Population Dynamics of Muikku

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http://users.jyu.fi/~tmarjoma/opetus.htm
Muikku (*Coregonus albula* (L.))

Vendace, Siklöja, Lakesild, Heltling, Рябушка, Rääbis, Repsis, Seliawa, Sielawa, Kleine Maräne

- Key pelagic planktivore
- Short-lived (<5 a)
- Small (<20 cm, <30 g)
- Mature after 2 summers
- Spawning October → hatching May
- Key prey for longer-lived generalist predators
Muikku (Coregonus albula (L.))

- Main target for commercial inland fishing
  - About 70 lakes, 15 000 km²
  - Annual yield 2 500 tn/a
  - Value 5 milj. €
  - About 300 fishers

- Recreational gill netting
  - Annual yield 1 600 tn/a
Muikku research in Finland

- Population studies since 1908 by T. H. Järvi
- 26 doctoral dissertations
- Over 40 populations
- Longest time series 40 years
- >>150 scientific publications

Why studied

- Resource use
  - Sustainable harvesting
  - Optimal harvesting

- Ecology
  - Understanding
    - Population regulation
    - Sources of variability

Royama: "Why do populations fluctuate as they do?"
Population monitoring

- Fishing log books + catch samples
  - Catch Per Unit Effort = abundance index (B, D)
  - Age distribution
  - Size, growth
- Echo sounding
  - Absolute density estimate (D)
  - CPUE calibration
- Larval Density estimation
Population monitoring

Fig. 1. Locations of the vendace populations (circles) and weather stations (crosses) used in the analysis.

Fig. 2. Time-series of (A) recruitment, (B) residuals of the density dependence model, (C) newly hatched larvae, and (D) spawing stock biomass or fecundity estimates used in the analysis; y-axis scale arbitrary.
Typical variability
Typical variability

Already T. H. Järvi, over 70 years ago listed:

- Strong interannual variability in year-class strength
- Tendency for 2-y cyclicity
- Occasional longer recession periods
- Spatial syncrony in year-class strength variability

Examples:
Typical variability: Year-class

Lake Puula (Marjomäki et al. 2014)
Typical variability: 2-y cycle

- Several lake specific case studies, e.g. Marjomäki et al. 2014
- meta-analysis (Marjomäki et al. unpublished):
  - 24 time series, 8-36 years
  - Significant 2-y cycle in recruitment

Onakmo: http://paijanne.org/cornet/tuloksia.htm
Typical variability: Recessions

KONNEVESI

Spawning B

Recruitment

Larval density

ONKAMO

HARVANSELKÄ

Valkeajärvi & Marjomäki2004
Typical variability: Spatial syncrony

Fig. 5. Correlation between mean temperature during four week period after the local ice break date at pairs of weather stations versus (A) distance, (B) north–south and (C) east–west vector of distance between the stations. Curves as in Fig. 3.

Fig. 3. Correlation of recruitment, residuals of the density dependence model, newly hatched larvae and spawning stock, between pairs of vendace stocks versus (A) distance, (B) north–south and (C) east–west vector of distance between the stocks. Fits of the models $r_i = r_0 \exp(-Dv^p)$ (black curve) and $r_i = r_0 \exp(-0.5(Dv^p)^2)$ (grey curve).

Marjomäki et al. 2004
But Why?

Analysis, hypotheses and speculation

Density dependent compensatory regulation
Density dependent compensatory regulation: Growth

- Strong negative relationship between D and G
  - E.g. Lake Puula age 1+ (first spawners)
    - Sparse stock (<100 ind./ha): 150 mm, 25 g
    - Dense stock (>1000 ind./ha): 115 mm, 11 g
Density dependent compensatory regulation: Growth

Consequences for **population fecundity**
- Egg number practically proportional to weight
  - Relative fecundity (eggs/g) marginally density dependent
- Egg wet weight rather constant

Consequences of **natural mortality**
- Predation mortality size dependent
Density dependent compensatory regulation: SB->R

Strong compensation

Lake Puula (Marjomäki et al. 2014)
Density dependent compensatory regulation: Previous R->R

- Strong compensation?
- Serial correlation in residuals -> 2-y damped oscillation, phase-forgetting quasi-cycles

Lake Puula (Marjomäki et al. 2014)
Density dependent compensatory regulation:

- Combining the compensatory effects of SB and prev. R -> no serial correlation in residual

Simulations with the artificially perturbed deterministic skeleton of the model produce two year *Phase-forgetting quasi-cycles* *(sensu Nisbet & Gurney 1982)*
Density dependent compensatory regulation:

Fig. 7 The transition lines in parameter space ($\gamma$, $-\theta$) between the regimes of damped 2-year oscillations and 2-year limit cycles for the recruitment time series simulated with the artificially perturbed deterministic population model incorporating recruitment function $R_t = \alpha SB_{t-1} \times R_{t-1}^\theta$ ($\alpha = 2000$). The different lines represent the transition lines for different levels of constant instantaneous total mortality $Z$. The cross indicates the parameter estimates for $\gamma$ and $-\theta$ (model 12 in Table 1).
Depensatory density dependence

- At least in theory
  - predation mortality if predator saturation possible

- In practice
  - commercial fishing aiming at constant catch (Marjomäki et al. 1996, 2005)

Density independent factors
Density independent factors

- Remember the spatial synchrony
- E.g. Wind forcing during larval period

Lake Puula (Marjomäki et al. 2014)
Density independent factors

- Predators?
  - E.g. perch + Temperature

Valkeajärvi & Marjomäki 2004
Analysis summary

Compensation

- Growth
- Natural mortality?
- Reproductive success

Depensation

Unpredictable environmental factors

- E.g. Wind
- E.g. Perch (mostly temperature related)
  - Recessions?
BUT WHY?
Facts and fiction about 2-y cycles
Why 2-y cycles

NOT Independent external force (Elton 1924)

\[ r = 0.22 \]

\[ r = -0.09 \]
Why 2-y cycles

- NOT induced by strong SB-R relationship
  - Over-compensation (Ricker 1954)
  - Generation cycle (Townsend 1990)
Why 2-y cycles

- NOT generation cycle
Why 2-y cycles

NOT TYPICALLY Generation cycle

- BUT POSSIBLE IF e.g. high fishing mortality
  - Low spawning stock
  - High adult mortality -> semelparity
Why 2-y cycles

- **Instant** density dependent inter-life stage effect

- In muikku: How could the previous year-class inhibit the next?
  - Egg and larval cannibalism *(Nordqvist 1944)*?
    • NOT LIKELY, *yet possible, common in lab* *(Urpanen et al. 2012)*
  - Older fish outcompete younger (0+)* *(Sandlund et al. 1991)*?
    • NOT LIKELY (yet possible)
Why 2-y cycles

**Delayed** density dependent effect (Ward & Larkin 1964)

= the regulatory process manifests itself with a delay

- A. **Exogenous** mechanism involving species interactions
  
  - Typically trophic interactions e.g.
    - the suppressing effect of this years cropping on the food resources in the following year (Auvinen 1988)
      » NOT LIKELY, yet possible, some association found
    - predator-prey cycles
      » **NO SHORT LIFE CYCLE SPECIALIST PREDATOR FOUND**
    - But remember perch and tendency for recessions with long cycle length
Why 2-y cycles

*Delayed* density dependent effect *(Ward & Larkin 1964)*

= the regulatory process manifests itself with a delay

- B. *Endogenous* dd parental effect e.g.
  
  - earlier experienced competition induces a cohort (generally sub-population) effect regulating
    
    - population fecundity and offspring number or/and
    
    - offspring mortality
Why 2-y cycles

*Delayed* density dependent effect *(Ward & Larkin 1964)*
=the regulatory process manifests itself with delay

- **B. *Endogenous* dd parental effect**
- Hypothesis for muikku *(Hamrin & Persson 1986)*:
  - Asymmetric inter-cohort competition in summer: an abundant year-class (0+) induces a sub-population effect on becoming spawners (1+->)
    - regulating
      - population fecundity and offspring number
        - YES, slightly, but compensated for in the models by using biomass in S-R-relationship
      - offspring mortality *(Experiments: Karjalainen et al. unpublished)*
        - fertilisation
        - Egg mortality in winter
        - larval mortality
"Experiments"
Why 2-y cycles

Conclusion:
- Several potential parallel forces
  - Cannibalism
  - Future food resources
  - Competition->Sub-population effect->egg/larval quality
  - Generation cycling in special cases

What next:
- Critical period
  - Preliminary analysis: 2-y c already in larval density???
    ->What happens in winter
- More experiments on parental effect
- Field observations on cannibalism
QUESTIONS? ANSWERS? COMMENTS?
References