



## Moving beyond the current paradigm in marine population connectivity: are adults the missing link?

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### Abstract

During the past century, the field of fisheries oceanography has dominated the study of population connectivity in marine environments. The influence of physical and biological processes and their relationship to transport and retention of early life history stages has been central in providing insight into population structuring and connectivity. However, the focus on dispersive early life history stages has meant that the role of adults has received less attention and is not fully understood or appreciated. We argue that adults play a vital role in population connectivity for a wide range of marine taxa and hypothesize that adult-mediated population connectivity commonly results in a diverse array of population structuring. Two case-studies on winter skate, *Leucoraja ocellata*, and winter flounder, *Pseudopleuronectes americanus*, are presented to illustrate the role adults play in marine connectivity at both broad and fine scales, respectively. Indeed, if adults are important for population connectivity, we argue that the role of larval processes is conditional on adult choice and only management and research pursuits that integrate the full life cycle of species will capture the full dynamics of metapopulation connectivity. Failure to include the roles of adults can lead to misinterpretation of the causes and consequences of changes in ecosystem structure and fisheries productivity.

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## Introduction

Since the pioneering work of Sars (1876) and Ljungman (1882), scientists have sought to understand the role of connectivity in marine fish populations. The current paradigm driving the understanding of population connectivity in marine ecosystems relies on the influence of physical and biological processes on patterns of early life stage dispersal and retention, resulting in structuring of populations at a variety of scales. The result has been the advancement of highly resolved, coupled physical–biological models (Miller 2007) that have contributed substantially to understanding patterns of population connectivity and isolation. For example, Cowen *et al.*'s (2006) analysis of connectivity in reef fish estimated larval dispersal of 10–100 km, a range that is not only ecologically relevant, but explains the low level of genetic structuring among some Caribbean reef fishes (Vasconcellos *et al.* 2008; Puebla *et al.* 2009; Purcell *et al.* 2009; Carson *et al.* 2011). In contrast to the scales of dispersal reported for Caribbean reef fish by Cowen *et al.* (2006), other species contain distinct local subpopulations despite highly dispersive early life stages. This suggests that genetic structuring at scales finer than dispersal capacity is not only possible, but likely (e.g. Mullan *et al.* 2002).

Part of the deficiency in the understanding of population structuring is that there are many species for which the early life history dispersal paradigm does not apply. For these species, population connectivity is either fully or partially mediated by adult life stages (see Table 1). Adult-mediated mechanisms result in fundamentally different population connectivity or structuring than displayed in the classic paradigm based upon physical–biological coupling during early life history. It has been argued (Frisk *et al.* 2008, 2010) that adult-mediated population connectivity (AMPC) may result in greater genetic connectivity than classical larval-mediated processes with exchanges among populations occurring over 100s–1000s of kilometres. The lack of appreciation of the role of adults in promoting connectivity (genetic and demographic) has been emphasized in recent mass migrations reported for several species with hypothesized mechanisms as density-dependent waves (Fauchald *et al.* 2006), food availability (Olsson *et al.* 2006) and the relationship between individual condition and environmental drivers (Frisk *et al.* 2008, 2010; Frisk 2010).

**Table 1** Definition and explanation of terms.

Terms and definitions
<i>Population</i> : A group of individuals living within a geographic area that has a high rate of interbreeding, but can consist of subpopulations or stocks
<i>Subpopulation and stocks</i> : Subpopulations represent unique population units or stocks that are defined by unique characteristics that can include genetic or demographic attributes. In the fisheries literature, it is common to define stocks based on characteristics related to fishery availability, political jurisdiction and biological characteristics, while subpopulations are delineated on biological characteristics
<i>Population structure</i> : Indicates the existence of subpopulations with genetic and or demographic differentiation
<i>Connectivity</i> : The exchange of individuals between subpopulations with demographic and or genetic consequences
<i>Genetic connectivity</i> : Indicates a level of genetic exchange between subpopulations where high connectivity would result in lower genetic stock structuring, and low connectivity would imply genetically distinct subpopulations
<i>Demographic connectivity</i> : Indicates a level of contribution by different demographic groups (e.g. age classes) that exchange individuals between regions occupied by different subpopulations
<i>Adult-mediated population connectivity (AMPC)</i> : Indicates connectivity maintained by adult spatial and temporal behaviour. AMPC can result in either genetic connectivity, demographic connectivity or a combination of both. For example, the case-studies presented suggest that winter skate ( <i>Leucoraja ocellata</i> , Rajidae) utilizes AMPC to maintain high stock connectivity over a large habitat range, while winter flounder ( <i>Pseudopleuronectes americanus</i> , Pleuronectidae) appears to utilize AMPC to maintain localized stock structuring of a demographic or genetic nature

The role that migration plays in the persistence of subpopulations has been studied in the broader ecological field, but to a lesser extent in fisheries ecology (Smedbol *et al.* 2002). The concept of metapopulation dynamics has been widely applied to model and understand the persistence and productivity of interconnected subpopulations. This concept generally describes the dynamics of a series of local subpopulations that undergo extirpation and colonization (Levins 1969; Hanski and Gilpin 1991; Hanski and Simberloff 1997; Smedbol and Wroblewski 2002). In metapopulations, structure develops through breeding, exchange of individuals and extirpation events (Hanski and Gilpin 1991; Hanski and Simberloff 1997; Smedbol and Wroblewski 2002). The applicability of the metapopulation concept to marine finfish has been hindered by the perception

of panmictic populations and a low probability of extirpation. This view stems from the current paradigm of marine connectivity where physical and biological processes and their relationship to transport and retention of early life history stages have been central in providing insight into population structuring and connectivity. Under this paradigm, it seems unlikely that most populations of marine finfish would be characterized by genetic structuring and unlikely that subpopulations undergo colonization-extirpation cycles as predicted by metapopulation theory (Smedbol and Wroblewski 2002). However, recent work on genetics (Mullon *et al.* 2002; Hoarau *et al.* 2004; Buckley *et al.* 2008; Zarronaindia *et al.* 2009, 2012), larval dynamics (Cowen *et al.* 2000) and migratory behaviour (Kerr and Secor 2009, 2012; Sagarese and Frisk 2011; Wingate *et al.* 2011) suggests that genetic and demographic population structuring may be a more common feature for marine finfish than might be expected.

If connectivity between subpopulations is assumed to be driven by large-scale dispersal of early life stages, resulting in panmictic populations, the stock concept underlying classical approaches to the management of fisheries holds that the dynamics of the population are regulated by internal processes of growth, recruitment and natural and fishing mortality. However, if local subpopulation productivity is significantly driven by exchange of individuals between subpopulations, as observed in metapopulation theory and proposed under AMPC, the classical approach to fisheries may be inadequate.

Here, we argue that AMPC is critical for understanding marine connectivity. We argue that the focus on larval-mediated connectivity has meant that the role of adults has been underappreciated resulting in an incomplete understanding of metapopulation structuring in marine fishes. Overcoming this information gap is critical for effective management of species and ecosystems and is essential for understanding the evolution of population structuring and species persistence. Specifically, we will present: (i) a conceptual framework for AMPC; (ii) two case-studies of marine species exhibiting AMPC, which illustrate the role of adults in genetic and demographic connectivity and thereby the importance of AMPC; and (iii) the management and evolutionary consequences of AMPC.

## Conceptual framework

At the beginning of the 20th century, the paradigms used to understand inter-annual variation in fish abundance commonly invoked movement of adults (Smith 1994). However, the focus quickly shifted to early life history-based hypotheses as evidence accumulated that suggested a greater contribution from larval dynamics towards explaining variation in local stock productivity. Specifically, fisheries oceanography's focus on larval processes to explain local variation in fish abundance originates from a series of hypotheses relating population fluctuations to recruitment in a select group of economically important temperate species, including Atlantic herring (*Clupea harengus*, Clupeidae) and Atlantic cod (*Gadus morhua*, Gadidae). It was Hjort's (1914) pioneering work that recognized the role of variability in early life survival as a dominant cause of variation in recruitment. Hjort (1914) was the first to suggest that critical periods of high mortality contribute to the high variation in survival between spawning and the age that individuals enter into a fishery. Later, the role of the environment during early life history would be further highlighted by Cushing's (1970) match/mismatch hypothesis, among others (See Leggett and DeBlois 1995 for review). These seminal works led to the propagation of biophysical modelling and have provided significant insight into the role of oceanography in controlling local abundance and productivity through dispersal and retention of offspring. While the role of adults has been inferred in ideas such as the member-vagrant hypothesis (Sinclair and Iles 1989) and the basin model (MacCall 1990), the focus on early life history has resulted in a disregard of the role of adult movements and behaviours in structuring populations and local productivity. For example, in a recent special issue of *Oceanography* (Vol 20, no. 3) dedicated to marine population connectivity, the role of older life stages receives only passing mention. Indeed, adult movements are discussed solely in relation to the effects of Marine Protected Area spillover on fishery yields (Fogarty and Botsford 2007) and not as a contributing factor in population connectivity.

Many species of teleost and elasmobranch fishes do not conform to the traditional view of larval-mediated connectivity. Species that are livebearers and mouth brooders, for example, are less likely to be constrained by larval dispersal because they

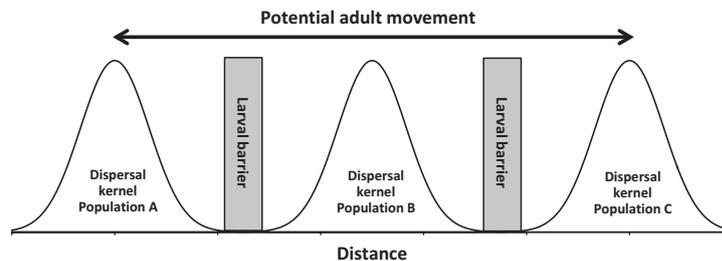
tend to produce advanced offspring that are deposited into optimal habitats. As species undergo ontogenetic shifts in habitat use, seasonal migrations or environmentally imposed decadal scale movements, opportunities to evolve AMPC become more likely. For example, reproductive migrations over great distances to optimal spawning/pupping areas (e.g. salmonids, spiny dogfish, *Squalus acanthias*, Squalidae, menhaden, *Brevoortia tyrannus*, Clupeidae) demonstrate how the degree of connectivity is determined by the behavioural ecology of adults. Recently, Palstra and Ruzzante (2011) found that the degree of connectivity in different salmon populations could be forecast from demographic and life history attributes. Thus, species that rely solely on AMPC will tend to have life histories characterized by some combination of low fecundity or production of large or protected offspring, which experience less variation in survivorship. The result is a key difference between pelagic coupling and AMPC where adults seek out optimal habitat both in terms of placement of young and feeding during gestation periods to maximize offspring survival and long-term reproductive investment (Cushing 1969, 1976; Helfman 1978; Macpherson and Duarte 1991). We suggest that the evolution of AMPC results in a much greater scale of interpopulation movement and potential connectivity than that mediated purely through larval transport.

Biophysical approaches to studying metapopulations involve considering the probability of 'self-recruitment,' the rate of dispersal away from the source populations and oceanographic links among systems (e.g. Cowen *et al.* 2007). When adult movement is greater than (or equal to) potential larval dispersal (Fig. 1), subpopulations can be connected through genetic or demographic

contributions (Table 1). Genetic connectivity would require that colonizing individuals contribute reproductively, whereas demographic connectivity would require that a component of a population moves between subpopulations.

In anadromy, where larval transport is constrained within a single watershed, it is clear that adult movement is the only method of connectivity among subpopulations. However, connectivity in species that have pelagic egg and larval stages can also be strongly dependent on AMPC. For example, in menhaden and bluefish (*Pomatomus saltatrix*, Pomatomidae), both common along the north-eastern US continental shelf, spawning occurs in coastal waters with the resulting offspring recruiting to inshore habitat, much the same as other species such as cod and herring. Although dispersal and settlement habitat selection control some of the patterns in survival, fall migrations to overwintering habitat at the southern extent of their ranges and the mixing of spawners during the spring create panmictic genetic populations (Warlen 1994; Lynch *et al.* 2010). These two species are examples in which the adult dispersal kernel exceeds or equals that of the pelagic egg and larval stages and is likely the primary factor in determining the overall population's demographics.

If patterns in recruitment are driven by adult movement, then unravelling a further layer of complexity that goes beyond larval dynamics will be required to understand population structuring. As a result, understanding metapopulation dynamics not only requires estimation of larval connectivity, but also variation in adult habitat choice and the environmental and resource drivers of individual adult movement. If AMPC contributes to population structuring, the role of larval pro-



**Figure 1** In species with adult-mediated population connectivity, metapopulation structuring is a function of smaller-scaled larval dynamics conditioned on larger-scaled adult movement, where kernels show the maximum larval dispersal for three populations (A, B, C). While persistent physical barriers limit larval transport and encourage retention and self-recruitment, the populations remain connected by adult movement.

cesses becomes conditional on adult choice. Models that ignore this added complexity will not capture the full dynamics of population connectivity. The result is a mismatch between ecological and management scales and a misinterpretation of the causes and consequences of changes in fisheries productivity.

## Case histories

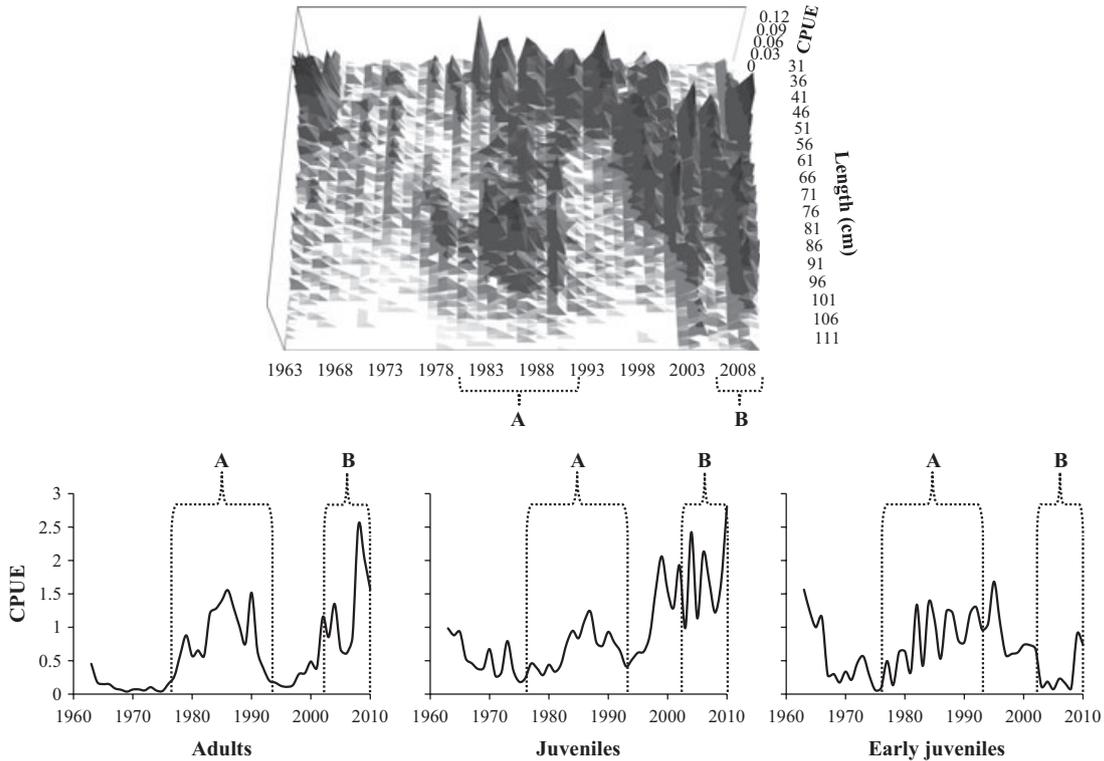
### Western Atlantic skates

Winter skate (*Leucoraja ocellata*, Rajidae) occurs in the north-western Atlantic from North Carolina, United States, to the Canadian coast and is characterized by AMPC (Frisk *et al.* 2008, 2010). Adult winter skate make regular seasonal movements between winter and summer habitats (Frisk 2010). During spring, the species is distributed broadly along the Atlantic coast, but by the fall, the population is clustered on Georges Bank and eastern southern New England, only to return to its broad coast wide distribution by winter (Frisk 2010). Although some egg production occurs year-round, spawning is concentrated in the fall and winter months (Frisk 2004; Frisk and Miller 2009). Females mature at 12 years and release 40–80 eggs per year (Sulikowski *et al.* 2005; Frisk and Miller 2009). Once released, the egg cases are anchored by four tendrils that attach to debris and are not readily moved by currents. Thus, seasonal movements of adults appear to be at least partially related to achieving optimal placement of offspring. The response to the seasonal environment suggests that drivers, such as temperature and resource availability, may provide cues for movement in the species. Frisk *et al.* (2008) argued that environmental change combined with a decrease in condition of winter skate on the Scotian Shelf may have triggered a large-scale movement of adults to Georges Bank in the 1980s. We hypothesize that the observed pattern of seasonal movement, driven by environmental cues, forms the mechanism for broad-scale exchange of individuals over a wide geographic region. Such events appear to occur occasionally, connecting regional subpopulations and altering the local demographics and likely genetic composition of populations.

One implication of AMPC is rapid changes in biomass within ecosystems resulting from exchange of individuals among populations. The consequences of these biomass transfers may be

perceived as regime shifts if keystone species (*sensu* Paine 1966) are involved and only small geographic components of the overall distribution are considered. Indeed, we have argued that AMPC underlies the well-documented regime shift on Georges Bank from a groundfish-dominated ecosystem to one in which elasmobranchs predominate (Frisk *et al.* 2008, 2010). Winter skate abundance increased dramatically on Georges Bank with contributions from adults and recruits between 1980 and 1982 (Fig. 2). This was originally hypothesized to be the result of predation and/or competitive release from decades of overfishing leading directly to an outbreak of elasmobranchs (Murawski 1991; Fogarty and Murawski 1998; many others). Further, the increase was feared to limit recovery of many commercially important groundfish (Murawski 1991; Fogarty and Murawski 1998). Frisk *et al.* (2008) provided a critique of the 'Elasmobranch Outbreak' hypothesis based on an examination of the size-structure of the winter skate population during this period and judged that the abundance increase resulted from movement of adults from either the deep off-shelf waters or the Scotian Shelf. The competitive and/or predation release mechanism is biologically unrealistic given the rapid and abrupt increase in fish 12 years and older (Frisk *et al.* 2008, 2010).

To formally examine whether population dynamics or adult migration was a more likely explanation for the changes in the winter skate population during the elasmobranch outbreak, Frisk *et al.* (2010) reconstructed the population dynamics of winter skate using a statistical-catch-at-age model. Models that included adult migration outperformed those that included only population dynamics. Simply stated, the appearance of a fully size-structured winter skate population is at odds with what is known of growth for this species, and the observed population increase (Fig. 2), assuming a closed system. The results did not rule out that competitive and/or predation release provided an advantage for recruiting skates. However, the model provided evidence that adult migration was a parsimonious explanation for the observed increase in winter skate on Georges Bank during the 1980s. Research has not been conducted to understand drivers behind adult winter skate movement and the location of the source population, leaving a critical gap in understanding connectivity for this species and overall ecosystem dynamics. This gap in knowledge has been high-



**Figure 2** Adult-mediated population connectivity has been implicated as the cause of the 1980s increase in adult winter skate (*Leucoraja ocellata*, Rajidae) on Georges Bank (Frisk et al. 2008, 2010) that in the past had been a hypothesized regime shift resulting from internal dynamics and self-recruitment of elasmobranchs in the absence of competition. However, the increase in abundance (CPUE) of adults (Period A), and a smaller increase in juveniles followed by a delayed increase in early juveniles, indicates this is not the case and that adults are controlling the shift. During the 2000s (Period B), adults and juveniles increased again, with recruitment appearing to increase at the end of the time series but never being the mechanism of population increase. Upper panel shows length frequency data for winter skate where maturity was assumed at a length of 80 cm or greater, juveniles ranged between 51 and 78 cm and early juveniles were <50 cm. The lower panel shows the aggregated abundance for adults, juveniles and early juveniles. Data are from the National Marine Fisheries Service’s annual autumn bottom trawl surveys.

lighted by a second unexplained increase in winter skate in 2008 that resulted in a biomass index increase from 3.85 to 9.5 kg per tow in a single year (NEFMC 2010). The New England Fishery Management Council Skate Plan Development Team argued in a 2008 memorandum that the increase in large skates could result from significant changes in catchability, a large recruitment event or a transient immigration of adult skates. Given that other surveys in the region were in agreement, no vessel or gear changes occurred and no apparent earlier cohorts could have produced the increase (Fig. 2), we argue that adult migration is the likely cause.

We speculate that AMPC plays a critical role in the closely related barndoor skate (*Dipturus laevis*, Rajidae) that has also shown large regional fluctu-

ations in abundance in the western Atlantic. Casey and Myers (1998) published a widely cited article claiming that barndoor skate had been extirpated in the western Atlantic and was headed for extinction. However, barndoor skate have gone through a rapid abundance increase in the last 10 years, far exceeding expected population growth rates for a long-lived species with a ‘slow’ life history (Frisk et al. 2001, 2002). The result is a dichotomy between population growth rates derived from life history characteristics (Casey and Myers 1998) and observed increases in population biomass over a 10-year interval (Cavanagh and Damon-Randall 2009). For example, a recent study used a density-dependent matrix analysis to model the increase in the barndoor skate population and estimated  $r_{\text{conditional}}$  (=intrinsic rate of increase as

used in the logistic equation) =  $0.41 \text{ year}^{-1}$  (Gedamke *et al.* 2007). The estimated population growth rate of 41% per year exceeds previous estimates of species with 'slow' life histories to which most large elasmobranchs conform. In support of this fast rate of population increase, Gedamke *et al.* (2007) point out that survey data in the early 1990s suggested the population increased annually at 43%.

At the core of these claims is the assumption that surveys represent the same proportion of the population year after year. These analyses (Casey and Myers 1998; Frisk *et al.* 2002; Gedamke *et al.* 2007) assume that the population is closed and decreases or increases in biomass are a function of local population dynamics and not migration or immigration to the system. However, if barndoor skate exhibit AMPC, the scale of the groundfish survey may not cover the spatial extent of their population dynamics adequately. For example, in the spring of 2006, the highest barndoor skate abundance since the inception of the spring groundfish survey in 1968 was observed with 192 barndoor skates being caught in 327 stations. Subsequently, in 2007, a single tow of the NMFS groundfish survey conducted at a depth of 296 m on the south-eastern flank of Georges Bank caught 277 barndoor skate including 110 adults (Sosebee, personal communication; Frisk *et al.* 2008). Thus, a single tow in 2007 exceeded the largest estimated abundance for an entire spring survey, and this tow was in deep-water that is not extensively sampled. The work of Kulka *et al.* (2002) demonstrated that catches of barndoor skate increased at depths greater than 450 m and were captured in the deepest of commercial trawls made (up to 1400 m) in the north-west Atlantic.

The contrasting views of barndoor skate population dynamics are difficult to reconcile. However, an understanding of AMPC may provide information to better understand the ecology of barndoor skate. We hypothesize that barndoor skate, like winter skate (Frisk *et al.* 2008, 2010), may undergo large-scale migrations, perhaps moving off-shelf during unfavourable environmental conditions. However, in the absence of a sampling program that covers the full spatial domain of the species, our current understanding of barndoor skate population structure, as well as the potential for AMPC and the link between local abundance and exploitation, will remain limited. For effective management of barndoor skate, we need to resolve

whether it is a species with a 'fast' life history headed for recovery or whether it is a species with a 'slow' life history which has evolved AMPC that may help it overcome the risk of extinction.

### Winter flounder

Historically, winter flounder has been a common flatfish in the north-western Atlantic and related coastal systems. It is a sought after commercial and recreational species that recently experienced a dramatic decline in abundance throughout its range and in some locations has become scarce. Winter flounder is a medium-sized flatfish reaching a total length of 46–67 cm that can live for 15 years (Klein-MacPhee 2002). Maturation occurs at 3 years for females and 2 years for males (Fields 1988; Klein-MacPhee 2002). Reproductively associated migratory movements between offshore and coastal habitats are common (Fields 1988; Klein-MacPhee 2002). Winter flounder spawn in inshore waters during late winter and early spring producing approximately 500 000 demersal eggs that develop into pelagic larvae (Lobell 1939; Perlmutter 1947; Bigelow and Schroeder 1953; Topp 1968; Pereira *et al.* 1999; Klein-MacPhee 2002; Wuenschel *et al.* 2009).

The view of population connectivity/structuring in winter flounder has varied over the decades. In the Long Island, NY region, early accounts suggest two distinct migratory groups termed 'bay fish' or resident individuals and 'offshore' or migratory individuals (Lobell 1939; Perlmutter 1947). Along coastal Connecticut, homing to local grass beds and population structuring was suggested through tagging studies conducted in the 1930s (Saila 1961). A recent microsatellite analysis provides evidence that suggests the species has a diverse population structure, as exemplified by claimings of 16 distinct genetic populations in Narragansett Bay, RI (Buckley *et al.* 2008).

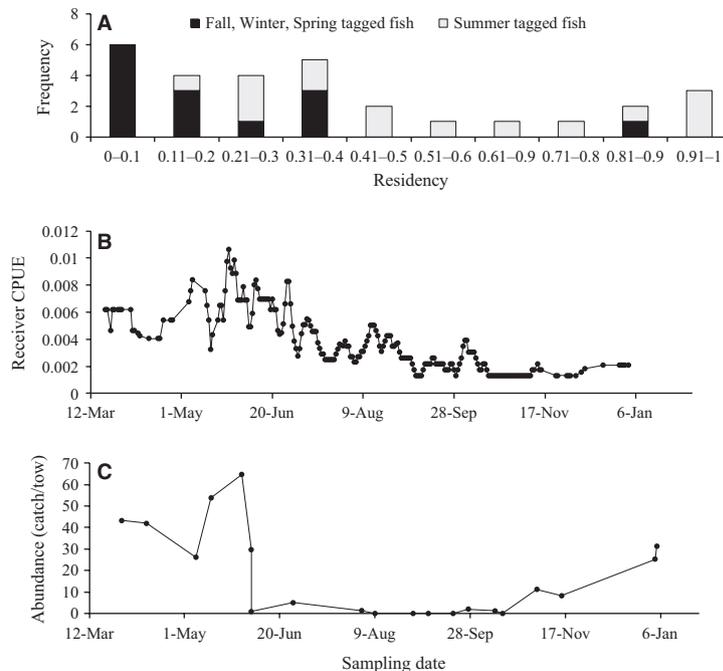
As the complexity of winter flounder life history is revealed, it is apparent that the accepted view whereby connectivity driven by larval dynamics and physical-biological processes that create genetic mixing and broad-scaled population structure (Chant *et al.* 2000) is being challenged by a new paradigm wherein adult behaviour plays a greater role (Wuenschel *et al.* 2009; DeCelles and Cadrin 2010; Sagarese and Frisk 2011). A greater understanding of metapopulation structure of win-

ter flounder requires an appreciation of the role of AMPC. To illustrate the potential metapopulation dynamics that can arise when AMPC is considered, we examine the work of Sagarese and Frisk (2011) and ongoing work in the coastal waters of Long Island, NY.

Recent acoustic tagging of adult winter flounder in Long Island bays has refined our understanding of life history diversity and provided support for the historical view of two distinct migratory contingents in the south shore bays of Long Island (Lobell 1939; Perlmutter 1947). Sagarese and Frisk (2011) identified contingents of winter flounder that remained within the bays of Long Island year-round and one that undertook offshore migrations. Analysis of acoustic data indicated that many individuals remained inshore during the spring and summer (Fig. 3). Confirming the behaviour, biological surveys conducted along the coast of Long Island showed a peak in abundance

during spawning periods from late fall to spring and a near complete absence of adult winter flounder in the ocean during the summer despite observations of adults continuously present within bays (Fig. 3; Sagarese and Frisk 2011). Thus, while migratory fish moved offshore, year-round residents remained in the bays of Long Island during the summer (Sagarese and Frisk 2011).

Further sampling identified a bimodal length distribution of young-of-year fish, which combined with results from acoustic tagging, an analysis of settlement patterns and coastal biological surveys, demonstrates strong evidence that two separate spawning populations co-occur within inshore habitat, a resident portion of the population persisting in the bay and a migratory portion that returns to the bay for a spawning period of variable length. The spatial overlapping of individuals with differing migration and spawning patterns raises the question of whether local genetic diver-



**Figure 3** Sampling in the New York coastal ocean and in Shinnecock Bay, along Long Island's southern shore, indicates diversity in migratory behaviour with implications for population structuring in winter flounder (*Pseudopleuronectes americanus*, Pleuronectidae). Frequency of residency levels are shown for winter flounder tagged during the summer, spring, fall and winter where residency is a proportion of days present in Shinnecock Bay (for details, see Sagarese and Frisk 2011) (Panel A, for details, see Sagarese and Frisk 2011). Receiver CPUE is shown for acoustically tagged winter flounder ( $n = 40$ ) in Shinnecock Bay (Panel B, for details, see Sagarese and Frisk 2011). Winter flounder were present in Shinnecock Bay, New York, during all seasons (Panels A and B), while they were nearly absent from the coastal ocean during the summer (Panel C). Note: Receiver CPUE provides an indicator of presence of winter flounder but does not necessarily represent abundance trends. The coastal survey was conducted in depths of 10–30 m in the ocean throughout the year; data are combined for years 2005–2007.

sity leads to the evolution of unique life histories. However, whether these two groups represent different behavioural contingents (Secor 1999) or two unique populations that occur seasonally in the same habitat is not clear. Current results suggest three possibilities for the spatial structuring of winter flounder in Long Island bays controlled by adult behaviour. The first is that migratory and spawning patterns result from genetically distinct populations occurring in overlapping habitat. In this scenario, different spawning peaks represent separate populations with one demonstrating the traditional on-offshore migration and one population remaining in coastal waters. The second is that temporal and spatial behaviours are conditional and set during early life history where individuals become migratory or resident but represent one genetic population (Secor 1999). The third is that the population is one genetic group with individuals making annual decisions to migrate or remain resident.

The evolutionary and population implications of the three potential life history strategies are a challenge to both scientists and management agencies. In a region where all indicators point to a collapse of winter flounder populations, understanding sources of variation in mortality, recruitment and gaining insight into the cause of winter flounder's decline is critically needed. Taylor and Norris (2007) recently developed a model to quantify how habitat change and migration survival might impact the relative proportions of resident and migratory individuals in a population. They assumed that (i) migration is genetically controlled and heritable, (ii) both survival and breeding success is density dependent, (iii) non-breeding habitat was the same for migrants and residents and (iv) no environmental stochasticity was present. They report two key findings that pertain to the life history variation observed in winter flounder if the relative quality of migratory habitat (non-shared) increases. First, the level of survival during the migrant stage required to favour complete (all individuals) migration decreases, and second, the proportion of residents in the population decreases. Thus, if the resident breeding habitat is degraded, long-term conditions would favour migrants and could reduce or perhaps lead to the elimination of residents. The theoretical model was not tailored to winter flounder; therefore, not all assumptions made by Taylor and Norris (2007) necessarily apply. Further, the model only

addressed genetic mechanisms of migratory behaviour. However, it elucidates the complex population dynamics that can arise between partial migration, long-term exploitation and habitat decline. Each of the three possible spatial life history strategies hypothesized for winter flounder has important implications regarding the ecological and evolutionary responses to habitat quality and environmental fluctuations including fishing, climate change and habitat alteration, among others. In our view, the often dominant focus on and general assumption of larval-mediated connectivity have left such dynamics unrecognized and/or understudied leaving a critical gap in our understanding of population structuring.

### Conclusions

AMPC emphasizes the roles of adults in connecting populations rather than the more common focus on dispersive larvae and changes the spatial scale over which population regulation occurs. If a species comprises several subpopulations connected by adult-mediated processes, the dynamics of all populations must be linked to fully understand the dynamics of the species. This is fundamentally different to species with larval-mediated connectivity in which recruitment subsidies can be viewed as stochastic events largely uncoupled from the dynamics of the focal population. In recent years, the importance of distributional changes in adult fish has been recognized (Lucey and Nye 2010; Nye *et al.* 2010, 2011) as have the implications of large-scale distributional shifts for defining management stocks (Link *et al.* 2011). As climate change continues, it will become increasingly important to understand the patterns and cues of adult movement.

We hypothesize that AMPC plays an important role in population connectivity for a wide range of species and life histories. We have provided a narrative describing how the role of adults in population connectivity can be conceptualized through two case-studies illustrating behaviours that can result in various degrees of population structuring. The degree to which subpopulations are connected to or isolated from adjacent populations through adult movement has important implications to the potential application of the metapopulation approach to marine finfish population dynamics and for determining appropriate management stock units. Unfortunately, even for the most

researched species, the drivers behind adult movement and their role in connectivity are unknown, leaving a large gap in understanding marine connectivity and its relationship to population and ecosystem dynamics.

The stock concept that underlies classical approaches to fisheries management holds that dynamics of the population are regulated by internal processes of growth, recruitment and natural and fishing mortality; such populations are termed closed. The central assumption of population closure leads to the management paradigm that declines in abundance can be compensated for by reductions in fishing mortality. However, if stocks are not effectively closed (i.e. winter skate) or are structured at fine scales (i.e. winter flounder), then abundance and fishing mortality may not be directly related; hence, reductions in fishing mortality may not lead to recovery. In open subpopulations, the additional processes of immigration and emigration, which serve to connect neighbouring stocks, must be considered. Similarly, for other species that display highly resolved population structuring, AMPC must be considered for management. It will no longer be sufficient to assume that reductions in fishing mortality will reduce or reverse rates of decline in abundance. This has consequences not only to single-species approaches to management but also to the emerging ecosystem-based approach. The ecosystem boundaries must be drawn to circumscribe all of the subpopulations for AMPC species, whereas this need not be the case for species connected via larval dispersal. We believe the lack of research on the role of AMPC has limited both scientific progress on metapopulation analysis in the marine environment and the effective management of critical resources.

While the number of marine finfish that display fine-scale genetic structuring clearly highlights the need to understand the role of AMPC, panmictic and/or demographically connected populations also have important metapopulation, ecosystem and management implications. In addition to the winter skate case-study, many potential species have evolved such a life history strategy. Prior to 1900, juvenile Atlantic menhaden were a common feature of coastal ecosystems along the coasts of New York, Connecticut, Massachusetts and Maine (Goode 1880). Reconstruction of the Great South Bay, New York, ecosystem indicated that the planktivorous Atlantic menhaden was the top-

ranking keystone species, removing large amounts of primary productivity from the system (Nuttall *et al.* 2011). The species spawns in the ocean producing pelagic eggs and larvae that are advected into coastal estuaries, where early juveniles develop (Quinlan *et al.* 2000; Karaköylü *et al.* submitted). Karaköylü *et al.* have hypothesized that the loss of juvenile productivity in the northern section of the species' range is a result of a reduced age-structure that has nearly eliminated older more northerly spawning individuals. The loss of menhaden has corresponded to a 100 year decline in the ecosystem structure and maturity of Great South Bay (Nuttall *et al.* 2011). The Atlantic menhaden story provides a clear example of a species where AMPC has important implications not only for the species management, but for ecosystems impacted by the behaviour of adults. Here, AMPC drives both the development of a broadly connected panmictic population and the geographic extent of this species' juvenile production.

We believe that a lack of attention to AMPC is due to dilution by the vast literature studying larval-mediated connectivity. In sharp contrast to the accepted paradigm, for species exhibiting AMPC, adults are the drivers behind shifts in regional production and resulting recruitment pulses in newly colonized areas. The potential for adults regulating marine connectivity is profound when viewed from a life history perspective and the contribution of different life stages to population growth rate. Life history analyses have shown that the contribution of early life stages to population growth is low compared to adult stages for many species (Heppell *et al.* 1999; Musick 1999; Frisk *et al.* 2005; Kinney and Simpfendorfer 2009). To elucidate population structuring in marine fishes, research that combines the vast amount of knowledge on larval-mediated connectivity, with the relatively understudied drivers of adult habitat choice and selection of offspring/spawning grounds, is needed. This approach would emphasize complete life history research that connects often divergent fields of enquiry, too focused on limited aspects of a species life cycle.

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