trend of observed and simulated recruitment supports the concept that recruitment strength develops from the interaction among relatively small-scale stochastic activating and larger-scale deterministic constraining factors. Activating factors affect all pre-recruitment stages, while constraint is mainly imposed on juvenile stages. Constraint can also occur at the larval stage; realistically however, because of its subtle effect, it will be difficult to detect at the recruitment phase after other constraining processes act on later stages (e.g., after predation and density dependence) have taken their toll on cohort abundance.

4.2. A conceptual model

Adopting the general theory of pattern formation described above, recruitment of pollock may be described as a complex process that is the outcome of the balance between activating and constraining processes embedded within a complex adaptive ecosystem (Fig. 5). The stochastic nature of recruitment is the cumulative product of the many episodic events and high frequency activating factors that may impact larval survival. Constraining factors are often deterministic processes that have regulatory effects on survival making it more predictable, such as mortality of juveniles due to a long term buildup of predators, or density dependence. It is recognized that some factors may fall between these categories, may operate at both levels, or otherwise be difficult to categorize. Given the hierarchical nature of this perspective, some factors may change roles at another scale of observation. For example, from a meso-scale perspective prey density may be an activating factor in larval survival; the prey field itself is more stochastic in nature and variable in time and space than the larval survival process that it affects. However, on a micro-scale prey density may be a constraining factor that controls the swimming behavior of larvae. When exposed to high prey
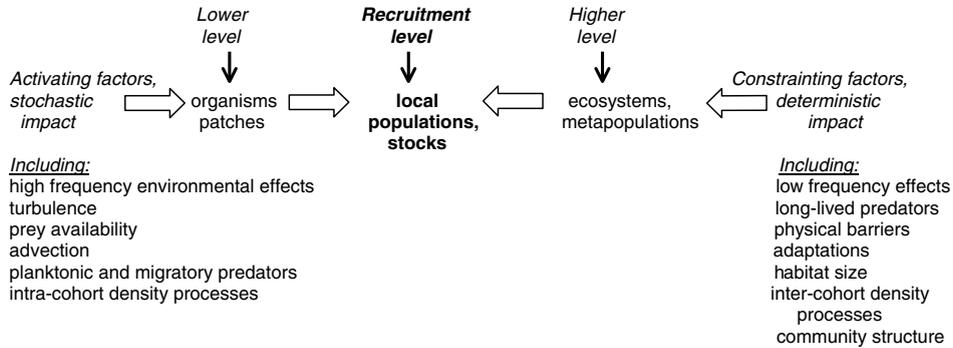
Fig. 5. A conceptual diagram of the organizing factors at different levels of the recruitment process for pollock in the Gulf of Alaska. The scale of observation ranges from organisms to ecosystems. At the scale of local populations, recruitment is a consequence of the dynamic tension between activating and constraining factors.

densities larvae make more turns and swim in a more horizontal aspect than they do in low densities of prey (Spring, 1996).

In our thinking, larval survival can be deterministic on an appropriate scale of observation; however, from the perspective of recruitment the factors influencing the survival process are complicated and interacting with many other factors. It is more practical to view the impact of larval mortality on recruitment years later as an outcome with a probability distribution rather than a certain outcome (i.e., it is stochastic). Conditions like wind intensity, turbulence and prey patchiness can change over relatively short scales (days and kilometers) in our study region and can result in episodic larval mortality, promoting variability in recruitment. The stochastic nature of recruitment is the cumulative product of many events and high frequency factors that impact larval survival. On the other hand, constraining factors change over large scales and introduce limits and impose stability or less variability in possible outcomes. For example, at later stages survival is mainly affected by groundfish predation and fall water temperature (as an accumulation of seasonal heating over months), which change over larger scales of months and hundreds of kilometers.

It is recognized that density-dependent processes are difficult to categorize as activating or constraining, although they are usually considered constraints. In fish population dynamics, strong non-linear density dependence can generate oscillations with increasing amplitude not distinguishable from chaos. However, moderately strong density dependence typically brings the population toward a stable equilibrium (May, 1976). Intra-cohort density dependence may change at a scale similar to the process it affects (recruitment) but inter-cohort density dependence, being the accumulated effect of several cohorts, changes at a lower frequency.

4.2.1. Activating factors

Factors that influence larval mortality (e.g., predation by invertebrates, storm events, transport into unfavorable nurseries, feeding success, etc.) change at a much higher frequency than recruitment, and are thus activating factors that promote change in the population. Mortality rates of early life stages of walleye pollock range from 4% to 40% per day (Bailey, Brodeur, & Hollowed, 1996; Bailey, Picquelle, & Spring, 1996) and are estimated over fairly small space and time scales: over areas of $10–30 \times 10^3$ km^2 and from 5 to 20 days.

The mechanism by which pollock larvae feed on prey and the dependence on turbulence and other environmental factors illustrate the complexity of these small-scale processes. Good survival of first-feeding larvae occurs during periods of low wind stress, whereas high winds are associated with low survival (Bailey & Macklin, 1994). Thus, high winds during the first-feeding period seem to disrupt feeding and survival. In addition, larval mortality rates are correlated with wind stress (Bailey, Brodeur, & Hollowed, 1996; Bailey,

Picquelle, & Spring, 1996), although there is an interaction with sea surface temperature associated with mixed layer stability. In a laboratory setting, turbulence is believed to impact larval fish contact rates with prey non-linearly (MacKenzie, Miller, Cyr, & Leggett, 1994). However, results testing this concept to date are complicated and contradictory (Dower, Pepin, & Leggett, 1998; Hillgruber & Klopmann, 2000; Landry, Miller, & Leggett, 1995; Reiss, Anis, Taggart, Dower, & Ruddick, 2002). Recently, it has been shown that pollock larvae will alter their vertical distribution to avoid turbulence (Davis, 2001), further complicating the effect of turbulence on feeding. In the field, there is also evidence that the vertical distribution of pollock larvae deepens in response to surface turbulence (Kendall, Incze, Ortner, Cummings, & Brown, 1994). Not only do larvae respond to turbulence, prey also have species-specific reactions to turbulence through avoidance and mixing (Incze, Hebert, Wolff, Oakey, & Dye, 2001). Porter et al. (in press) found that there is an interaction effect of light and turbulence on larval feeding such that high turbulence and low light are associated with poor feeding conditions, but high turbulence and high light are associated with optimal feeding conditions. Presumably, high turbulence causes larvae and prey to concentrate at depth in calmer waters, where feeding is enhanced but only when light levels are high.

Prey abundance, another factor influencing contact rates, has been linked with feeding success and mortality rates of pollock larvae (Bailey, Canino, Napp, Spring, & Brown, 1995), and prey levels have been correlated with the condition and growth of larvae as well (Haldorson, Paul, Sterritt, & Watts, 1989; Theilacker, Bailey, Canino, & Porter, 1996). Poor larval condition due to food deficiencies influences the behavior (Davis & Olla, 1992) and ability of larvae to locate and capture prey. Pollock larvae alter their swimming behavior in patches of prey, swimming slower, turning more, and increasing the horizontal aspect of their paths (Spring, 1996). Pollock larvae exhibit selectivity in feeding on different species of copepod nauplii (Hillgruber, Haldorson, & Paul, 1995), for example selecting against *Oithona* sp., even though it was the most abundant species of nauplii. High densities of pollock larvae can impact prey number, possibly to the point of depleting their own food resources (Duffy-Anderson, Bailey, & Ciannelli, 2002). Other factors known to be important for larval feeding success include sea surface temperature and light levels (Paul, 1983; Porter et al., in press).

Predation, advection, and disease also affect survival of early life stages, and numerous interactions are involved in each of these processes. For example, predation on larvae is influenced by stage and condition of larvae, the distribution, and abundance of many different predators, their overlap with their prey, their feeding rates, interactions with alternative prey, and environmental conditions (such as turbulence, temperature, and vertical structure in the water column). Variability in transport of eggs and larvae is also thought to be important to survival of early life stages (Hinckley, Bailey, Picquelle, Schumacher, & Stabeno, 1991; Incze, Kendall, Schumacher, & Reed, 1989; Kim & Kendall, 1989). Variability in transport is, among other factors, related to variations in the vertical structure of the water column, the vertical distribution of larvae, larval size, variations in current strength and direction, formation and location of meso-scale features such as eddies and meanders exporting water from, and carrying it onto the shelf (Sponaugle et al., 2002; Vastano, Incze, & Schumacher, 1992). Bailey (2000) speculated that anomalous transport away from the normal predatory field might contribute to the appearance of strong year classes.

4.2.2. Constraining factors

Constraining factors tend to have lower frequency oscillations compared to the recruitment process and the activating factors directly affecting larval mortality. Large-scale conditions like temperature anomalies, currents, and physical boundaries may impose order or constraints on change in ecological communities by their effects on species distribution and species interactions. Constraints may also arise in pollock populations from adaptations to their environments, such as the constancy of the timing and location of spawning (Bailey et al., 1999).

Habitat size is a condition that imposes constraints on the population level of pollock (Fig. 6) and other fishes (Sissenwine, 1984). Competition for prey, and possibly space, as limited resources, are presumably
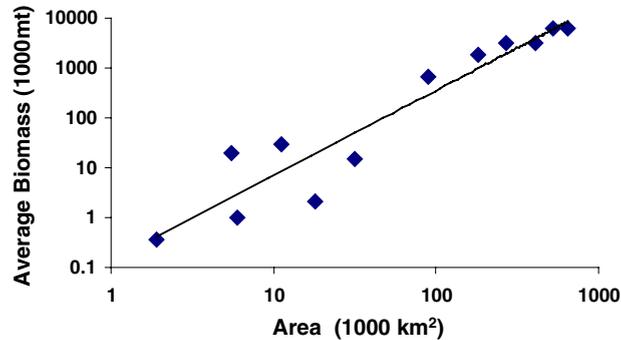
Fig. 6. The (log–log scale) relationship between the average biomass estimated from VPA (or stock assessment surveys) and the area of the continental shelf occupied by each of 13 different stocks. The continental shelf occupied was estimated as the area between the 50 and 200 m isobaths determined from digitized maps. The biomass levels are from the following stocks (from references in Bailey et al., 1999; Palsson et al., 1996 and unpublished reports): Sea of Okhotsk, west Kamchatka, west Bering Sea, Gulf of Alaska, north Puget Sound, south Puget Sound, eastern Bering Sea, northern Japan, Dixon Entrance, Queen Charlotte, West Vancouver, Strait of Georgia, and Prince William Sound.

underlying the constraints of available habitat. In the case of pollock, which are cannibalistic, crowding in space may be undesirable and lead to expansion beyond the optimal habitat to avoid predation. Size of habitat may also impose constraints on complex interactions with predators, including predation effects upon density dependence, availability of refuges from predation, and other considerations. For example, juvenile pollock tend to inhabit the upper and warmer part of the water column, where they also find shelter from their groundfish predators (Brodeur & Wilson, 1996). In years when fall temperature is high, presumably the depth of the thermocline is shallower, imposing a serious constraint on habitat availability for juvenile pollock. In addition, in a warmer and thinner upper layer, juvenile pollock may easily incur food limitations, as a result of their increased energetic demands (Ciannelli, Brodeur, & Buckley, 1998). Thus, in years characterized by warm fall sea surface temperature juvenile pollock may suffer from higher predation, as a result of limiting shelters, and increased density dependence, as a result of limiting food availability (Ciannelli et al., 2004).

Community structure, especially at higher trophic levels, is another constraining influence on recruitment. In general, changes in the predator community occur at a lower frequency than interannual variability in recruitment. An example is the buildup of large and long-lived predatory fishes that occurred after the late 1970s regime shift in the Gulf of Alaska and its effect on juvenile pollock mortality (Bailey, 2000). Low frequency changes in the plankton community may also impact recruitment through bottom-up processes (Beaugrand, Brander, Lindley, Souissi, & Reid, 2003) or trophic mismatches (Edwards & Richardson, 2004).

Constraints may be self-generated by density dependence in pollock populations. Density-dependent mortality from cannibalism or from food limitation are deterministic processes known to influence pollock recruitment (Fig. 7). In walleye pollock, density-dependent mortality can occur during the late-larval to early juvenile stage because of prey shortages (Bailey, Brodeur, & Hollowed, 1996; Duffy-Anderson et al., 2002). The intensity of density dependence is mediated by the external environmental variables that also have a direct effect upon survival (i.e., wind speed, water temperature, and predation). These changes of density dependence are essential to explain the dynamics of pollock recruitment, since they account for both, the non-additive effects of the environment and the shifts in recruitment dynamics reported in Ciannelli et al. (2004). In the Bering Sea, pollock are highly cannibalistic (Wespestad & Quinn, 1996), causing inter-cohort density dependence, although such a high degree of cannibalism is not observed in the Gulf of Alaska population (Bailey et al., 1999).
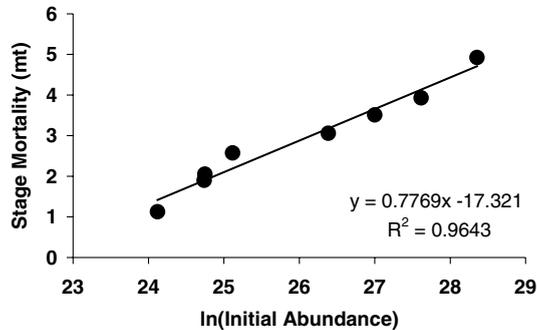
Fig. 7. Total mortality (mt, product instantaneous rate of mortality, m, during stage and stage duration, t) of Gulf of Alaska pollock from the late-larval to early juvenile stage plotted against the initial cohort density.

Egg production, as the product of individual fecundity and numbers of adult females, is also a constraining factor that limits recruitment and varies on a lower frequency than recruitment, since the numbers of females are aggregated over 10 or more annual cohorts. Furthermore, the age structure of adult spawning pollock possibly affects the size and condition of larvae, which has been observed for west coast rockfishes (Berkeley, Chapman, Sogard, 2004). However, in the case of pollock there has been no observed relationship between maternal size and egg size (and thus larval size through the relationship of egg and larval size) (Hinckley, 1990).

Fishing pressure on pollock may be a constraint, although the long-term effects of fishing pressure on pollock recruitment have been difficult to demonstrate. Human exploitation is known to cause population trends in other marine fishes (Bjørnstad, Fromentin, Stenseth, & Gjoesaeter, 1999). From simulations of the eastern Bering Sea pollock stock, Wespestad and Quinn (1996) showed that fishing has little effect on pollock recruitment, and possibly has a positive effect due to the removal of cannibalistic adults. Other aspects of harvesting are relatively unexplored in pollock population dynamics; these include interactions between fishing and population genetic effects on age and size at maturity (Hutchings, 2004), effects of age structure on spawning time and fitness of eggs and larvae (Berkeley, Hixon, Larson, & Love, 2004), and effects of fishing on depletion of local stocks (Bailey et al., 1999).

4.3. Other conceptual models

There are numerous conceptual models describing control of the recruitment process. Most of these models involve dichotomies, such as pre- or post-settlement (Hixon, 1998), top-down or bottom-up (Menge et al., 1999), and density-dependent versus density-independent control (Clark et al., 1999; Holm, 1990). Similarly, factors influencing recruitment have been dichotomized, such as subtle processes versus episodic events (Houde, 1989), extrinsic or intrinsic (Carr & Reed, 1993; Robertson, 1990), deterministic versus stochastic (Fowler, Doherty, & Williams, 1992), biotic versus abiotic (Lecchini & Galzin, 2003), and high or low frequency factors (Hollowed, Bailey, & Wooster, 1987). Some other concepts provide mechanisms, for example, the match or mismatch of larval feeding readiness to prey availability (Cushing, 1975) and starvation versus predation hypotheses (Wooster & Bailey, 1989). The primary difference between the activating-constraining concept and these others is that the former is defined by its effect, rather than an inherent property. Classification of factors based on activation and constraint is mechanistic, inclusive of these other concepts, and based on ecological theory. In our model the categorization of a factor depends on its observational scale of variability, and the result is a dynamic balance between processes occurring at different scales. This conceptual view not only provides a mechanistic understanding of how factors affect the system variability, but also provides insight on the possible outcome of the dynamic balance between such factors.

The bottom-up versus top-down model, although being clear in the mechanisms, does not account for the fact that survival of a cohort may be bottom-up at the larval stage and top-down at the juvenile stage; there is not an obvious place for density dependence and no consideration of scale. The categories extrinsic versus intrinsic, deterministic versus stochastic, subtle or episodic, high, and low frequency are conceptually appropriate in that they explain some particular way that a factor operates, but do not provide mechanistic explanations, nor do they provide insight on the outcome. The category density-dependent versus density-independent does not account for the fact these two factors may often interact, and therefore cannot be isolated from each other. In the category biological versus environmental, almost all biological events can be linked with environmental causes and making this dichotomy seems too simplistic.

Another conceptual model of pollock recruitment in the GOA, known as the 'switch model' (Megrey et al., 1996), described recruitment as a series of switches each corresponding to an early life stage. External environmental variables regulated the magnitude of survival, depicted by the position of the switch: high survival in its 'on' position and low in the 'off' position. Our conceptual model shares with the switch model the concept that recruitment results from a series of survival events occurring over temporally and spatially segregated stages. However, we emphasize the presence of internal regulatory forces (i.e., density dependence) and the interaction of factors.

Hunt et al. (2002) proposed a conceptual model of pollock recruitment in the Bering Sea, in relation to climate and environmental forcing, known as the 'oscillating control hypothesis' (OCH). This view of pollock recruitment in the Bering Sea shares with us the presence of different environmental phases with different mechanisms of recruitment control within each phase. However, it also bears a number of differences. First, the OCH was mainly focused on trophic interactions and relative effect on the survival of walleye pollock juvenile stages (i.e., bottom-up versus top-down forcing) while we also emphasize the demographic effects of environmental variability (i.e., density dependence). Second, the OCH only dealt with the survival during the juvenile stage, while we cover also the larval stage. Finally, and most importantly, the OCH is hitherto untested, mainly because of the limited time series of environmental data available for the Bering Sea. Thus, our study, though focused on a different system, partly corroborates the OCH view of environmentally driven phase transitions of pollock recruitment dynamics. In Hunt's view the recruitment phase transitions depend on the dominance of bottom-up or top-down regulatory forces. Here, we claim that the relative dominance of activating or constraining mechanisms is responsible for the phase transitions of pollock recruitment dynamics.

5. Recruitment forecasting

Forecasts of recruitment are currently used by the National Marine Fisheries Service to provide guidance to the North Pacific Fisheries Management Council, which establishes harvest quotas. The effects of alternative harvest strategies and recruitment scenarios are used to project future abundance and risk associated with management actions (Megrey et al., 1996). The projected status of stocks is extremely sensitive to recruitment assumptions, and recruitment forecasts are utilized to limit the possible scenarios to those most probable. So far, forecasting recruitment of pollock has met with modest success. Forecasts have been made from both quantitative models (the non-linear transfer function model described above) and from a forecast algorithm based on quantitative and qualitative data not included in the model (such as larval abundance and length–frequency composition in annual acoustic surveys) using a combined measure of the information weighted by data source and type (Megrey et al., 1996). Currently, the recruitment prediction strategy is to classify each annual forecast into one of five possible scenarios (strong, average-strong, average, weak-average or weak year-class strength). In 11 years of forecasting attempts, the predictions have resulted in no exact forecasts, 7 near-correct forecasts (one classification scenario off, e.g., average-strong prediction turned out to be a strong year class), 3 near-misses (2–3 classes off) and one miss

(four classes off) (http://www.pmel.noaa.gov/foci/forecast/bullseye.html). The current forecast uses data on winter–spring precipitation, winter–spring wind mixing, advection from drogued drifters, larval counts during the late-larval period, and the strength of prior year classes given the empirical relationship among year classes with a 2-year lag (http://www.pmel.noaa.gov/foci/forecast/04.pdf).

The conceptual picture of recruitment as a complex process impacts the strategy to forecast recruitment. When dynamics are complex due to non-linear systems and interactions, predictions become more uncertain as the time between initial conditions and the prediction target increases. In the case of pollock, correlations with recruitment improve steadily as the temporal proximity of input variables gets closer to the age of recruitment. Forecasts are difficult to make years in advance from environmental conditions during early life (egg and larval) stages because of the variability introduced by mortality during a long juvenile stage. There is not a statistically significant relationship (or even a noticeable trend) among the conditions (egg abundance, or any combination of egg abundance and environmental conditions such as wind speed and temperature) during the initial stages of year class formation and eventual year-class strength. Correlations between recruitment and cohort abundance at young stages of development improve steadily with proximity of cohort age to the age of recruitment (Fig. 8(a)). By the late-larval stage there is a noticeable trend between recruitment and larval abundance (Fig. 8(b)), and a significant trend with age-0 juveniles (Fig. 8(c)). Finally, age-1 abundance is highly correlated with recruitment (Fig. 8(d)). The difficulty of forecasting recruitment from environmental conditions (Walters & Collie, 1988) or abundances of early life stages has been suggested previously (Bradford, 1992). For example, in a meta-analysis of marine fish populations, Bradford (1992) found that egg and larval abundances were imprecise as predictors of future recruitment, whereas juvenile abundances performed better.

The problem of forecasting fishery recruitment has some parallels with forecasting seasonal to interannual weather. In both cases, account must be made for complicated interactions between a host of processes over a wide range of spatial and temporal scales. In addition, much of the potential predictability resides in relatively large-scale and slowly changing aspects of the respective systems (for example, SST for the weather and abundance of long-lived predators for fishery recruitment). Long-term weather forecasting is difficult, especially in the extra-tropics, because the memory of the initial state of the atmosphere is short.
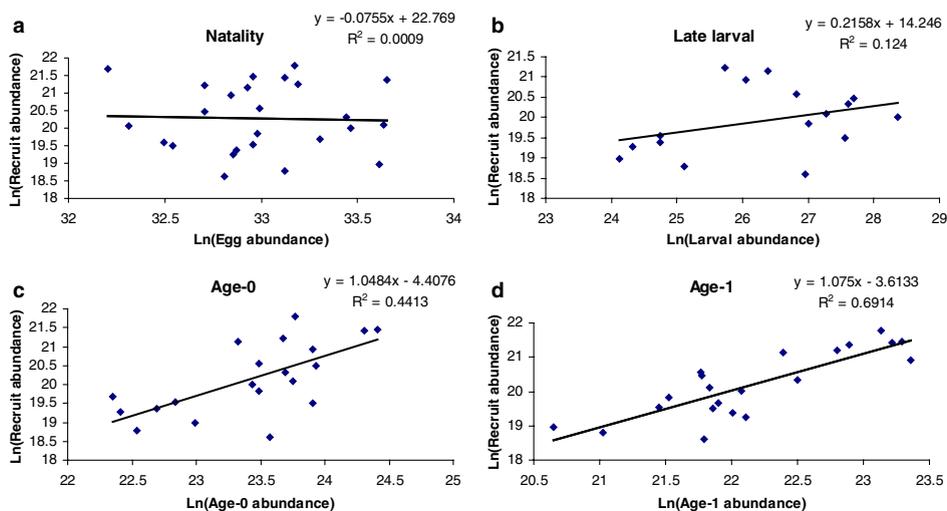
Fig. 8. Comparison of Gulf of Alaska pollock the natural logarithm of recruitment at age-2 from catch-at-age models to the natural logarithm of stage specific abundance of each cohort determined from life tables (e.g., Bailey, Brodeur, and Hollowed, 1996; Bailey, Picquelle, and Spring, 1996) at: (a) egg stage, (b) late-larval stage, (c) age-0 juvenile stage, and (d) age-1 juvenile stage.

Marine communities may have similar phases over which the system memory is short or long (short-lived pelagic versus long-lived demersal fish dominated communities).

As complex systems (Rind, 1999), weather patterns exhibit self-organization into preferred modes of variability, at least on large spatial and temporal scales. It should also be recognized that long-term weather forecasts, by nature, can only provide information over broad spatial and temporal perspectives. But it is often the regional weather that is of tangible importance, and the weather on this scale is subject to local influences that are often only weakly linked to the large-scale flow. For example, while the North Pacific basin displays much of its variability on decadal time scales in association with the Pacific Decadal Oscillation (Mantua, Hare, Zhang, Wallace, & Francis, 1997), the coastal winds along the Gulf of Alaska fluctuate much more on subseasonal to interannual time scales (Stabeno et al., 2004). The experience gained in long-term weather forecasting suggests that fishery recruitment forecasting should be even more difficult and less reliable. We have more complete knowledge of the physics controlling the weather than the mechanisms impacting recruitment. Therefore, we also have a better foundation for establishing causal links in statistical models and estimating the processes in dynamical models for the weather than for recruitment. Since statistical models perform about as well as dynamical models in terms of the long-term weather (e.g., Goddard et al., 2001), and because of the large uncertainties in ecosystem processes, it is reasonable to expect that statistical models are apt to be more reliable for fishery recruitment forecasting in the near future. While statistical models for fishery recruitment hold some promise, they are limited by factors similar to those for long-term weather forecasts, and the relative importance of the various mechanisms influencing recruitment is liable to be a function of the background state or regime.

For pollock the background state of the environment can generate a change in the mechanisms of recruitment control (Ciannelli et al., in press). For example, the importance of constraining factors is accentuated during environmental regimes that promote high predation and density dependence, i.e., high fall temperature and high groundfish predator density. During such environmental regimes the magnitude and variability of pollock recruitment are on average low, and recruitment control is delayed to the juvenile stages (age-0 and age-1). During opposite environmental regimes, there is lack of constraint on the abundance of juvenile stages. As a consequence, recruitment is strongly influenced by the factors that affect larval survival (i.e., the activating factors). During such regimes, pollock recruitment dynamics exhibit higher average magnitude and variability and earlier stage of recruitment control. There is an emerging principle among fisheries oceanographers that in the presence of regime-dependent recruitment dynamics the management of harvestable marine resources should adapt to the incumbent climate scenario (Duffy-Anderson et al., in press; Rothschild & Shannon, 2004; Steele, 1996). However, the challenge is not only to understand the intricacies by which the environment affects recruitment, but also to synthesize them in a fashion that is of use to managers. Our hope is that the view under which we present pollock recruitment dynamics will facilitate the understanding of a causal and more workable link between environmental variability and recruitment control.

Acknowledgements

References

Anderson, P. J., & Piatt, J. F. (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology-Progress Series, 189*, 117–123.

Bailey, K. M. (2000). Shifting control of recruitment of walleye pollock (*Theragra chalcogramma*) after a major climate and ecosystem change. *Marine Ecology-Progress Series, 198*, 215–224.

Bailey, K. M., Brodeur, R. D., & Hollowed, A. B. (1996). Cohort survival patterns of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska: a critical factor analysis. *Fisheries Oceanography, 5*(Suppl. 1), 179–188.

Bailey, K. M., Canino, M. F., Napp, J. M., Spring, S. M., & Brown, A. L. (1995). Contrasting years of prey levels, feeding condition and mortality of larval walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. *Marine Ecology-Progress Series, 119*, 11–23.

Bailey, K. M., Ciannelli, L., & Agostini, V. N. (2003). Complexity and constraints combined in simple models of recruitment. In H. I., Browman, & A. B. Skiftesvik (Eds.), *The big fish bang: Proceedings of the 26th annual larval fish conference* (pp. 293–302). Bergen, Institute of Marine Research, Bergen, Norway.

Bailey, K. M., & Macklin, A. (1994). Analysis of patterns in larval walleye pollock *Theragra chalcogramma* survival and wind mixing events in Shelikof Strait, Gulf of Alaska. *Marine Ecology-Progress Series, 113*, 1–12.

Bailey, K. M., Picquelle, S. J., & Spring, S. M. (1996). Mortality of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, 1988–91. *Fisheries Oceanography, 5*(Suppl 1), 124–136.

Bailey, K. M., Quinn, T. J., Bentzen, P., & Grant, W. S. (1999). Population structure and dynamics of walleye pollock, *Theragra chalcogramma*. *Advances in Marine Biology, 37*, 179–255.

Beamish, R. (1994). Climate change and exceptional fish production off the west coast of North America. *Canadian Journal of Fisheries and Aquatic Science, 50*, 2270–2291.

Beaugrand, G, Brander, K. M., Lindley, J. A., Souissi, S., & Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature, 426*, 661–664.

Berkeley, S. A., Chapman, C., & Sogard, S. M. (2004). Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology, 85*, 1258–1264.

Berkeley, S. A., Hixon, M. A., Larson, R. J., & Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries, 29*, 23–32.

Bjørnstad, O. N., Fromentin, J-M., Stenseth, N. C., & Gjoesaeter, J. (1999). Cycles and trends in cod populations. *Proceedings of the National Academy of Sciences of the Unite States of America, 96*, 5066–5071.

Bjørnstad, O. N., & Grenfell, B. T. (2001). Noisy clockwork: time series analysis of population fluctuations in animals. *Science, 293*, 638–642.

Bograd, S. J., Stabeno, P. J., & Schumacher, J. D. (1994). A census of mesoscale eddies in Shelikof Strait, Alaska, during 1989. *Journal of Geophysical Research, 99*, 18243–18254.

Botsford, L. W. (2001). Physical influences on recruitment to California Current invertebrate populations on multiple scales. *ICES Journal of Marine Science, 58*, 1081–1091.

Bradford, M. J. (1992). Precision of recruitment predictions from early life stages of marine fishes. *Fishery Bulletin, United States, 90*, 439–453.

Brodeur, R. D., & Wilson, M. T. (1996). A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fisheries Oceanography, 5*(Suppl. 1), 148–166.

Brown, J. H., Gupta, V. G., Li, B-L., Milne, B. T., Restrepo, C., & West, G. B. (2002). The fractal nature of nature: power laws, ecological complexity and biodiversity. *Philosophical Transactions of the Royal Society of London B, 357*, 619–626.

Brown, J. H., Whitham, T. G., Morgan, S. K., & Gehring, C. A. (2001). Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science, 293*, 643–650.

Carr, M. H., & Reed, D. C. (1993). Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Canadian Journal of Fisheries and Aquatic Science, 50*, 2019–2028.

Ciannelli, L., Bailey, K. M., Belgrano, A., & Stenseth, N.C. (in press). Climate change causing phase transition of Walleye Pollock (*Theragra chalcogramma*) recruitment dynamics. *Proceedings of the Royal Society B*.

Ciannelli, L, Brodeur, R. D., & Buckley, T. W. (1998). Development and application of a bioenergetics model for juvenile walleye pollock. *Journal of Fish Biology, 52*, 879–898.

Ciannelli, L., Chan, K. S., Bailey, K. M., & Stenseth, N. C. (2004). Nonadditive effects of the environment on the survival of a large marine fish population. *Ecology, 85*, 3418–3427.

Clark, W. G, Hare, S. R., Parma, A. M., Sullivan, P. J., & Trumble, R. J. (1999). Decadal changes in growth and recruitment of Pacific halibut (*Hippoglossus stenolepsis*). *Canadian Journal of Fisheries and Aquatic Science, 56*, 1–11.

Cushing, D. H. (1975). *Marine ecology and fisheries*. Cambridge: Cambridge Univ. Press.

Davis, M. W. (2001). Behavioral responses of walleye pollock, *Theragra chalcogramma*, larvae to experimental gradients of sea water flow: implications for vertical distribution. *Environmental Biology of Fishes, 61*, 253–260.

Davis, M. W., & Olla, B. L. (1992). Comparison of growth, behavior and lipid concentrations of walleye pollock *Theragra chalcogramma* larvae fed lipid-enriched, lipid-deficient and field-collected prey. *Marine Ecology-Progress Series, 90*, 23–30.

Dixon, P. A., Milicich, M. J., & Sugihara, G. (1999). Episodic fluctuations in larval supply. *Science, 283*, 1528–1530.

Dorn, M., Barbeaux, S., Guttormsen, M., Mergrey, B., Hollowed, A., Wilkins, M., & Splalinger, K. (2003). Assessment of walleye pollock in the Gulf of Alaska. In *Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska*. Anchorage, AK: North Pacific Fishery Management Council.

Dower, J. F., Pepin, P., & Leggett, W. C. (1998). Enhanced gut fullness and an apparent shift in size selectivity by radiated shanny (*Ulvaria subbifurcata*) larvae in response to increased turbulence. *Canadian Journal of Fisheries and Aquatic Science, 55*, 128–142.

Duffy-Anderson, J. T., Bailey, K. M., & Ciannelli, L. (2002). Consequences of a superabundance of larval walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska in 1981. *Marine Ecology-Progress Series, 243*, 179–190.

Duffy-Anderson, J., Bailey, K., Ciannelli, L., Cury, P., Belgrano, A., & Stenseth, N. C. (2005). Phase transitions and climate-environmental variability in marine fish recruitment processes. *Ecological Complexity, 2*, 205–218.

Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature, 430*, 881–884.

Estes, J. A., Tinker, M. T., Williams, T. M., & Doak, D. F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science, 282*, 473–476.

Fowler, A. J., Doherty, P. J., & Williams, DMcB. (1992). Multi-scale analysis of recruitment of a coral reef fish on the Great Barrier Reef. *Marine Ecology-Progress Series, 82*, 131–141.

Fromentin, J-M., Gjoesaeter, J., Bjørnstad, O. N., & Stenseth, N. C. (2000). Biological processes and environmental factors regulating the dynamics of the Norwegian Skagerrak cod populations since 1919. *ICES Journal of Marine Science, 57*, 330–338.

Goddard, L., Mason, S. J., Zebiak, S. E., Ropelewski, C. F., Basher, R., & Cane, M. A. (2001). Current approaches to seasonal-to-interannual climate predictions. *International Journal of Climatology, 21*, 1111–1152.

Haldorson, L., Paul, A. J., Sterritt, D., & Watts, J. (1989). Annual and seasonal variation in growth of larval walleye pollock and flathead sole in a southeastern Alaskan bay. *Rapports et Procès-Verbaux des Réunions. Conseil International Pour L' Exploration de la Mer, 191*, 220–225.

Hillgruber, N., Haldorson, L. J., & Paul, A. J. (1995). Feeding selectivity of larval walleye pollock *Theragra chalcogramma* in the oceanic domain of the Bering Sea. *Marine Ecology-Progress Series, 120*, 1–10.

Hillgruber, N., & Klopmann, M. (2000). Vertical distribution and feeding of larval blue whiting in turbulent waters above Porcupine Bank. *Journal of Fish Biology, 57*, 1290–1311.

Hinckley, S. (1990). Variation of egg size of walleye pollock *Theragra chalcogramma* with a preliminary examination of the effect of egg size on larval size. *United States Fishery Bulletin, 88*, 471–483.

Hinckley, S., Bailey, K. M., Picquelle, S., Schumacher, J. D., & Stabeno, P. J. (1991). Transport, distribution and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. *Canadian Journal of Fisheries and Aquatic Science, 48*, 91–98.

Hixon, M. A. (1998). Population dynamics of coral-reef fishes: controversial concepts and hypotheses. *Australian Journal of Ecology, 23*, 192–201.

Hollowed, A. B., Bailey, K. M., & Wooster, W. S. (1987). Patterns in recruitment of marine fishes in the Northeast Pacific Ocean. *Biological Oceanography, 5*, 99–131.

Hollowed, A. B., Hare, S. R., & Wooster, W. S. (2001). Pacific basin climate variability and patterns of Northeast Pacific marine fish production. *Progress in Oceanography, 49*, 257–282.

Holm, E. R. (1990). Effects of density-dependent mortality on the relationship between recruitment and larval settlement. *Marine Ecology-Progress Series, 60*, 141–146.

Houde, E. D. (1989). Subtleties and episodes in the early life of fishes. *Journal of Fish Biology, 35*(Suppl. A), 29–38.

Hunt, G. L., Jr., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M., et al. (2002). Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Research. Part II, 49*, 5821–5854.

Hutchings, J. A. (2004). The cod that got away. *Nature, 428*, 899–900.

Incze, L. S., Hebert, D., Wolff, N., Oakey, N., & Dye, D. (2001). Changes in copepod distributions associated with increased turbulence from wind stress. *Marine Ecology-Progress Series, 213*, 229–240.

Incze, L. S., Kendall, A. W., Schumacher, J. D., & Reed, R. K. (1989). Interactions of a mesoscale patch of larval fish (*Theragra chalcogramma*) with the Alaska Coastal Current. *Continental Shelf Research, 9*, 269–284.

Incze, L. S., Ortner, P. B., & Schumacher, J. D. (1990). Microzooplankton, vertical mixing and advection in a larval fish patch. *Journal of Plankton Research, 12*, 365–379.

Kendall, A. W., Incze, L. S., Ortner, P. B., Cummings, S., & Brown, P. K. (1994). Vertical distribution of eggs and larvae of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska. *Fishery Bulletin, United States, 92*, 540–554.

Kendall, A. W., & Picquelle, S. J. (1990). Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. *Fishery Bulletin, United States, 88*, 133–154.

Kim, S., & Kendall, A. W. (1989). Distribution and transport of larval pollock (*Theragra chalcogramma*) in Shelikof Strait, Gulf of Alaska, in relation to water movement. *Rapp. Proc-verb. Reun. Cons. Int. Explor. Mer., 191*, 127–136.

Landry, F., Miller, T. J., & Leggett, W. C. (1995). The effects of small-scale turbulence on the ingestion rate of fathead minnow (*Pimephales promelas*) larvae. *Canadian Journal of Fisheries and Aquatic Science, 52*, 1714–1719.

Lecchini, D., & Galzin, R. (2003). Influence of pelagic and bethic, biotic and abiotic, stochastic and deterministic processes on the dynamics of auto-recruitment of coral fish. *Cybium, 27,* 167–184 (English abstract).

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology, 73,* 1943–1967.

Levin, S. A., & Pacala, S. W. (1997). Theories of simplification and scaling of spatially distributed processes. In D. Tilman & P. Kareiva (Eds.), *Spatial ecology* (pp. 271–295). Princeton, NJ: Princeton University Press.

Longhurst, A. R. (1976). Vertical migration. In D. H. Cushing & J. J. Walsh (Eds.), *The Ecology of the seas* (pp. 116–137). Philadelphia: W.B. Saunders Co..

MacKenzie, B. R., Miller, T. J., Cyr, S., & Leggett, W. C. (1994). Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnology and Oceanography, 39,* 1790–1799.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society, 78,* 1069–1079.

Maurer, B. A. (1999). *Untangling ecological complexity*. Chicago: University of Chicago Press.

May, R. M. (1976). Simple mathematical models with very complicated dynamics. *Nature, 261,* 459–467.

Megrey, B. A., Bograd, S. J., Rugen, W. C., Hollowed, A. B., Stabeno, P. J., Macklin, S. A., et al. (1995). An exploratory analysis of associations between biotic and abiotic factors and year-class strength of Gulf of Alaska walleye pollock (*Theragra chalcogramma*). *Canadian Special Publication of Fisheries and Aquatic Sciences*, 227–243.

Megrey, B. M., Hollowed, A. B., Hare, S. R., Macklin, S. A., & Stabeno, P. J. (1996). Contributions of FOCI research to forecasts of year-class strength of walleye pollock in Shelikof Strait, Alaska. *Fisheries Oceanography, 5*(Suppl. 1), 189–203.

Menge, B. A., Daley, B. A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P. M., et al. (1999). Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological Monographs, 69,* 297–330.

Merrick, R. L., Chumbley, M. K., & Byrd, G. V. (1997). Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. *Canadian Journal of Fisheries and Aquatic Science, 54,* 1342–1348.

Musgrave, D. L., Weingartner, T. J., & Royer, T. C. (1992). Circulation and hydrography in the northwestern Gulf of Alaska. *Deep-Sea Research, 39,* 1499–1519.

Napp, J. M., Incze, L. S., Ortner, P. B., Siefert, D. W., & Britt, L. (1996). The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival. *Fisheries Oceanography, 5*(Suppl. 1), 19–38.

Napp, J. M., Kendall, A. W., & Schumacher, J. D. (2000). A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. *Fisheries Oceanography, 9,* 147–162.

Omori, M., & Kawasaki, T. (1995). Scrutinizing the cycles of worldwide fluctuations in the sardine and herring populations by means of singular spectrum analysis. *Bulletin of the Japanese Society of Fisheries Oceanography, 59,* 361–370.

Palsson, W. A., Hoeman, J. C., Bargmann, G. G., & Day, D. E. (1996). 1995 status of Puget Sound bottomfish stocks, Washington Department of Fish and Wildlife, Olympia, WA.

Pascual, M., Roy, M., & Franc, A. (2002). Simple temporal models for ecological systems with complex spatial patterns. *Ecology Letters, 5,* 412–419.

Paul, A. J. (1983). Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae *Theragra chalcogramma*. *Marine Ecology-Progress Series, 13,* 175–179.

Porter, S. M., Ciannelli, L., Hillgruber, N., Bailey, K. M., Chan, K. S., Canino, M. F. & Haldorson, L. J. (in press). Analysis of factors influencing larval walleye pollock *Theragra chalcogramma* feeding in Alaskan waters. *Marine Ecology-Progress Series*.

Quinn, T. J., III, & Niebauer, J. J. (1995). Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to oceanographic variables. *Canadian Special Publication of Fisheries and Aquatic Sciences, 121,* 497–507.

Reed, R., & Schumacher, J. D. (1987). Physical oceanography. In D. W. Hood, S. T. Zimmerman (Eds.), *The Gulf of Alaska: Physical environment and biological resources* (pp. 57–75). Minerals Management Service Pulb. No.: MMS86-0095, DOC/NOAA, DOI.

Reiss, C., Anis, A., Taggart, C. T., Dower, J., & Ruddick, B. (2002). Relationships among vertically structured in situ measures of turbulence, larval fish abundance and feeding success and copepods on Western Bank, Scotian Shelf. *Fisheries Oceanography, 11,* 156–174.

Rind, D. (1999). Complexity and climate. *Science, 284,* 105–107.

Robertson, D. R. (1990). Differences in the seasonalities of spawning and recruitment of some neotropical reef fishes. *Journal of Experimental Biology and Ecology, 144,* 49–62.

Rothschild, B. J. (2000). Fish stocks and recruitment: the past thirty years. *ICES Journal of Marine Science, 57,* 191–201.

Rothschild, B. J., & Shannon, L. J. (2004). Regime shifts and fishery management. *Progress in Oceanography, 60,* 397–402.

Royer, T. C. (1981). Baroclinic transport in the Gulf of Alaska. Part II. Fresh water driven coastal current. *Journal of Marine Research, 39,* 251–266.

Royer, T. C. (1998). Coastal processes in the northern North Pacific coastal segment. In A. R. Robinson & K. H. Brink (Eds.). *The sea* (Vol. 11, pp. 395–414). New York: J. Wiley and Sons.

Schumacher, J. D., Stabeno, P. J, & Bograd, S. J. (1993). Characteristics of an eddy over a continental shelf: Shelikof Strait, Alaska. *Journal of Geophysical Research, 98,* 98395–98404.

Schumacher, J. D., Stabeno, P. J., & Roach, A. T. (1989). Volume transport in the Alaska Coastal Current. *Continental Shelf Research, 9*, 1071–1083.

Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M, et al. (1999). Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science, 21*, 289–347.

Sissenwine, M. P. (1984). Why do fish populations vary. In R. M. May (Ed.), *Exploitation of marine communities* (pp. 59–94). Heidelberg: Springer-Verlag.

Southward, A. J., Boalch, G. T., & Maddock, L. (1988). Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th Century. *Journal of the Marine Biological Association of the United Kingdom, 68*, 423–445.

Sponaugle, S., Cowen, R. K., Shanks, A., Morgan, S. G., Leis, J. M., Pineda, J. S., et al. (2002). Predicting self-recruitment in marine populations: biolphysical correlates and mechanisms. *Bulletin of Marine Science, 70*, 341–375.

Spring, S. (1996). *Swimming behavior of walleye pollock larvae Theragra chalcogramma in relation to zooplankton*. M.S. Thesis, Univ. of Wash., Seattle WA, unpublished.

Springer, A. M. (1992). A review: walleye pollock in the North Pacific. How much difference do they really make? *Fisheries Oceanography, 5*, 205–223.

Stabeno, P. J., Bond, N. A., Herman, A. J., Mordy, C. W., & Overland, J. E. (2004). Meteorology and oceanography of the northern Gulf of Alaska. *Continental Shelf Research, 24*, 859–897.

Stabeno, P. J., Reed, R. K., & Schumacher, J. D. (1996). The Alaska coastal current: continuity of transport and forcing. *Journal of Geophysical Research, 100*, 2477–2485.

Stabeno, P. J., Schumacher, J. D., Bailey, K. M., Brodeur, R. D., & Cokelet, N. D. (1996). Observed patches of walleye pollock eggs and larvae in Shelikof Strait, Alaska: their characteristics, formation and persistence. *Fisheries Oceanography, 5*(Suppl. 1), 81–91.

Steele, J. H. (1996). Regime shifts in fisheries management. *Fisheries Research, 25*, 19–23.

Stenseth, N. C., Bjørnstad, O. N., Falck, W., Fromentin, J-M., Gjoesaeter, J., & Gray, J. S. (1999). Dynamics of coastal cod populations: intra- and inter-cohort density dependence and stochastic processes. *Proceedings of the Royal Society of London B, 266*, 1645–1654.

Stenseth, N. C., Chan, K. S., Framstad, E., & Tong, H. (1998). Phase-dependent population dynamics in Norwegian lemmings: interaction between deterministic and stochastic processes. *Proceedings of the Royal Society of London B, 265*, 1957–1968.

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K-S., & Lima, M. (2002). Ecological effects of climate fluctuations. *Science, 297*, 1292–1296.

Theilacker, G., Bailey, K. M., Canino, M. F., & Porter, S. (1996). Variations in larval walleye pollock feeding and condition: a synthesis. *Oceanography, 5*(Suppl. 1), 112–123.

Vastano, A. C., Incze, L. S., & Schumacher, J. D. (1992). Observation and analysis of fishery processes: larval pollock at Shelikof Strait, Alaska. *Fisheries Oceanography, 1*, 20–31.

Walters, C. J., & Collie, J. S. (1988). Is research on environmental factors useful to fisheries management? *Canadian Journal of Fisheries and Aquatic Science, 45*, 1848–1854.

Wespestad, V. G., & Quinn, T. J., II. (1996). Importance of cannibalism in the population dynamics of walleye pollock, *Theragra chalcogramma. NOAA Technicl Report NMFS* 126 (pp. 212–216).

Wilson, J. G., & Overland, J.E. (1986). Meterology of the northern gulf of Alaska. In Hood, D. W., Zimmerman, S. T. (Eds.), *The Gulf of Alaska: Physical environment and biological resources* (pp. 31–54). Minerals Management Service Pulb. No.: MMS86-0095, DOC/NOAA, DOI.

Wooster, W. S., & Bailey, K. M. (1989). Recruitment of marine fishes revisited. *Canadian Special Publication of Fisheries and Aquatic Sciences, 108*, 153–159.