**The idea: Spatial structure and local density-dependence within stock complexes could drive surprises in population dynamics, especially at low abundances.**

**Potential lab paper**

**Related topics:** Disassembly rules, metapopulation, biocomplexity, density-dependence, spatial structure.

**Background.** Fisheries generally manage and harvest stock complexes consist of multiple populations using different habitats. For example, fisheries harvest multiple populations of salmon or cod. For each of these populations, density-dependence can operate at the local (population-level) scales. For example, spawning habitat or rearing habitat in salmon may be limited. Thus, different populations will have different relationships between spawners and recruits depending on their local productivity and capacity (thin orange lines). However, management generally operates on the spawner-recruit relationship of the aggregate stock complex (thick blue line).

Recruits (e.g., smolts)

Spawners

If the local habitats are filled up evenly/randomly, then this spatial structure doesn’t matter much. However, if there are patterns in terms of how total numbers of returning fish are distributed into the local habitats, then this spatial structure and density dependence may shift the aggregate stock-recruit relationship. This is important because fisheries management is generally based on historic stock-recruit relationships of the aggregate.

We previously explored this idea with Keogh River steelhead (Atlas et al. 2015). Atlas et al. hypothesized that prolonged periods of poor marine survival drives spatial contraction of populations. This means that, even if overall there is low total abundance, locally populations were at high densities and at habitat capacity. This will decrease the compensatory capacity of populations (compensatory capacity is the ability of populations to be productive at low populations).

I think that this is rich topic that would warrant a group project. A paper could consist of the following sections.

**Review.**

**Atlas et al. (2015)** simulation model had no harvest – just trends & variation around marine survival. Watershed network had both smolts and adults. No age/size structure or age at spawning.

Could add… different network topologies particularly with an adult “marine” patch. Harvest (maybe even size-selective harvest) that occurs in the “marine” patch. Temporal variation in the adult “run” times. Temporal variation in harvest (harvest occurs disproportionately early, or targets the timing of the larger populations). Plastic age at spawning. Age/size structure.

Structure -> give each local patch a unique stochastic CR and, perhaps, constant K. Fit a “watershed” recruitment curve. Derive CR (compensation ratio) for the whole watershed. Run the model and harvest the fishery in the “marine” patch. Refit the recruitment curve and calculate CR.

**The Einum papers:**

Einum et al. 2005 – patchiness in densities of breeding sites within a river leads to DD survival. Can be mitigated by earlier hatch/fertilized.

The spatial distribution of suitable breeding sites limits density-dependent early juvenile survival. Hypothesis supported in Einum et al. 2008.

Einum et al. 2006 – Spatial distribution of suitable breeding sites induced density-dependence in early survival and late juvenile growth. Density-dependence affects both mean performance and variation in performance (i.e., body size and survival).

Einum et al. 2008 – Patchy v. continuous breeding distributions in early life cause spatial structure due to limited dispersal of small fishes > 250m and variable habitat quality for the early life stage

Patchiness disrupts linkages between habitat quality and density. Leads to over-dispersed density distribution where early juveniles aggregate in larger than expected, which may incur increased density-dependent mortality and/or reduced density-dependent growth. Relationship breaks down if mobility changes with body size.

**Schtickzelle and Quinn (2007) –** populations of anadromous fishes, like salmon watersheds, are *likely* metapopulations but this depends on the spatial scale and amount of dispersal between patches, the patchiness of suitable habitats at relevant life stages, and asynchrony. I would argue this last point is debatable… but they seem very conservative on linkages to metapopulation theory.

**Thomas et al. (1999)** – compelling review on the spatial structure of populations. Decouples categories of spatial structure into two spatially based process axes: population compensation (births > deaths & emigration > immigration) and regional mobility axis (total movers > total birth/death). The compensation axis is the attractor in demographic space where population dynamics circle around, i.e., it is dynamic and density-dependent. This counters some of **Schtickzelle and Quinn’s** comments that metapopulations are very specific and categorical things, suggesting instead that a metapopulation is an outcome that may vary along a continuum of at least two kinds of stochastic processes. That being said, they relate to one another in that identifying the appropriate spatial scale of dispersal and population dynamics helps to identify where along these demographic processes the population is being regulated.

**Courcham et al. (1999)** – reviews the Allee effect and some mechanisms in which we might expect to see one. Allee effect defined as change from negative to positive density-dependence in population growth at low population sizes. This may be caused by many factors like finding mates, exacerbated predation events, etc. The linkage to salmon watersheds occurs through selective harvest of populations based on size/productivity that selectively reduces densities and induces spatial changes to population structure, this can then feedback to demographic processes like density-dependent dispersal and population productivity. So a question becomes: does selective harvest of local populations lead to state shifts, like Alee effects or hysteresis, in the whole “metapopulation”. Do we see this evidence associated with these mechanisms in other spatially structured fish populations like salmon watersheds, lake districts, coral reefs, etc.?

**Saether et al. (1999)** – use a Levin’s metapopulation model to look at effect of density-dependence in either emigration and/or immigration on habitat occupancy. Positive density-dependence in immigration reduces rate of change in occupancy and lowers “K” – the number of patches occupied at equilibrium high-densities – compared to negative density-dependent immigration or density-independence. Conversely, negative density-dependent emigration reduces rates of changes in occupancy and lowered “K”. Either way, if extinction and dispersal depends on occupancy, then there is an unstable equilibrium at low occupancy leading to an Allee effect. Theoretically demonstrates that reduced site occupancy in a metapopulation can lead to state shift and Allee effect for whole watershed because of reduced dispersibility and stochastic local demographic processes.

**Some remaining questions:** how different is *straying* v. *dispersing*? Salmon literature treats this quite differently. Schtickzelle and Quinn link straying as “maladaptive” dispersal… but that isn’t empirically supported in that particular review.

Do discrete habitats we are looking at arise because of different local streams in a regional watershed or the ontogeny associated with anadromy and dispersal or both?

**Background theory.**

**A simulation model. Anticipated key findings:**

* Altered compensatory capacity
  + Lower compensatory capacity
  + Increased compensatory capacity (if less productive populations go first)
* Hysteresis
* Mediated by:
  + Dispersal
  + Habitat preference by productivity relationships (assembly rules)
  + Vulnerability by productivity relationship (disassembly rules)
    - E.g, mortality is not random across the landscape? (e.g., selective fisheries).
    - Disassembly rules for populations: linkages between vulnerability and function (Zavaleta et al. 2009, Moore and Olden 2017).
* Thoughts:
* Will need to think about stochasticity and how partitioned among sub-populations. Is this a model of biocomplexity?
* No evolution/local adaptation (Yeakel et al. 2018).

**Case studies:**

* Atlantic Salmon (Einum et al. 2006, 2008a, 2008b)
* Steelhead (Atlas et al. 2015)
* Snake River Chinook (Achord et al. 2003)(Dan Isaak, Jim Thorson, Scheuerell))
* Cod or Herring? (Ruzzante et al. 2006, Hutchinson 2008)
* Coral Reef fish? (Hixon? or maybe Osenberg, Schmitt and Holbrook)

**Management Implications**

* Careful about harvest selection (disassembly rules)
* Less or more resilient
* Stock-recruit functions may shift through time
  + emphasize that these are *apparent* SR relationships at a watershed scale

**Some references**

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