

The year-class phenomenon and the storage effect in marine fishes

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Abstract

Factors contributing to population growth through strong year-class formation have driven a century of directed research in fisheries science. A central discovery of Hjort's paradigm was that multiple generations overlap and longevity is matched with frequency of strong recruitments. Here, I elaborate on this tenet by examining how intra-population modalities in spawning and early habitat use favour population resiliency. A modern theory that has application is the storage effect [Warner, R.R., Chesson, P.L., 1985. Coexistence mediated by recruitment fluctuations – a field guide to the storage effect. *Am. Nat.* 125, 769–787], whereby spawning stock biomass accumulates each year so that when early survival conditions are favourable, stored egg production can result in explosive population growth. I review two early life history behaviours that contribute to the storage effect: split cohorts (i.e., seasonal pulses of eggs and larvae) and contingent behaviour (i.e., dispersive and retentive patterns in early dispersal). Episodic and pulsed production of larvae is a common feature for marine fishes, well documented through otolith microstructure and hatch-date analyses. In temperate and boreal fishes, early and late spawned cohorts of larvae and juveniles may have differing fates dependent upon seasonal and inter-annual fluctuations in weather and climate. Often, a coastal fish may spawn for a protracted period, yet only a few days' egg production will result in successful recruitment. In these and other instances, it is clear that diversity in spawning behaviour can confer resilience against temporal variations in early survival conditions. Although many factors contribute to intra-population spawning modalities, size and age structure of adults play an important role. Contingent structure, an idea dating to Hjort (herring contingents) and Gilbert (salmon contingents), has been resurrected to describe the diversity of intra-population modalities observed through otolith microchemical and electronic tagging approaches. Retentive and dispersive behaviours confer resiliency against early survival conditions that vary spatially. Examples of contingent structure are increasingly numerous for diadromous fishes. Here, a nursery habitat associated with a contingent behaviour may make a small contribution in a given year, but over a decade contribute significantly to spawning stock biomass. For flatfish and other marine fishes, contingent structure is probable but not well documented. Proximate factors leading to contingent structure are poorly known, but for diadromous fishes, time of spawning and early life history energetic thresholds is hypothesized to lead to alternative life cycles. Here again time of spawning may lead to the storage effect by hedging against spatial variance in early vital rates. Managing for the storage effect will be promoted by conservation of adult age structure and early habitats upon which both strong and weak year-classes rely.

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1. Introduction

The storage effect has been suggested as an important mechanism in regulating marine fish populations (McCann, 1998; Secor, 2000a; Frank and Brickman, 2001; Francis, 2003; Berkeley et al., 2004). The central theory, originally developed by Warner and Chesson (1985) to explain species co-existence, is that overlapping generations (age structure) results in the accumulation of adult biomass over many year-classes, and this acts as a ‘seed bank’ that improves the chance for future population growth. In this essay, I elaborate on this basic concept by considering how diversity in spawning behaviour by adults and early dispersal by juveniles may contribute to the accumulation of spawning stock biomass by hedging against failed year-classes. Further, I argue that adult age structure itself can contribute to diversity in spawning behaviours and early dispersal. If such a relationship can be established, then maintenance or recovery of age structure is supported in fisheries management as a means to conserve population resiliency (Marshall et al., 2003).

2. What is the storage effect?

The storage effect concept originated from studies on reef fish diversity. Sale’s competitive lottery system (Sale, 1977) explained high species diversity in systems where recruitment was space limited. The hypothesis specified that recruitment only occurred when space opened up (e.g., due to predation, fishing, or a storm event) and other patches on the reef were held by juveniles and adults. Under the assumption of a ready supply of larvae competent to settle onto this new space, settlement fortuitously occurred on a first come, first serve basis. This random allocation of space maintained species co-existence and high diversity in reef systems. Chesson and Warner (1981) identified problems with this concept. In particular, if there occurs any competitive edge among larvae competent to settle (e.g., due to relative abundance, swimming ability, or responsiveness to settlement cues), then over generations, competitive exclusion by a single species occurs (Chesson and Warner, 1981). In modelling exercises, Chesson and Warner found that this prediction was robust under constant or varying environments. Indeed, coexistence was only stable when species had identical demographic attributes, which was deemed highly unlikely.

Warner and Chesson (1985) imposed three necessary conditions that would permit patterns of stable coexistence in systems where recruitment was space limited: (1) early vital rates and larval supply among species is

variable across years; (2) adults survive over long periods of poor recruitments; and (3) episodic recruitments (i.e., high rates of settlement) are matched by generation time. They termed this suite of demographic conditions the storage effect because strong recruitments were figuratively stored in the adult population. The storage effect has broad application in entomology, where storage occurs during long duration pupating stages; and in botany where storage occurs in seed banks. What is common about these taxa and marine fishes is that one life stage is driven by environmental variability and the other is buffered against competitive and environmental loss.

As an example of the storage effect, consider the recovery of Chesapeake Bay striped bass *Morone saxatilis*, a large temperate sea bass (female maturation at c. 7 y) that supports important fisheries in US Atlantic waters. Due to depressed spawning stock abundance in the early 1980s, strong fishing controls were implemented during the late 1980s. Subsequently, a population boom occurred during the 1990s, stimulated by strong year-classes that predated 1970. Striped bass can live in excess of 30 years, and demographic analysis showed that egg production stored in spawners >15 years in age was a key element in their rapid recovery (Secor, 2000a).

The storage effect, as a mechanism of promoting resiliency in populations through interactions among year classes (overlapping generations), has only recently been discussed for marine fishes (Frank and Brickman, 2001; Berkeley et al., 2004) but the idea has been implicit in the way we understand marine population dynamics since Hjort and his team’s discovery of the year-class phenomenon. A single very strong year-class (e.g., the 1904 year-class of Atlantic herring) is expected to sustain recruitments for a decade or longer. Further, a single strong year-class is expected to contribute to subsequent strong year-classes. Thus, scientists and managers have long recognized that longevity and age structure serve to span relatively long dry spells in year-class strength.

Here, I propose that larval cohorts spawned at different times but within the same year-class also contribute to the storage effect. Recruitment variances are typically treated on an annual basis (Myers, 2001; Marshall et al., 2003), but within an annual cohort, high variances in survival of weekly or monthly cohorts of larvae are common. Episodic and pulsed production of larvae is a common feature for marine fishes, well documented through otolith microstructure and hatch-date analyses (Limburg, 2002). I use the term ‘split cohorts’ (usage after Post et al., 1997) to differentiate within year-class variability from between year-class variability. Modalities in early dispersal and habitat use

patterns also represent an important sub-annual source of variance in early survival rates. I propose that these two cohort types, divested in time or space, contribute to sustain year after year accumulation of spawning stock biomass and thereby provision the storage effect much like annual investments in a seed bank (Fig. 1). Below, I give several examples of split cohorts in marine fishes and discuss ways in which these cohorts contribute to the storage effect.

3. Temporally split cohorts

Seasonal egg and larval production is often mistimed with periods of favourable survival conditions (Cushing, 1975; Rothschild, 1986), and spawning behaviour is viewed as one of the chief means by which variances in early survival can be reduced. As an example, Fogarty et al. (2001) contrasted Atlantic cod with haddock, which showed ten fold higher recruitment variability than cod. A 46% higher interannual variance in mean date of hatching in cod was attributed to an increased likelihood that cohort production would be well matched with favourable survival conditions. They concluded that the “lower variability in cod recruitment is consistent with ... a risk-spreading reproductive strategy and a protracted spawning season and broader spatial structure relative to haddock”. Similarly, for other marine fishes, recruits are often drawn from a relatively narrow period of a given population’s spawning interval.

For example, Hovenkamp (1991) observed that larvae and juvenile North Sea plaice were drawn from a relatively restricted period of egg production. Egg

productions across five North Sea regions were protracted and occurred from December to April for the period 1987–1989. But hatch-date distributions analyzed from immigrating larvae to the Wadden Sea were principally drawn from week-to-month-long periods. Further, these periods of peak representation varied among years. In 1987 and 1989, most larvae originated from eggs produced in December or January; in 1988, virtually all larvae originated from eggs produced during a two week period in March. Hovenkamp (1991) found it...“remarkable that in all years egg-production curves extended over several months, but that the influx of larvae peaked during only few, sometimes short periods”.

Differential transport of larvae to settlement areas may be important in controlling recruitment in flatfishes (Bailey et al., 2005). In their classic study on the tidal stream transport of metamorphosing Japanese flounder larvae in Shijiki Bay (Nagasaki), Tanaka et al. (1989) observed that settling larvae were most abundant during spring tides, perhaps indicative of favourable tidal conditions for inshore larval transport. Here as in the Hovenkamp (1991) study, a protracted spawning season would insure sufficient larval supply for favourable transport to nursery habitats. In a separate study, Noichi et al. (1994) back-calculated spawn-dates for over 1500 juvenile Japanese flounder from Yanagihima Beach (Nagasaki) and estimated that spawning occurred every day from late January through late April in 1990 and 1991. Over this protracted spawning period, recruitment (settlement) was pulsed corresponding to spring tides.

Long-term settlement patterns were linked to larval supply for winter flounder by Sogard et al. (2001). Over

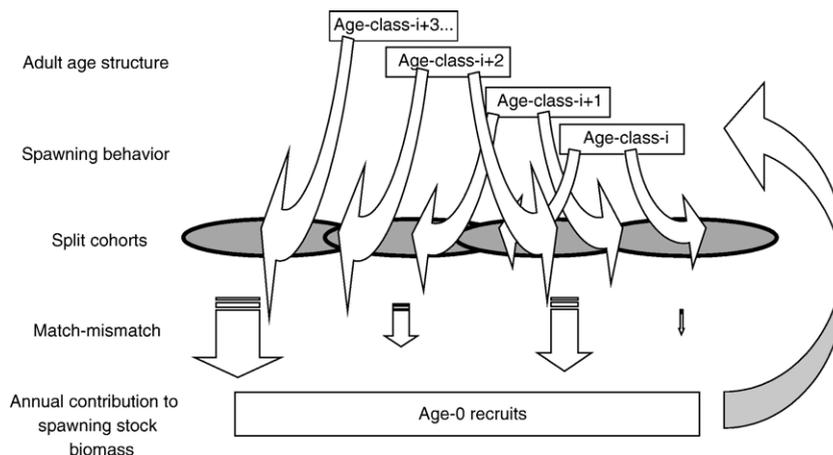


Fig. 1. Conceptual diagram representing how split cohorts contribute to the storage effect. Age structure contributes to a range of spawning behaviours, which in turn contributes to temporal and spatial diversity in larval production and utilization of nursery habitats represented by split cohorts. Each of these seasonal cohorts confronts different early survival conditions and thus, differentially contributes to future recruitments to the adult population. Because early survival conditions vary both seasonally and interannually, the storage effect guards against complete year-class failure and guarantees continued year-upon-year accumulation of spawning stock biomass.

the period, 1989–1999 in Great Bay, New Jersey (US), larval supply showed pulses in some years at c. bi-weekly cycles over a two-month period, but not all pulses equally contributed to the production of newly settled juveniles (Fig. 2). Timing of settlement was driven by climatic factors, where colder winters resulted in delayed settlement, yet larval supply did not show the same degree of dependence upon winter conditions. Here again is evidence that a protracted spawning season may be important in reducing recruitment variability by improving the odds that some but not all cohorts will be well matched with favourable early survival conditions.

As another example of an offshore coastal spawner, Atlantic coast bluefish exhibit seasonal pulses of larvae and juveniles that may lead to reduced recruitment

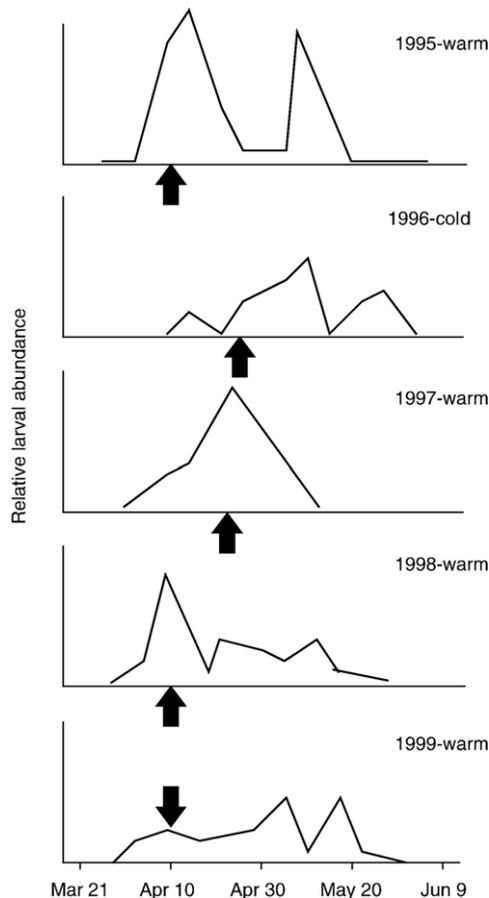


Fig. 2. Relative abundance of winter flounder larvae collected in Great Bay, New Jersey US (figure modified from Sogard et al., 2001). Filled arrow indicates mean back-calculated settlement date from juveniles collected during early summer months. Note that juvenile recruits come from a relatively restricted pulse of larvae on an annual basis and that the time of peak settlement varies across years.

variability. In early spring, bluefish adults move from overwintering habitats northerly along US coastal Atlantic waters. They congregate in US South Atlantic waters and spawn (Fig. 3). Another northerly migration occurs in early summer to US mid-Atlantic Bight latitudes where a subsequent pulse of spawning occurs. This pattern of spawning results in two main pulses of young recruits moving into nearshore coastal and estuarine nursery habitats (Nyman and Conover, 1988; Hare and Cowen, 1996; Munch and Conover, 2000). In trawl and seine collections in these habitats, modal progressions are typically observed during summer and fall months associated with spring and summer spawned cohorts (Fig. 3).

In fall months, a US federal survey program collects juvenile bluefish from Massachusetts to North Carolina (Munch and Conover, 2000). Based upon the length of those juveniles captured, Conover et al. (2003) classified spring and summer cohort juveniles, and inferred a recent shift in cohort representation. During the 20-y period 1973–1993, the spring cohort dominated. But in the more recent period, 1994–2002, the summer cohort dominated. The reason for this shift in cohort representation is unknown. Still, without contributions by the summer cohort in recent years, recruitment would be lower and over the entire series more variable. Thus, we find circumstantial evidence that spatially and seasonally split cohorts may contribute to the storage effect in Atlantic bluefish.

Because Chesapeake Bay striped bass spawn in restricted habitats—tidal freshwater regions in estuaries—several studies have effectively matched periods of egg production with subsequent larval and juvenile production (Rutherford and Houde, 1995; Secor and Houde, 1995, 1998; Houde, 1997). Indeed, daily ageing has allowed weekly resolution of cohorts of larvae. Striped bass are capital spawners, spawning in waves, cued by periods of rising temperature (Fig. 4a, cohorts C, E, F, and G). Still, not all spawners follow such cues (Fig. 4a, cohort D). Interestingly, in 1991, a poor overall year for recruitment, offspring resulting from an anomalous period of egg production encountered very favourable early survival conditions and contributed disproportionately to recruitment (Fig. 4a, b, cohort D; Secor and Houde, 1995). Note, also that favourable temperatures for larvae only occurred during a narrow window of the larval production period. Due to inter-annual variations in climate, this window of favourable conditions is a moving target, thus selecting for a range of spawning times.

In striped bass and other diadromous species, there are numerous studies that show that recruits result from variable periods of egg and larval production across

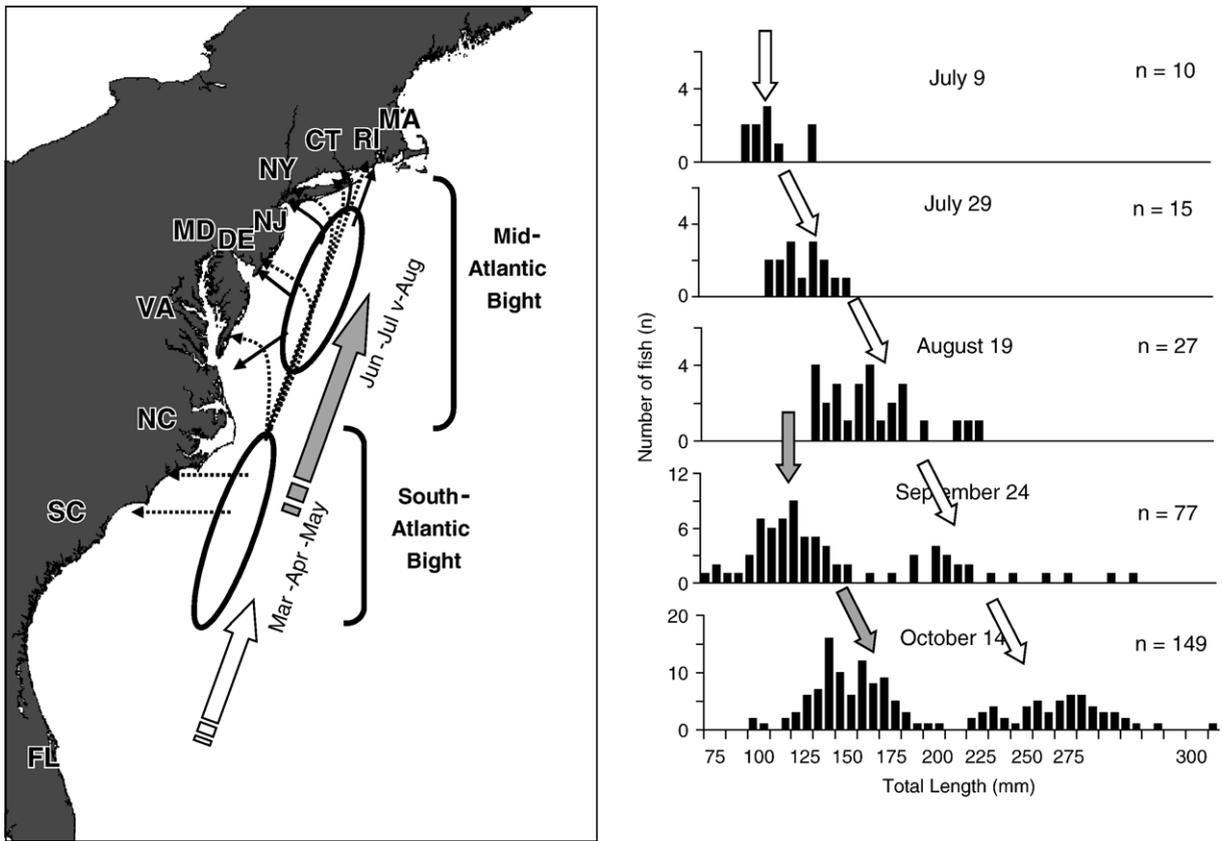


Fig. 3. Pulsed spawning behaviour and split cohort production in bluefish. (Left panel) Adult bluefish migrate from southern US Atlantic offshore waters (open arrow) and initially spawn March-May in coastal regions of the US South-Atlantic Bight. A second northern migration (filled arrow) and spawning period follows in the US Mid-Atlantic Bight. This spawning pattern results in pulsed delivery of early stage juveniles to inshore Mid-Atlantic nursery areas (shown by narrow arrows). (Right panel) Shown here are modal progressions for spring (open arrows) and summer (filled arrows) spawned cohorts collected in Maryland coastal waters (Secor, unpubl. data).

years (Crecco and Savoy, 1985; Rutherford and Houde, 1995; Limburg, 1996; Limburg et al., 1999). Much like Atlantic cod (Fogarty et al., 2001), the protracted nature of spawning results in split cohorts of larvae and juveniles, and is expected to dampen the effect of environmental variability on early vital rates. This in turn contributes to the storage effect by insuring that some minimal amount of recruitment occurs each year.

These examples of split cohorts highlight how a protracted and/or episodic delivery of eggs and larvae can contribute to the storage effect by improving the chance that some larvae will be well matched to favourable survival conditions. This tactic will not typically result in the explosive year-class phenomenon that has captured the attention of fisheries ecologists in the past. Rather, it will provision the year after year accumulation of adult biomass that insures that when overall environmental conditions favour a strong year-

class, there is sufficient egg and larval production upon which those conditions can act.

4. Spatially split cohorts

Split cohorts may serve not only to dampen temporal sources of variations in early survival conditions, but also spatial sources of recruitment variability. Intra-annual cohorts are delivered to different nursery environments by dint of spawning behaviours, dependent upon where and when parents spawn. Diversity in patterns of early habitat use serve to reduce variability associated with more restricted early dispersal and habitat use migration patterns. For instance, consider a population that relies exclusively upon a single tidal creek. A single catastrophic storm event might eliminate nursery function for this tidal creek yet leave adjacent nursery habitats less affected. The spreading of risk through diverse patterns of habitat use has been termed

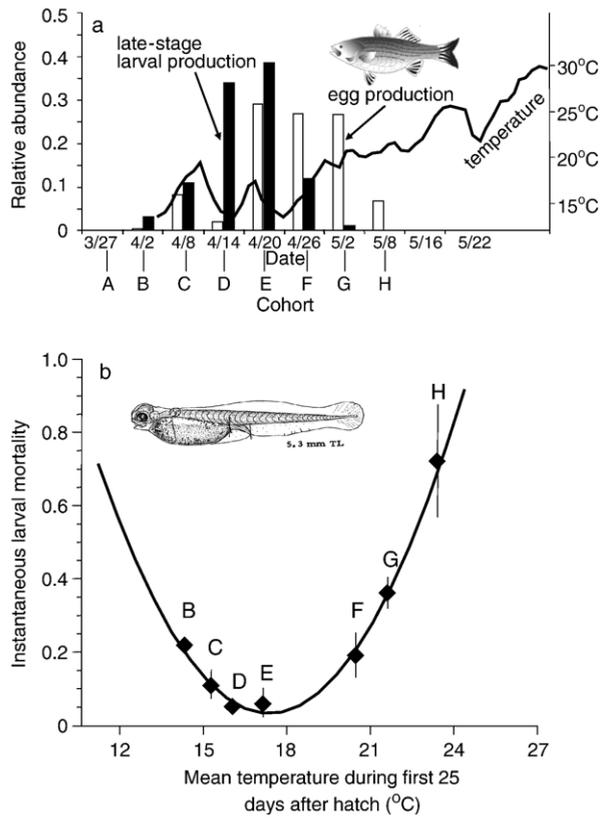


Fig. 4. (a) Striped bass egg and larval production for eight week split cohorts during spring 1991. Note that spawning is cued to periods of increasing temperature, but that cohort D is the exception to this rule. Also, note differential representation of late stage larvae respective to egg production across the weekly cohorts. (b) Larval striped bass mortality rate of weekly cohorts versus early temperature conditions. Mortality rates (shown with standard error bars) estimated through daily ageing and catch curve analysis. Note that early and late cohorts experience unfavourable survival conditions, while cohorts spawned at intermediate dates experienced the lowest mortality rates. Figures adapted from Secor and Houde (1995).

the rescue effect, where minority habitats may serve to subsidize spawning stock biomass in most years, but occasionally preserve the population should the majority habitat be catastrophically altered (Ray, 1997; Kraus and Secor, 2005).

White perch are an anadromous species closely related to striped bass, but restricted in their distribution to estuaries. In the Patuxent River estuary (Chesapeake Bay), Kraus and Secor (2004) observed two principal habitat use patterns—juveniles either remained in freshwater, natal or dispersed to brackish water nursery habitats. Using otolith microchemical analysis, they estimated that dispersal to brackish water nursery habitats occurred during the late larval-early juvenile period, analogous to settlement in flatfish and other coastal

species. Interestingly, those juveniles that exhibited rapid larval growth rates tended to remain in freshwater, while those with lower growth rates dispersed to brackish water nursery habitat. Because larval growth rate can vary substantially between early and late season cohorts (Limburg et al., 1999), there is an expectation (albeit as of yet untested) that spawning behaviour may be associated with the two patterns of early habitat use.

During the period 1989–2000, Kraus and Secor (2004) evaluated the relative contribution of the two patterns of early habitat use to adult recruitment (Fig. 5). They observed that in most years, and in particular those years producing large year-classes, the brackish water mode produced >90% of the recruits to the adult stock. However, for the weakest year-classes, those associated with drought spring and summer conditions, only the freshwater mode contributed to recruitment. Thus, for some years of poor juvenile production, only the minority behaviour and habitat contributed to recruitment. Under the expectation that prolonged periods of drought and poor year-class strengths can infrequently occur, Kraus and Secor (2004, 2005) argued that the retentive freshwater larval and juvenile behaviour may be important for long-term population resilience.

Other examples exist for early modal patterns of migration behaviour, particularly for diadromous species (Secor, 1999). Spatial cohorts within populations that exhibit similar migration patterns are termed contingents (Gilbert, 1914; Hjort, 1914; Secor, 1999, 2004). Contingents parcel spatial variances in recruitment through alternate recruitment pathways. Contingent structure and population consequences have been shown for many salmon and char populations (Nordeng, 1983; Thorpe et al., 1998), but also for Japanese, European and American eels (Tsukamoto et al., 1998; Tzeng et al., 2000; Tsukamoto and Arai, 2001; Morrison et al., 2003), American shad (Limburg, 2001), blueback herring and alewife (Limburg, 1998), striped bass (Secor et al., 2001), white perch (Kraus and Secor, 2004), ayu (Tsukamoto et al., 1987), and Japanese sea bass (Secor et al., 1998).

In coastal spawning fish, evidence for divergent patterns of either inshore-coastal or estuarine nursery habitat use exists through coincident occurrence of individuals in these two habitat types. Flatfish figure heavily into the view that estuaries serve as potentially higher ranked nurseries (*sensu* Beck et al., 2001). Yamashita et al. (2000) examined patterns of past habitat use in stone flounder, which settled in either estuarine or exposed inshore-coastal areas of Sendai Bay, Japan. They used Sr/Ca ratio in otoliths (Sr/Ca was elevated in the more stressful and environmentally fluctuating estuarine habitats) to determine pattern of recruitment

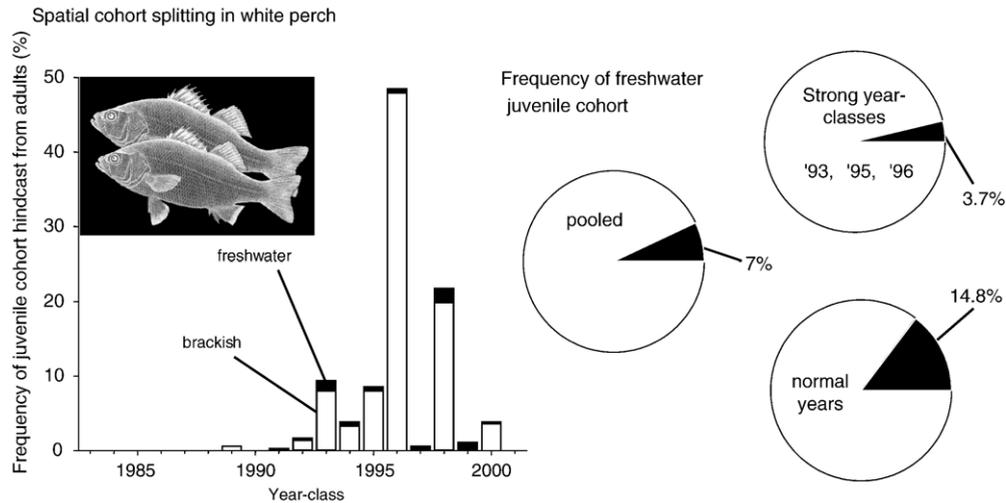


Fig. 5. Contribution of freshwater and brackish nursery habitats to spawning stock biomass in Patuxent River (Chesapeake Bay) white perch. Left panel: Adults classified using otolith microchemical analysis of their core region to two source habitats for year-classes 1989–2000. Right panel: Classification of adults by nursery habitat for pooled, dominant, and ‘normal’ year-classes (filled wedge is freshwater cohort). Note that in years not characterized by high recruitment, the freshwater nursery makes a relatively higher contribution to adult production. Analyses and graphic modified from Kraus and Secor (2004, 2005).

to age 1 and 2 years. Contribution rates varied between the two year-classes (Fig. 6). From 1994 and 1995 year-classes respectively, 65% and 32% of the samples resulted from production in estuarine nursery habitats. Although sample sizes were small (~20 each year), the example suggests that spatial splitting of cohorts might vary in a manner similar to white perch, where the consequences of alternative habitat use patterns vary across years. In a similar study, Brown (2006) inferred that adult English sole sampled in the Monterey Bay region (California, USA) originated from both coastal and estuarine habitats in similar proportion. Because estuarine nursery habitats were much smaller in areal extent, she concluded that estuaries were higher ranked nurseries.

5. Factors leading to split cohorts

A central remaining question is how do adult spawning behaviours (i.e., time, place, duration, amplitude of egg production) contribute to split cohorts. Further, how is diversity of spawning behaviours maintained within populations? Environmental cues are certainly important in causing variations in spawning duration and amplitude in flatfish and other marine fishes (Gibson, 1997). In flatfish aquaculture, spawning is responsive to temperature, photoperiod and salinity (e.g., Watanabe et al., 2001; Nissling et al., 2002; Kayaba et al., 2003). Learned behaviour, schooling, and mating systems are also important determinants in spawning behaviours. Further, because flatfish and most

other marine fishes are not single event spawners, spawning duration, amplitude and frequency will be influenced by factors related to condition, size and age (Rijnsdorp, 1994).

Here, I stress age structure as a factor that contributes to diversity in spawning behaviours. In flatfish and other species, older fish spawn at different times than younger fish, which may hedge against a seasonal mismatch. Rijnsdorp (1994) reported that older plaice spawn earlier than younger smaller plaice. This same pattern has been observed in striped bass (Cowan et al., 1993), Atlantic herring (Lambert, 1987) and Atlantic cod (Hutchings and Myers, 1993). Lambert (1987) found that increased numbers of adult age-classes were associated with an earlier and more protracted spawning period in Atlantic herring. Secor (2000b) showed that higher age diversity in Chesapeake Bay striped bass was positively, albeit insignificantly, associated with an increased number of spawning days. Several studies on Icelandic cod have shown that age structure strongly influences the timing and duration of egg production, and recruitment success (Marteinsdóttir and Thorarinnsson, 1998; Scott et al., 1999; Begg and Marteinsdóttir, 2000).

Although less well studied, spawning behaviours (and associated age structure) may also affect the early dispersal behaviours of young. Early life history thresholds, similar to those documented for salmonids (Metcalf and Thorpe, 1992; Økland et al., 1993) and for Chesapeake Bay white perch (Kraus and Secor, 2004), are proposed as a principal mechanism underlying contingent structure. Threshold cues for early

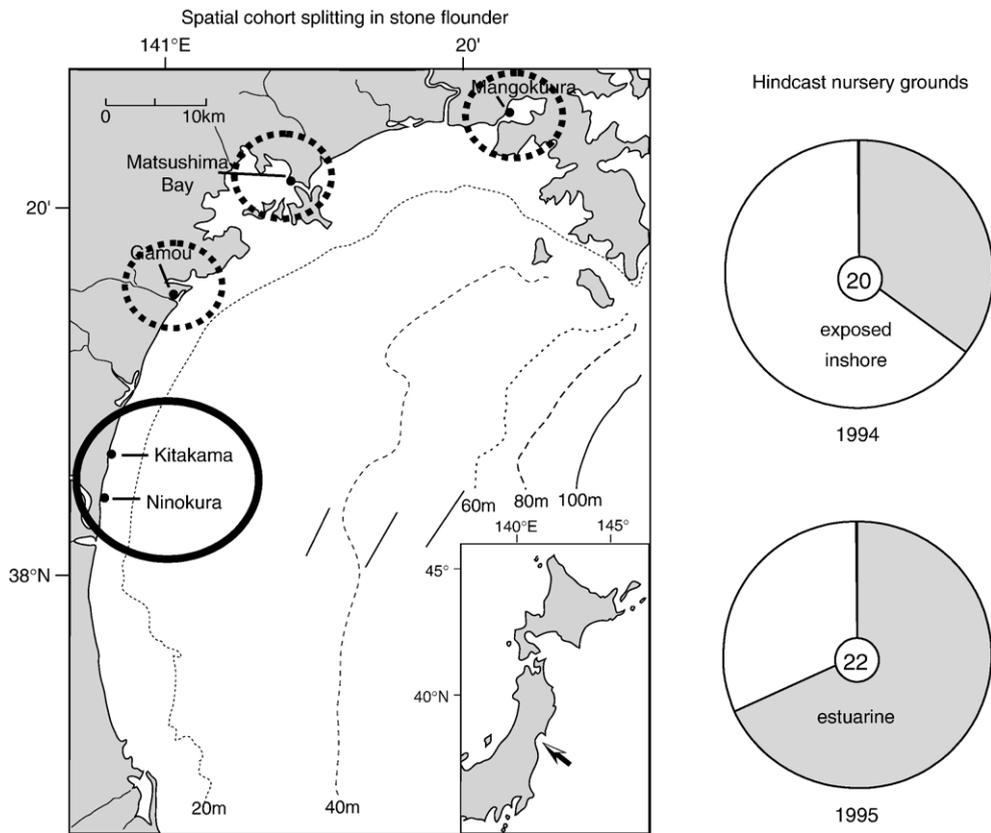


Fig. 6. Contributions of exposed inshore and estuarine nursery habitats to two year-classes (1994 and 1995) of age-1 and age-2 stone flounder in Sendai Bay. Nursery habitats were classified using otolith microchemical analysis. Map at left shows exposed inshore sites (solid line circle) and estuarine sites (dashed line circle). Central number in pie charts to right is sample size for age-1 (year-class 1995) and age-2 (year-class 1994) flounder. Data and graphics modified from Yamashita et al. (2000).

dispersal behaviours should vary with season and thus be related to specific periods of offspring production. Lake Biwa ayu (*Plecoglossus altivelis*) is a fascinating example of how a protracted and pulsed period of egg production can contribute to contingent structure (Tsukamoto et al., 1987). The annual population comprises a lake resident contingent and a stream migratory contingent. Both groups spawn in lacustrine habitats, but the resident contingent spawns earlier and its offspring attain a larger size by the end of the first growth season than the offspring of the migratory contingent, enabling an upstream migration by their offspring. Thus, due to the influence of female size and spawning behaviour, the offspring of migratory spawners become resident and the offspring of resident spawners become migratory (Fig. 7).

A common theme in these examples is that spawn date may link adult age structure to split cohorts in time and space. Bluefish represent a good example of how spawn date may be related to spawning location, resulting in spatially and temporally split cohorts. But

other examples are rare, perhaps because such studies require simultaneous sampling of eggs, larvae, and juvenile recruits. Here, I wish to emphasize that examination of spawning and hatch-dates is a productive means to evaluate how adult attributes are linked to recruitment variability.

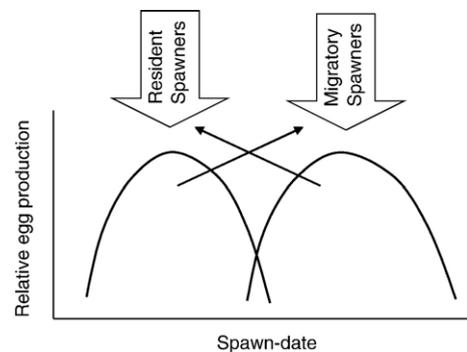


Fig. 7. Influence of spawn date (split cohorts) on migratory and resident contingent structure for Lake Biwa ayu. Interpretation of results from Tsukamoto et al. (1987).

6. Longevity and the storage effect

The storage effect comes from ecological theory, but has obvious parallels to Hjort and his team’s early work on Atlantic herring (Hjort, 1914). One of the principal discoveries related to the formation of strong year-classes was the presence of multiple and overlapping age classes. Fisheries ecology subsequently focused on factors leading to dominant year-classes, but relatively little attention has been given to the role of overlapping generations and longevity on recruitment variability. Age structure is most often viewed as the consequence of variations in recruitment success, rather than a causative agent itself in influencing recruitment variability. In this section, I review the evidence that longevity results in decreased recruitment variability. Such evidence provides indirect support of the view that overlapping generations and longevity are factors contributing to the storage effect.

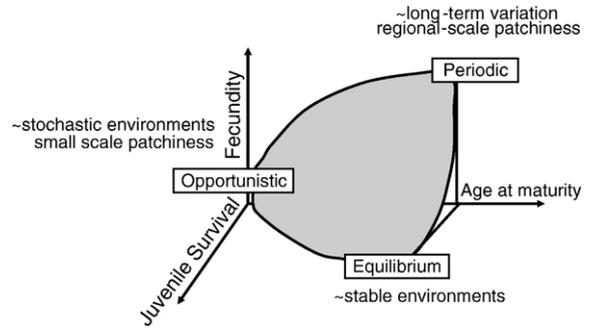


Fig. 9. Conceptual diagram representing three principal life history strategies in marine teleosts (modified from Winemiller and Rose, 1992). Note that Pleuronectidae epitomize the life history traits for a periodic species, which include late maturation, long reproductive life span, repeat spawning, high individual fecundity, and low (and variable) juvenile survival.

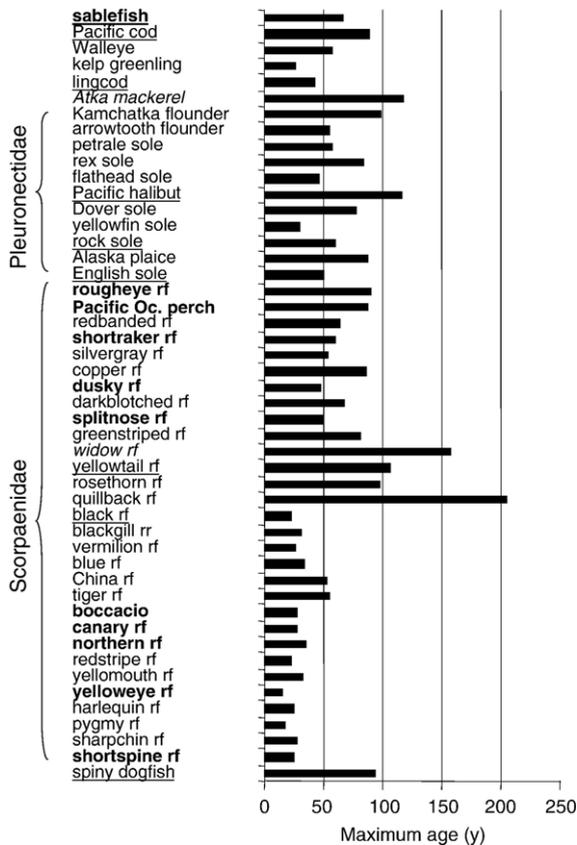


Fig. 8. Maximum ages reported for Alaska and British Columbia groundfish species. Common names for those species where longevity has been validated are indicated by underline (chemical OTC marking), bold face (radiometric validation), and italics (marginal increment analysis). rf=rockfish. Data from Munk (2001).

With the advent of improved means to age fishes, new maximum age estimates present new challenges to fisheries ecologists: Why do some fishes live so long? Are the oldest members of populations important to population dynamics? Since Beamish and McFarlane’s (1983) admonishment that age determination procedures lacked scientific rigor, large revisions in age structure of many marine species have occurred due to increased reliance on otolith structures, improved interpretations based upon verification studies and more consistently applied methods, and the application of geochronological tracers. Consider the subject of Beamish and McFarland’s review—sablefish, for which maximum age was revised upward from 6 to 90 y (Fig. 8). Pacific rockfish are in particular biblical in their longevities with several species exceeding 100 years in age. Although flatfish do not show such extreme ages, longevities >30 y are not uncommon (e.g., Fig. 8; Nash and Geffen, 2005).

From first principles, Charnov and Schaffer (1973) resolved Cole’s (1954) paradox that semelparous and iteroparous reproductive rates were nearly equivalent by showing that iteroparity was favoured when early survival \ll adult survival. Because low survival rates are expected to generate a higher scope of variability in survival than a high rate, variability in recruitment should be positively related with iteroparity and its associated trait, longevity. In empirical studies, Leggett and Carscadden (1978) and Schaffer and Elson (1975) showed for American shad and Atlantic salmon, respectively that among populations, longevity and the degree of iteroparity were positively correlated with latitude. Under the assumption that higher latitudes cause higher variations in recruitments (due, for instance

to more extreme seasonal and interannual fluctuations in temperature), these studies are central case studies substantiating the theoretical expectation for increased longevity with increased recruitment variability (see also Van der Veer and Leggett, 2005).

Over the past 20 y, meta-analyses have confirmed patterns of increased recruitment variability with longevity across the majority of marine fish taxa investigated. Winemiller and Rose (1992) compiled life history traits for 216 marine and freshwater fishes. Using multivariate analyses, they observed three dominant vectors (Fig. 9): (1) opportunistic species showing low individual fecundity, low early survival and rapid maturation; (2) equilibrium species showing low individual fecundity, high early survival and late maturation; and (3) periodic species exhibiting high individual fecundity, low early survival, and late maturation. Periodic species are arguably representative of most temperate and boreal marine fishes. These species are associated with infrequent cycles of favourable conditions for early survival and broad spatial patchiness in early survival conditions. In summary, Winemiller and Rose’s meta-analysis of life history traits supports life history theory: longevity (late maturation) is associated with low and variable early survival rates.

A large recruitment database of over 200 stocks of marine fishes (Myers, 2001) supported a recent analysis between recruitment variability and longevity (Longhurst, 2002). For several important taxa—Atlantic herring, Atlantic cod, hake, whiting, and mackerels—significant positive correlations were found between recruitment variability and longevity. On the other hand, Pleuronectidae showed a weakly negative relationship. Further, Longhurst noted that the coefficient of variation for recruitments, ~50%, was substantially less for flatfish than for other taxa in the database. Not surprisingly, smaller data sets examined by Mann and Mills (1979) and Roff (1991) also failed to find significant relationships between flatfish recruitment variability and longevity. Density-dependent regulation during the juvenile period is thought to be of increased importance in flatfish in comparison to other taxa (Iles and Beverton, 2000; Van der Veer et al., 2000a,b), possibly offsetting the influence of longevity on recruitment variability.

7. Can we manage for the storage effect?

Managing for the storage effect is in effect managing for increased diversity within a population. Age diversity metrics have been developed for several species including

Age diversity index based upon age-specific reproductive rates

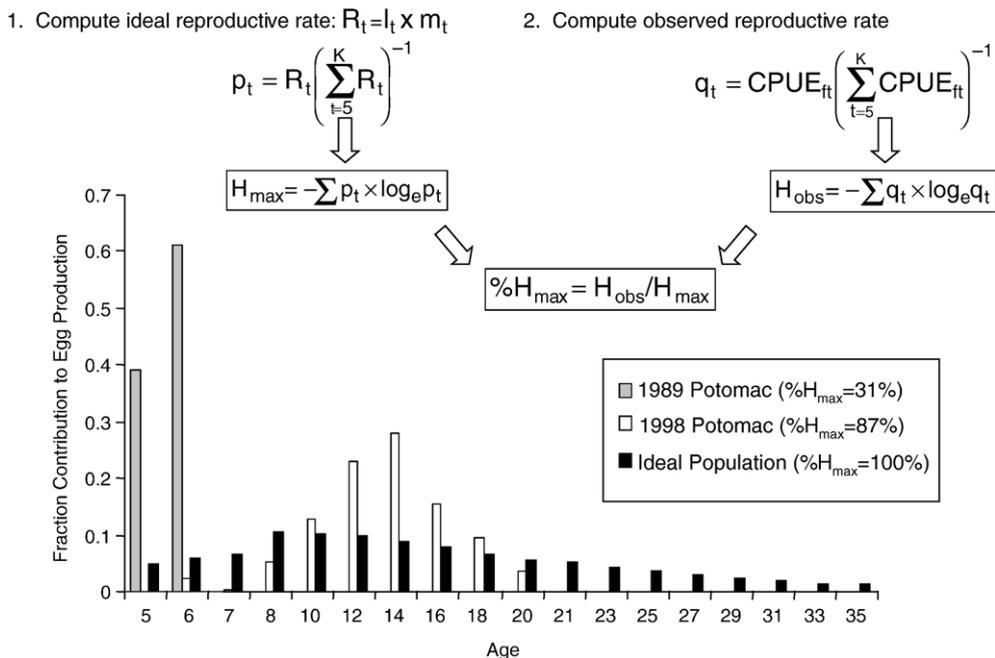


Fig. 10. Comparison of age-specific reproductive rates in an unexploited (ideal) striped bass population and observed reproductive rates for the Potomac River population in 1989 and 1998. Steps for computing the age diversity index are presented. l_t =survival to age t , m_t =fecundity at age t , $CPUE_{ft}$ =adult biomass at age $t \times m_t$. Graphic and analyses from Secor (2000b) and Marshall et al. (2003).

Atlantic herring (Lambert, 1987, 1990), Icelandic cod and striped bass (reviewed in Marshall et al., 2003). As an example, Secor (2000b) developed a method similar to the egg-production-per-recruit index in which observed age-specific reproductive rates are compared with those expected for an unexploited population (Fig. 10). Diversity and evenness-based indices of the distribution of individuals across age-classes serve to index the storage effect, which depends upon the accumulation of spawning stock biomass across many age-classes rather than the production of single strong year-classes (which would give low diversity and evenness scores). Age diversity indices could serve as metrics or targets in stock assessments ancillary to the current standards: stock abundance and exploitation rate (Marshall et al., 2003).

The storage effect will also be influenced by the rescue effect—where multiple nursery habitats contribute to the accumulation of spawning stock biomass (Bailey, 1997; Able, 2005; Ray, 2005). As shown for Chesapeake white perch and suggested for stone flounder, minority habitats in a given year can make important contributions over a longer period of time. Further, to improve a population's resiliency to anthropogenic, climate-driven, and other catastrophic loss of nursery habitats, the approach of assigning high conservation priority to only the most productive nursery habitats (e.g., Beck et al., 2001) may be flawed (Kraus and Secor, 2005). Such assignments should be based on habitat use studies that match in duration the generation time of the species of interest.

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