

Connectivity effects on productivity, stability, and persistence in a herring metapopulation model

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Diverse and interacting spawning groups of Atlantic herring (*Clupea harengus*) have varying degrees of independence to environmental conditions. How these population components respond independently to the same set of environmental conditions, and are connected through straying or entrainment, will contribute to the aggregate metapopulation dynamics. The consequences of connectivity for productivity, stability, and persistence were evaluated in an age-structured model of a two-component metapopulation. Simulation scenarios of straying and entrainment were developed to examine the effects of component interchange and recruitment covariance on metapopulation attributes. Asynchronous component responses should result in reduced variance in metapopulation dynamics, which was measured as the portfolio effect (PE). Most types and magnitudes of connectivity reduced metapopulation productivity and stability. Increased connectivity tended to increase instability of a component by distributing the effect of strong year classes among components and disrupting the “storage effect” within components. Density-dependent straying and entrainment, respectively, showed stabilizing and destabilizing feedback cycles on metapopulation stability and persistence. Furthermore, high rates of connectivity tended to result in increased synchronous responses between components and depressed metapopulation productivity, stability, and PE. Exploitation on a metapopulation should similarly depress independence among components because high mortality will dampen component responses to environmental forcing.

Keywords: Atlantic herring, connectivity, entrainment, metapopulation, portfolio effect, straying.

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Introduction

Philopatry, the multigenerational return by adults to a specific location to breed (Sinclair, 1988), is a basic concept in the assessment of marine fisheries that enables fishery management to be scaled appropriately to underlying population production rates (Secor, 2005). Complex life cycles have arisen to ensure life-cycle closure in highly fecund fish with dispersive early stages. Philopatry directs migration and spawning behaviour and increases the probability of young encountering favourable ocean conditions, thus enhancing survival (Cushing, 1975; Sinclair, 1988). On the other hand, strict philopatry entails inertia to environmental change. As Harden Jones (1968, p. 185) observed for Atlantic herring: “Homing could be a disadvantage when fish persist in returning to the same spawning area or ground where conditions have become unfavourable . . . The only biological insurance against this is a satisfactory level of straying and a multiplicity of spawning grounds . . .”. We examine how small to moderate deviations from philopatry—also known as connectivity—contribute to productivity, stability, and persistence in a hypothetical herring (*Clupea harengus*) metapopulation.

The overall response of a metapopulation to environmental forcing will depend on the individual dynamics and pattern of connectivity among constituent subpopulations. Here, linked

herring spawning groups are considered as a patchy metapopulation (Harrison and Taylor, 1997), where the emergent metapopulation responses are dependent on demographic exchanges among subpopulations (here referred to as spawning components: Smedbol and Stephenson, 2001) that occur at ecological time-scales (Kritzer and Sale, 2004). Stability is conferred to a metapopulation when its components respond asynchronously to the same environmental conditions. Differences in component life histories are important for stability, because they lead to differential responses to interannual variations in environmental conditions (i.e. the “storage effect”; Warner and Chesson, 1985; Secor, 2007). Asynchronous component responses should result in reduced variance in metapopulation dynamics, which can be measured as the portfolio effect (PE; Doak *et al.*, 1998; Tilman *et al.*, 1998). Here, the PE is defined as the degree to which variance in metapopulation biomass is reduced owing to asynchronous spawning-component responses to climate and other environmental forcing.

Two types of connectivity—straying and entrainment—were contrasted in their effects on metapopulation productivity, stability, and the PE. Straying represents the movement of individuals away from their natal population and does not depend on interactions among individuals between components. In contrast,

entrainment does depend on behavioural interactions, which draw individuals from one spawning component into another during the periods of spatial overlap (McQuinn, 1997a; Corten, 2002). Therefore, straying rate only depends on the component that generates the strays; entrainment rate depends on the relative abundance and degree of overlap between spawning components.

In addition to its role in colonizing new spawning habitats (Cury, 1994), straying can contribute to metapopulation structure and overall resilience (Smedbol and Stephenson, 2001; Ware and Schweigert, 2001). Ware and Schweigert (2001) modelled the possible influence of density-dependent straying among five stocks of Pacific herring. Straying was shown to confer persistence to less productive stocks, dependent on subpopulation proximity and their relative densities. Density-dependence increased natal homing when subpopulations were declining and promoted resilience in smaller subpopulations through subsidies from more abundant ones.

The entrainment hypothesis stems from Corten's (2002) view that life-cycle closure and population structure result from memorization of migration routes by adults, rather than imprinted environmental cues during the larval stages. This view was supported by circumstantial evidence, such as the rapid return of spawning herring to Aberdeen Bank after a generation of absence (Corten, 1999). Following establishment of a migration circuit by a component, those behaviours were hypothesized to be conserved across generations through social transmission from adults to juveniles (McQuinn, 1997a; Corten, 2002). While tagging data have provided direct evidence of straying in many fish species, little direct evidence has been collected in support of entrainment (ICES, 2007). For Gulf of St Lawrence herring, McQuinn (1997b) used otolith characteristics to show substantial mixing by spring-spawned herring in spawning aggregations during autumn. In contrast, Brophy *et al.* (2006), using otolith microstructure analysis, detected little exchange (<10%) between seasonal spawning contingents in the Celtic and Irish Seas.

Despite limited direct evidence, the entrainment hypothesis provides a tractable alternative explanation for the observed pattern of loss and colonization of spawning grounds by herring (Corten, 2002; ICES, 2007). Naïve juveniles can stray and successfully colonize new habitats, and transmit novel migration patterns within a single generation, potentially resulting in rapid population growth associated with range expansions. This type of connectivity conforms to the rapid population-growth cycles observed in sardine (*Sardina pilchardus*), where expanding habitat volumes are hypothesized to be rapidly capitalized through social transmission (ICES, 2007).

The obstinacy with which fish come back to the same spawning grounds as their ancestors can be counteracted by both types of connectivity, but these may have different consequences for metapopulation growth, stability, and persistence. We hypothesize that exchange resulting from entrainment can confer instability on individual components because of a positive feedback loop between their growth and the "capture" of individuals from smaller components. In contrast, density-dependent straying should regulate exchange rates based on the relative abundances of the components. To investigate how these two types of exchange operate, a hypothetical metapopulation simulation model was developed that comprised two age-structured components.

Methods

Metapopulation system

The hypothetical metapopulation comprised two spawning components, of which one (C_A) was more productive than the other (C_B). Further, recruitment to C_A correlated positively with the North Atlantic Oscillation (NAO; January/February/March annual index; Hurrell *et al.*, 2003), whereas recruitment to C_B fluctuated randomly. Assessment data from the Celtic Sea and the Irish Sea stocks of Atlantic herring (ICES, 2008) were used as the basis for parameter estimates for C_A and C_B , respectively, because these stocks may be independent in their response to the environment in terms of recruitment, differ in their relative biomass and have shown small to moderate straying rates (Brophy *et al.*, 2006). Mixing (straying or entrainment) was assumed to occur only among adults (ages 2–9). For the sake of simplicity, seasonal cohorts of each component were not tracked.

Age-structured model

Two age-structured spawning components were constructed that included nine age groups (age 1–9). Recruitment-at-age-1 (R) was calculated separately for each component, using the "hockey-stick" type of stock–recruitment model

$$R = \alpha \min(S, S^*) = \begin{cases} aS & \text{if } S < S^* \\ aS^* & \text{if } S \geq S^* \end{cases} \quad (1)$$

where S^* is the spawning-stock biomass that triggers a difference in the response of R (C_A : $S^* = 44\,446$ t; C_B : $S^* = 19\,089$ t) and a the gradient (9600 for both populations). For C_B , stochastic recruitment was modelled as random variation around the maximum number of recruits (asymptote of "hockey-stick" stock–recruitment model). The magnitude in recruitment variation was scaled to achieve a coefficient of variation (CV) in age-1 recruitment equal to 40%.

Recruitment variation in C_A was modelled similarly but included the NAO index as a multiplier. S at time t was calculated as a function of the number-at-age ($N_{t,a}$), average weight-at-age (W_a ; 1998–2007), and the mean fraction mature-at-age (P_a ; Celtic Sea schedule applied to both components; ICES 2008):

$$S_t = \sum_{a=1}^{a=\infty} N_{t,a} W_a P_a \quad (2)$$

Abundance-at-age for ages 2–9 was calculated by

$$N_{t+1,a+1} = N_{t,a} e^{-Z_a} \quad (3)$$

where Z_a is the total adult mortality rate (0.6 year⁻¹ for both components).

Straying and entrainment scenarios

A series of 500 stochastic model runs, each conducted over a 150-year period, was performed for each scenario (only the last 100 years were used in the analyses, to allow the model to eliminate the effects of initial conditions). Simulations included a baseline without connectivity (discrete components), as well as various straying and entrainment scenarios (Figure 1). Straying or entrainment dynamics between components were assumed to be governed by the relative biomass of adults (ages 2–9). As somatic growth rates were only slightly curvilinear, abundance and biomass were well correlated (500 simulations: $r > 0.97$; $p <$

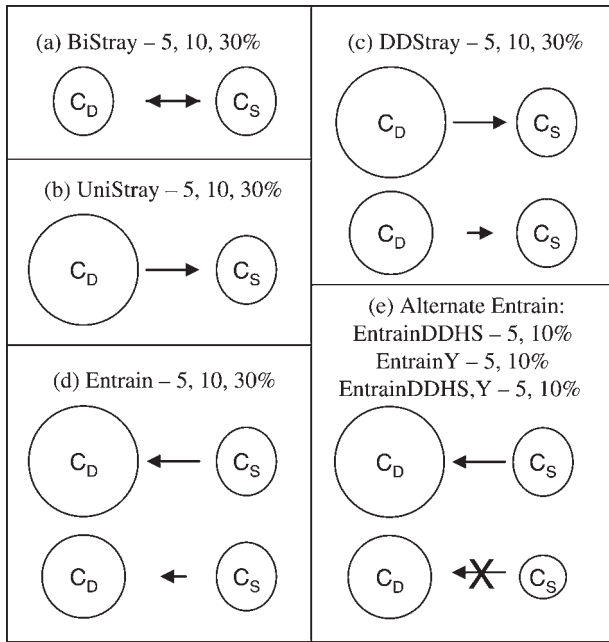


Figure 1. Model scenarios of connectivity (arrows qualitatively indicate amplitude; rates simulated in %) between two metapopulation components, C_D (dominant component) and C_S (subordinate component): (a) BiStray, bidirectional straying; (b) UniStray, unidirectional straying; (c) DDStray, density-dependent straying, with maximum straying rate occurring at either the stock–recruitment biomass trigger S^* (DDStray) or the 80th percentile S trigger (DDStray2; see Figure 2); (d) Entrain, entrainment of dominant component. A group of entrainment scenarios (e) precluded entrainment under certain conditions (represented by “X”) and included EntrainDDHS, density-dependent habitat selection (see text), and EntrainY, entrainment only in years exceeding the 90th percentile recruitment level of the dominant component. Note that the initially dominant component, indicated elsewhere as C_A , occasionally became subordinate in scenarios owing to environmental forcing; therefore, a different notation has been used here (C_D).

0.001). Therefore, abundance responses would be similar to those shown for biomass.

For some scenarios, the more productive C_A could become subordinate to C_B owing to its correlation with NAO. To describe straying and entrainment scenarios, it was convenient to use notations C_D and C_S for dominant and subordinate components, respectively (Figure 1). Bidirectional and unidirectional straying was specified at 5, 10, and 30% of S . These straying rates span values reported in the herring literature (McQuinn, 1997b; Ware and Schweigert, 2001; Brophy *et al.*, 2006). In unidirectional straying scenarios, straying was only from C_D to C_S . Density-dependent (DD) straying was modelled from 0 to 30%, using the hockey-stick approach based upon S^* (DDStray) or the 80th percentile of spawning biomass for C_D (DDStray2; Figure 2) as a trigger for maximum straying.

For entrainment scenarios, biomass entrainment (S_E) was only from C_S to C_D (Figure 1). Entrainment rates (5, 10, and 30%) were applied to the difference in spawning biomass (S) between the two components:

$$S_E = \text{entrainment rate } (S_D - S_S). \quad (4)$$

In one set of entrainment scenarios, the concept of DD habitat selection (DDHS) was introduced, which is based on the idea

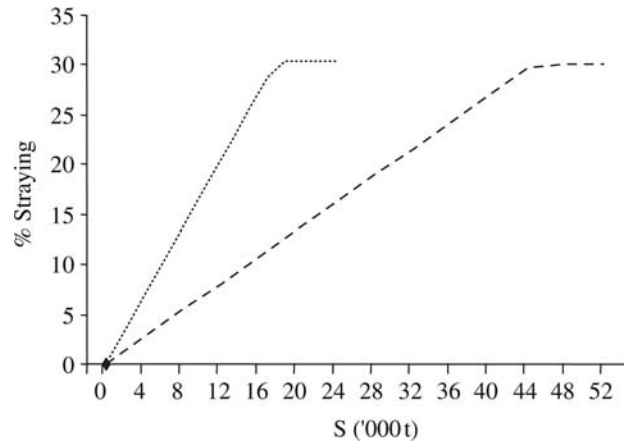


Figure 2. Model used for density-dependent straying for components C_A (dashed line) and C_B (dotted line) when maximum straying was set at S^* .

that, at low densities, C_S was less likely to disperse because of improved habitats at lower densities (cf. the basin model; MacCall, 1990). In this case, C_S was protected from complete entrainment by retaining 30% of its mean S . Finally, a scenario (Y) was evaluated where entrainment was restricted to the presence of very large year classes in C_D (McQuinn, 1997b; ICES, 2007): entrainment from C_S was only when S_D was greater than the 90th percentile of its distribution.

Mean S for each component and for the overall metapopulation was calculated as a metric of productivity, whereas the mean coefficient of variation [(s.d./ μ)·100] of S represents a measure of component or metapopulation instability. The numbers of times recruitment failed ($R=0$) and an entire simulation failed ($S=0$) were tallied as indices of persistence for each scenario.

Portfolio effect

Finally, an index was constructed to examine how the two components independently responded to the environmental forcing and thereby reduced the variance observed at the metapopulation level—i.e. the PE of each scenario on metapopulation stability. To measure this, CV at each component scale (subscript C : attributable to C_A and C_B) were compared with the CV observed at the metapopulation scale (subscript M). First, CV_C and CV_M were estimated for a 100-year time-frame. Then, by weighting the individual CV_C according to their respective spawning biomasses (S_C), the metapopulation CV_M^* was estimated as if the two components were responding in complete synchrony to environmental forcing:

$$CV_M^* = \sum_{C=1}^{C=k} \left(\frac{S_C}{S_M} CV_C \right), \quad (5)$$

where $k=2$ (the number of components). A comparison of the CV_M with CV_M^* provides an estimate of the extent to which variance is dampened owing to independence between components in their contribution to an aggregate metapopulation biomass. This has been termed the PE (Doak *et al.*, 1998):

$$PE = 1 - \left(\frac{CV_M}{CV_M^*} \right). \quad (6)$$

PE positively scales with metapopulation stability, but also indicates how component independence contributes to overall

stability. For instance, what additional stability is conferred by considering components as part of a metapopulation vs. considering component stabilities on an individual basis? For a two-component system with no correlation between components ($r=0$), the PE would be 30% according to the modified formula from Doak *et al.* (1998):

$$CV_M = CV_C \frac{[1 + r(k-1)]^{0.5}}{k^{0.5}}. \quad (7)$$

Results

Projected biomass of the metapopulation (S_M) for the baseline model was stable and showed the expected effects of long-term NAO forcing on S_A , and a less productive S_B that varied independently (Figure 3a). The CV of the two components and metapopulation were approximately twofold less (Figure 4a, b) than the input recruitment variation (40%), indicative of the dampening effect of age structure and mortality. For instance, a strong year class would cause a degree of autocorrelated response in S over a 5–9-year period. The PE was estimated at 26% (Figure 4e), which indicates that independence in recruitment between the two components caused increased stability at the metapopulation level, nearly in accordance with independent populations of equivalent abundance (PE=30%; see Methods). None of the simulated population components crashed; there was no recruitment failure for C_B , but it failed in 1 of 100 years for C_A .

The lowest rates of bi- and unidirectional straying (5%) gave similar results to the baseline simulation, but high levels of straying resulted in increased instability within components (Figure 4a, b). As an example, unidirectional straying at 30% caused heavy subsidy of C_B from C_A (Figure 3b). Large depletions of strong year classes, caused by this straying, are expected to reduce the

autocorrelation contributed by age structure because these year classes are transferred to the alternate component in ways that are unrelated to environmental forcing or internal population dynamics. Higher CVs for both components translate to a higher PE for this scenario (Figure 4e). Measures of persistence were the same as for the baseline simulation except that, at 30% straying, recruitment failed in 2 of 100 years for C_A .

DD straying scenarios caused components to show correlated responses. The overall difference in S between the components was lowest for this class of scenarios when compared with other straying and entrainment scenarios (Figure 3c). Furthermore, the NAO forcing on C_A was apparent in oscillations in C_B because of the transfer of large numbers of strays from the dominant component. Although DD straying tended to regulate abundances in both components and reduced their respective CVs, the PE at the metapopulation level was low (Figure 4e) because both components were responding with greater synchrony to environmental forcing. Measures of persistence were the same as for the baseline simulation.

Entrainment caused extirpation of C_B at all but the lowest (5%) level of entrainment (Figure 4d). For 5, 10, and 30% entrainment, simulated C_B crashed 8, 21, and 100% of the time, respectively (likewise, recruitment to C_B failed in 4, 67 and 100% of run years, respectively). Depressed persistence was insensitive to whether entrainment happened in all years or only during periods of high biomass. Simulating DDHS allowed for persistence of C_B (Figure 4d), but created an unexpected dynamic. On rare occasions for scenarios with >5% entrainment, C_B (the originally subordinate component) became dominant and entrained members of C_A (Figure 3d). This was the only scenario in which this occurred. Recruitment was more persistent in C_B , with recruitment failure in <10% of run years at 5 and 10% entrainment rates.

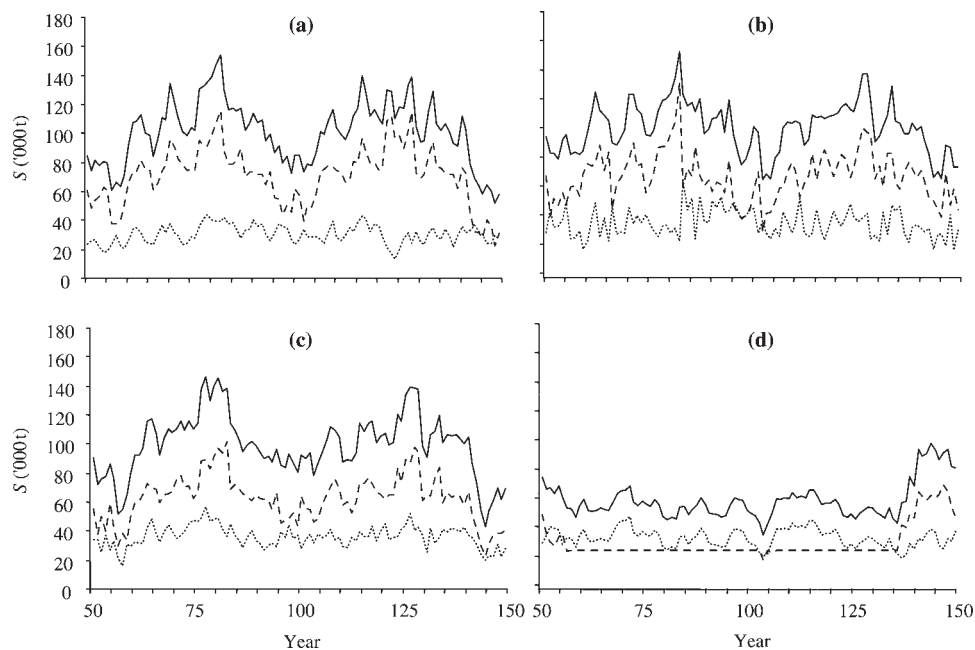


Figure 3. Simulated spawning-stock biomass (S) from alternative scenarios: (a) baseline (no connectivity); (b) 30% unidirectional straying; (c) density-dependent straying (maximum 30% and a biomass trigger for the dominant component); and (d) 5% entrainment with density-dependent habitat selection by the subordinate component. Components C_A , C_B , and metapopulation biomass are represented as dotted, dashed, and solid lines, respectively.

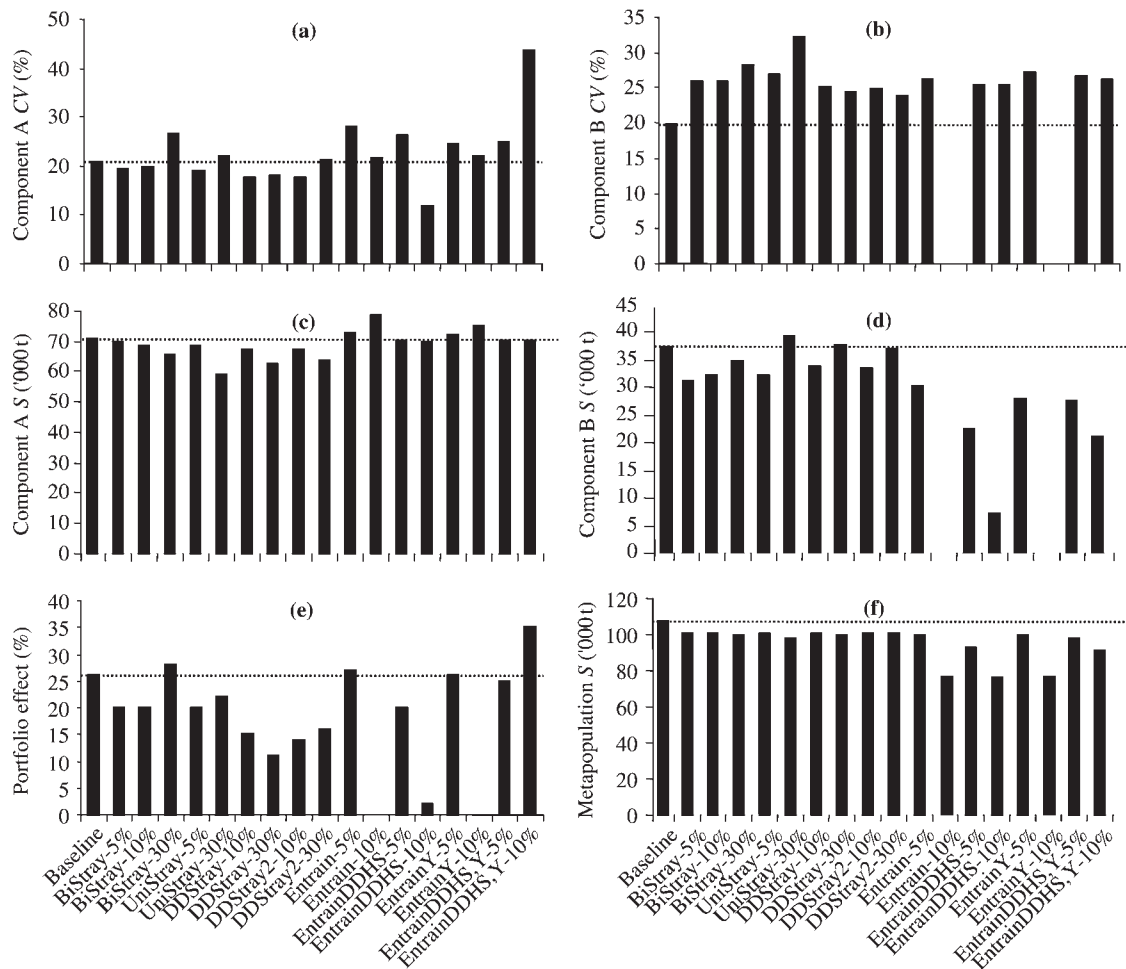


Figure 4. Coefficients of variation (CV) for (a) C_A and (b) C_B ; biomass (S) for (c) C_A and (d) C_B ; (e) PE; and (f) metapopulation spawning biomass across all scenarios. Dotted line indicates baseline (no connectivity). For scenario codes, see Figure 1.

Across all scenarios, straying and entrainment tended to cause reduced component and metapopulation S and decreased stability (increased CV and lower PE; Figure 4). Exceptions included high rates of straying and entrainment, which caused S_B and S_A , respectively, to exceed the baseline. Even so, the overall metapopulation S_M was consistently below the baseline scenario (Figure 4f). Lower component CVs were associated with DD straying (Figure 4c, d), and the only incidences of the PE exceeding the baseline were for high rates of straying or entrainment (Figure 4e).

Discussion

Connectivity is a research priority in the management of marine systems for the protection of vital components of populations of species and their essential habitats. Our results indicate that connectivity through straying or entrainment may involve a cost in terms of lost productivity, stability, and persistence. Small rates of connectivity (5%) showed minimal losses to productivity and stability, but higher rates potentially disrupt the influence of periodic contributions of strong year classes to internal metapopulation dynamics, and reduce independence among constituent components in their contribution to metapopulation stability and persistence.

Correlated dynamics between components were observed for DD straying and entrainment scenarios, which showed contrasting

consequences to metapopulation stability (Figure 5). DD straying resulted in a proportional transfer from one component to the other, according to each component's adult biomass. This served to dampen variance within components, but also resulted in transfers that minimized the relative difference in component biomass. The negative feedback cycle of straying and component biomass also resulted in correlated dynamics between components. In the modelled metapopulation, the more productive C_A experienced the greatest degree of increased stability (reduced CV), but at the metapopulation level, the PE (stability) was reduced owing to increased synchrony in component dynamics. DD straying has been ascribed to Pacific herring by Ware and Schweigert (2001). Based upon a decade of tagging returns (1977–1998), they showed that individuals among five regions along the northeastern Pacific dispersed according to the relative densities attributed to these regions. However, because natal origins of the adults tagged among regions were not determined, the relevance in terms of metapopulation structure remains uncertain.

In contrast to DD straying, entrainment operates as a positive feedback cycle, where capture by the dominant component can serially deplete the subordinate component (Figure 5). If the entire subordinate component is subject to entrainment, the model suggests that even small rates of entrainment (5%) would eventually lead to extirpation of that component. If some

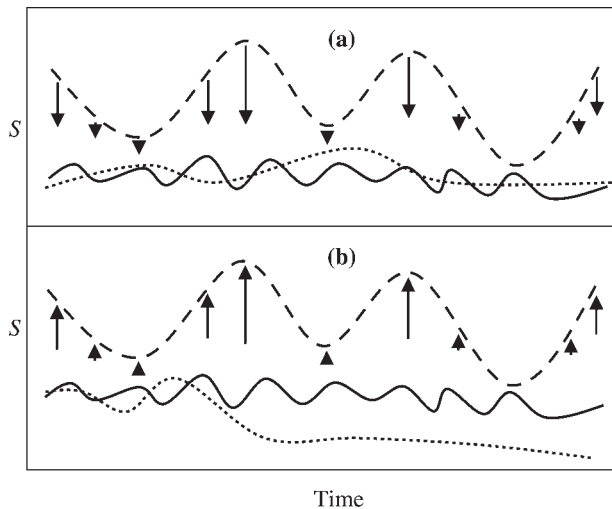


Figure 5. Conceptual diagram displaying temporal development of spawning biomass (S) for: (a) density-dependent straying vs. (b) density-dependent entrainment for C_A (dashed line) and C_B (dotted line). Solid lines represent the baseline scenario for C_B (no connectivity). Arrows indicate direction and amplitude of connectivity.

portion is protected against entrainment (in this case through DDHS), the simulations suggest that entrainment may result in oscillations in the ordering of dominant and subordinate components. Such cycles of entraining members of different components could impart resilience to a metapopulation when the components respond differently to environmental forcing. This mechanism might also increase overall metapopulation productivity by allowing periodic entrainment by the favoured component during certain environmental regimes (ICES, 2007).

Entrainment has been modelled here naively as a density-dependent “capture process”, as has been suggested for sardine populations (ICES, 2007). Entrainment has also been associated with other population attributes, such as variable growth rates of juveniles originating from sympatric seasonal spawning events (McQuinn, 1997a) or population crashes, which could support a rapid adoption of a new migration behaviour (Corten, 2002).

In retrospect, the negative association between connectivity and PE is intuitive. Metapopulation stability depends on the independence (or negative covariance) of constituent populations, but connectivity will diminish independence. Although the PE of connected populations was less than the baseline scenario, it was generally $>20\%$, indicating that, even in the face of environmental forcing, substantial metapopulation stability can be maintained at low and even moderate levels of connectivity.

Productivity and stability are but two of several metapopulation parameters of interest. Other important factors include persistence and resilience (Kerr *et al.*, in press). Metapopulations require some level of connectivity among components for long-term persistence, but the issue is how much? A metapopulation cannot persist with high rates of both component connectivity and synchrony. The trade-offs emerge from our results, where high rates of connectivity resulted in enhanced synchrony in responses to NAO forcing and depressed metapopulation productivity and stability. Similarly, exploiting all components at the same rate at the metapopulation scale should depress

independence among components and depress metapopulation stability and productivity.

Mitigation against destabilization of metapopulations, whether caused by fishing or environmental forcing, could include management strategies to: (i) preserve age structure; (ii) avoid fishing on aggregations of mixed spawning components; (iii) target large year classes; or (iv) maintain biomass in constituent components to minimize differences among them. The goal of such strategies would be to reduce the degree of dominance as well as the covariance among components in the target metapopulation. Conserving biomass among multiple components may also serve as bet-hedging against catastrophic losses of entire herring stocks (Smedbol and Stephenson, 2001). Such strategies may need to be supported by potentially costly expanded research and monitoring programmes. Continuing studies on genetic tags, otolith structure, and electronic tags (ICES, 2006; 2007) will indicate the effectiveness of such conservation measures.

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References

- Brophy, D., Danilowicz, B. S., and King, P. A. 2006. Spawning season fidelity in sympatric populations of Atlantic herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 607–616.
- Corten, A. 1999. The reappearance of spawning herring on Aberdeen Bank (North Sea) in 1983 and its relationship to environmental conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2051–2061.
- Corten, A. 2002. The role of “conservatism” in herring migrations. *Reviews in Fish Biology and Fisheries*, 11: 339–361.
- Cury, P. 1994. Obstinate nature: an ecology of individuals. Thoughts on reproductive behavior and biodiversity. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 1664–1673.
- Cushing, D. H. 1975. *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge, UK. 277 pp.
- Doak, D. F., Bigger, D., Harding, E. K., Marvier, M. A., O’Malley, R. E., and Thomson, D. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist*, 151: 264–276.
- Harden Jones, F. R. 1968. *Fish Migration*. Edward Arnold Ltd, London. 325 pp.
- Harrison, S., and Taylor, A. D. 1997. Empirical evidence for metapopulation dynamics. *In Metapopulation Biology: Ecology, Genetics and Evolution*, pp. 27–42. Ed. by I. A. Hanski, and M. E. Gilpen. Academic Press, New York. 512 pp.
- Hurrell, J. W., Kushnir, Y., Visbeck, M., and Ottersen, G. 2003. An overview of the North Atlantic Oscillation. *In The North Atlantic Oscillation: Climate Significance and Environmental Impact*, pp. 1–35. Ed. by J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck. Geophysical Monograph Series, 134. 279 pp.
- ICES. 2006. Report of the Study Group on Regional Scale Ecology of Small Pelagic Fish (SGRESP), 27 February–2 March 2006, Galway, Ireland. ICES Document CM 2006/LRC: 05. 45 pp.
- ICES. 2007. Report of the Workshop on Testing the Entrainment Hypothesis (WKTEST), 4–7 June 2007, Nantes, France. ICES Document CM 2007/LRC: 10. 107 pp.

- ICES. 2008. Report of the Herring Assessment Working Group for the Area South of 62° (HAWG), 11–19 March 2008. ICES Headquarters, Copenhagen. ICES Document CM 2008/ACOM: 02. 601 pp.
- Kerr, L. A., Cadrin, S. X., and Secor, D. H. The role of spatial dynamics in the stability, resilience, and productivity of fish populations: an evaluation based on white perch in the Chesapeake Bay. *Ecological Applications*, in press.
- Kritzer, J. P., and Sale, P. F. 2004. Metapopulation ecology in the sea: from Levin's model to marine ecology and fisheries science. *Fish and Fisheries*, 5: 131–140.
- MacCall, A. D. 1990. *Dynamic Geography of Marine Fish Populations*. Washington Sea Grant Program, Washington University Press, Seattle. 153 pp.
- McQuinn, I. H. 1997a. Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries*, 7: 297–329.
- McQuinn, I. H. 1997b. Year-class twinning in sympatric seasonal spawning population of Atlantic herring, *Clupea harengus*. *Fishery Bulletin US*, 95: 126–136.
- Secor, D. H. 2005. Fish migration and the unit stock: three formative debates. *In* *Stock Identification Methods*, pp. 17–44. Ed. by S. X. Cadrin, K. D. Friedland, and J. R. Waldman. Elsevier, Burlington, MA. 717 pp.
- Secor, D. H. 2007. The year-class phenomenon and the storage effect in marine fishes. *Journal of Sea Research*, 57: 91–103.
- Sinclair, M. 1988. *Marine Populations: an Essay on Population Regulation and Speciation*. Washington Sea Grant Program, Washington University Press, Seattle. 252 pp.
- Smedbol, R. K., and Stephenson, R. 2001. The importance of managing within-species diversity in cod and herring fisheries of the north-western Atlantic. *Journal of Fish Biology*, 59: 109–128.
- Tilman, D., Lehman, C. L., and Bristow, C. E. 1998. Diversity–stability relationships: statistical inevitability or ecological consequence? *American Naturalist*, 151: 277–282.
- Ware, D., and Schweigert, J. 2001. Metapopulation structure and dynamics of British Columbia herring. *Canadian Stock Assessment Secretariat Research Document 2001/127*. 27 pp.
- Warner, R. R., and Chesson, P. L. 1985. Coexistence mediated by recruitment fluctuations—a field guide to the storage effect. *American Naturalist*, 125: 769–787.

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