



Population Dynamics of Muikku

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Timo J. Marjomäki

Aquatic Sciences

Fish resource biology & management

<http://users.jyu.fi/~tmarjoma/opetus.htm>

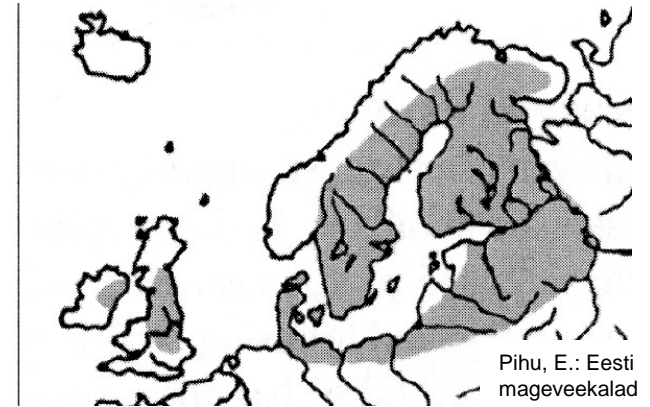


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Muikku (*Coregonus albula* (L.))

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

Abb. 1. Zugnetzfisherei bei der Zugnetzstelle Koratinniemi in den Wassern von Taimonniemi. (Jugendjahre 1913) T. H. J—1.

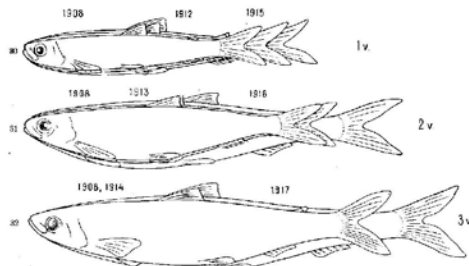


Abb. 20—22. Mittlere Länge (mit Orbsen) der ein-, zwei- und dreijährigen Keitele. Nadir. Die Jahreszahlen bezeichnen die Fangjahre. 1 v.—3 v.—1—3-jährige. Die Höhen mit den Jahren gewachsen.

Järvi T. H. 1919: Muikku ja muikkukannat 1. Keitele. Suomen Kalatalous 5.



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Abb. 16

Why studied

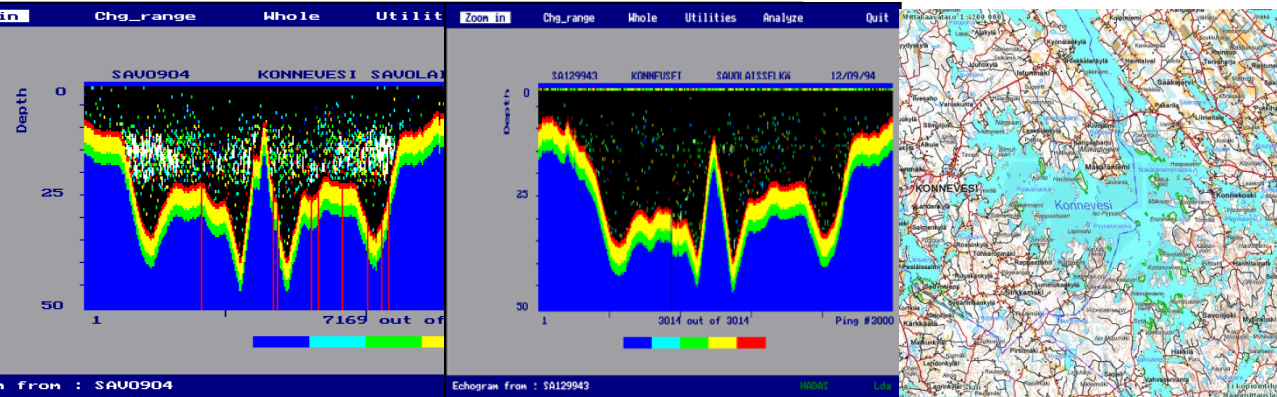
- Resource use
 - Sustainable harvesting
 - Optimal harvesting
- Ecology
 - Understanding
 - Population regulation
 - Sources of variability

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

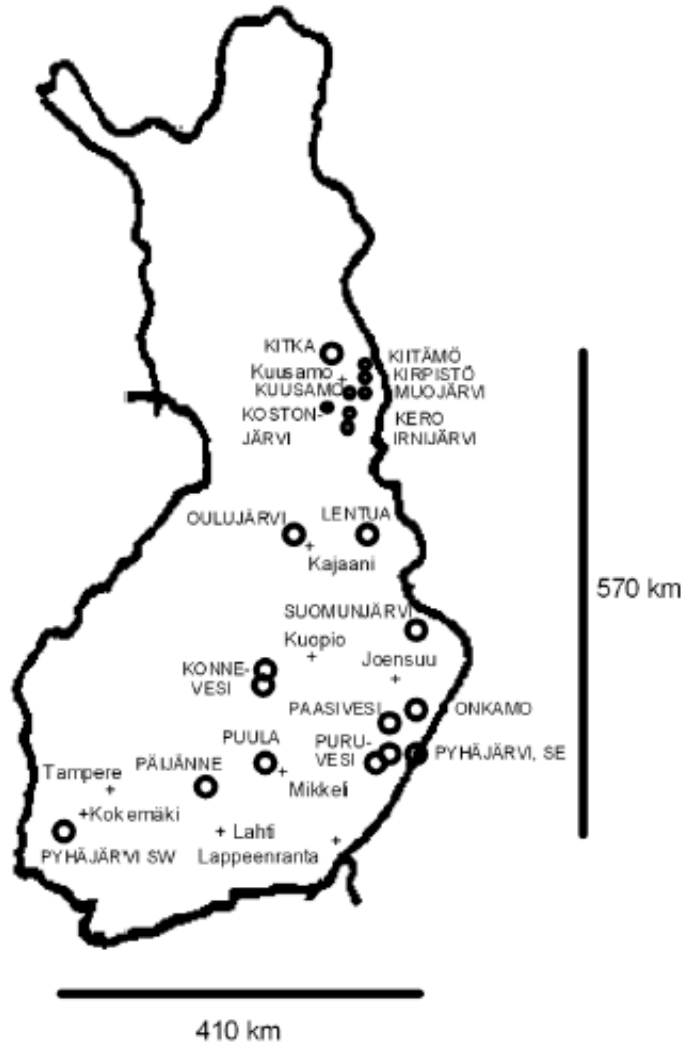


Fig. 1. Locations of the vendace populations (circles) and weather stations (crosses) used in the analysis.

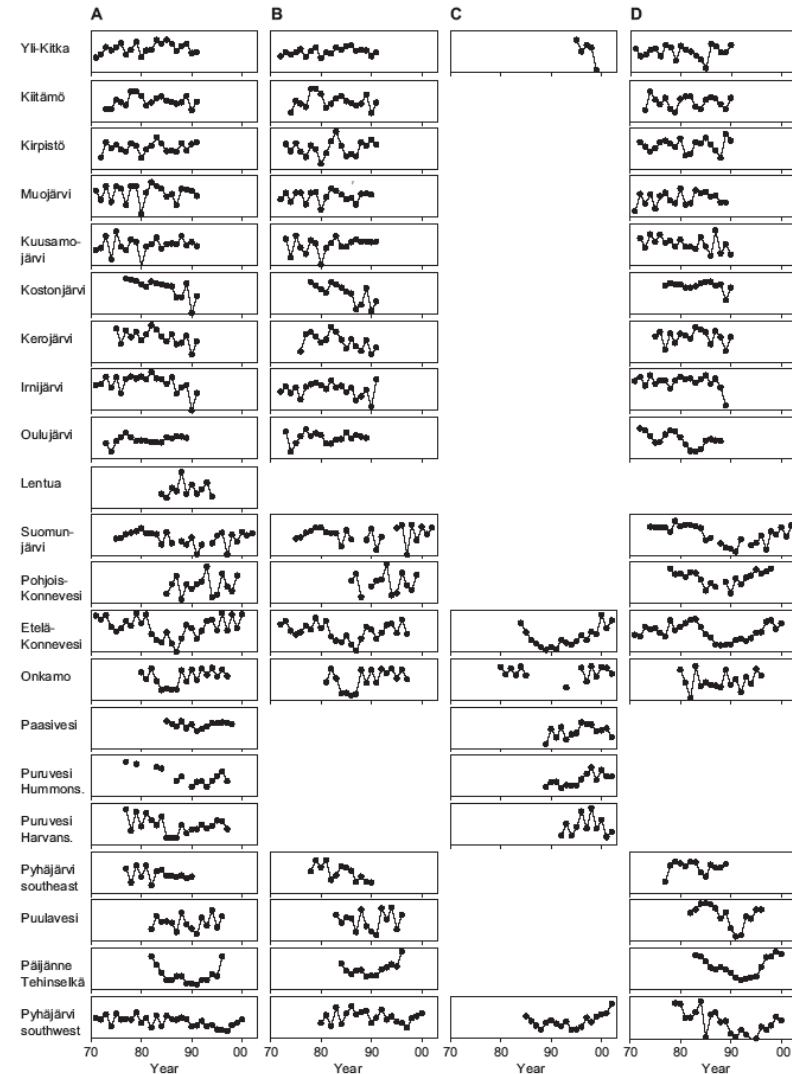


Fig. 2. Time-series of (A) $\ln(\text{recruitment})$, (B) residuals of the density dependence model, (C) $\ln(\text{newly hatched larvae})$ and (D) $\ln(\text{spawning stock biomass or fecundity estimate})$ used in the analysis; y-axis scale arbitrary.

Typical variability



Typical variability

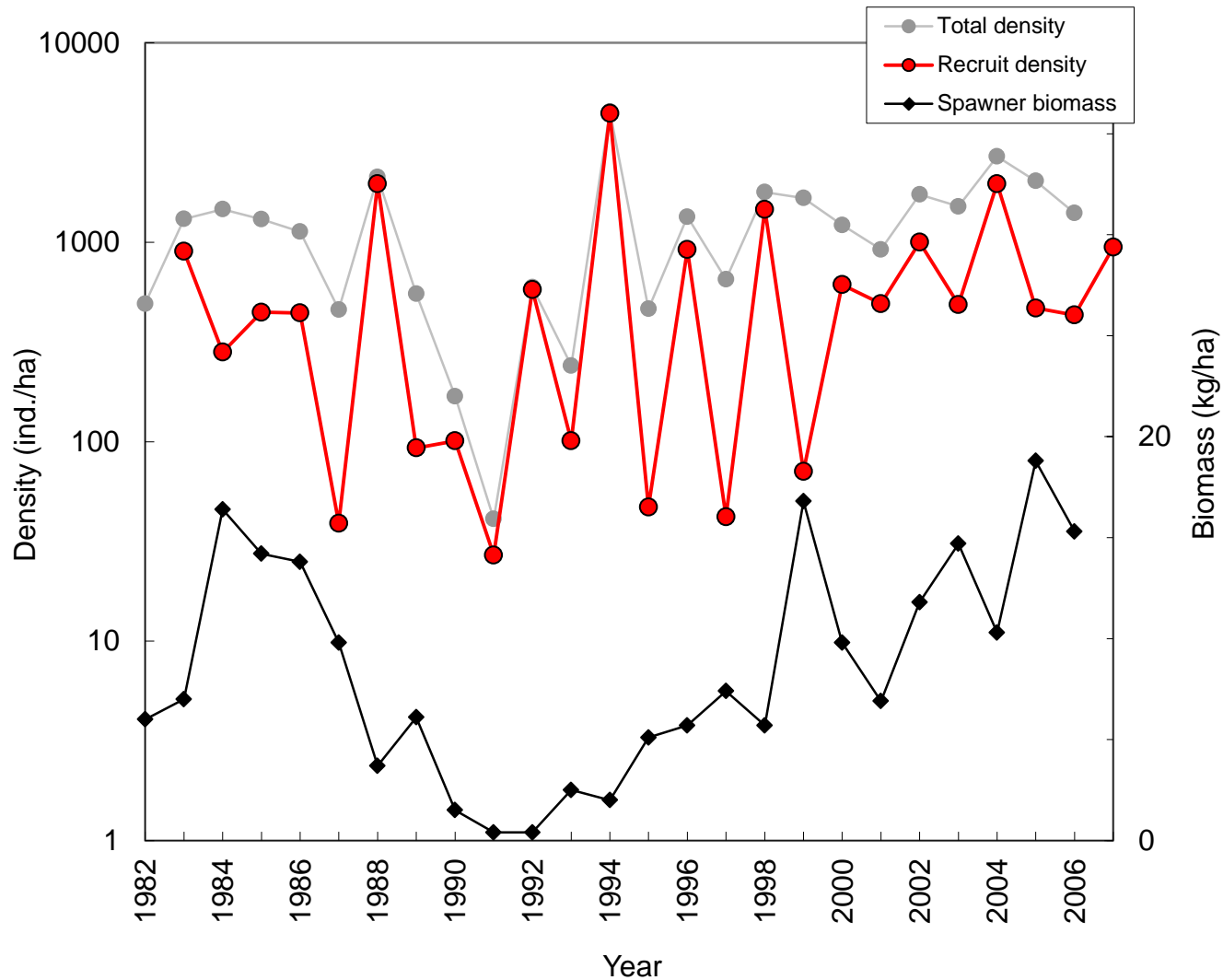


- Already T. H. Järvi, over 70 years ago listed:
 - Strong interannual variability in year-class strength
 - Tendency for 2-y cyclicity
 - Occasional longer recession periods
 - Spatial synchrony in year-class strength variability

■ Examples:



Typical variability: Year-class



Lake Puula (Marjomäki et al. 2014)

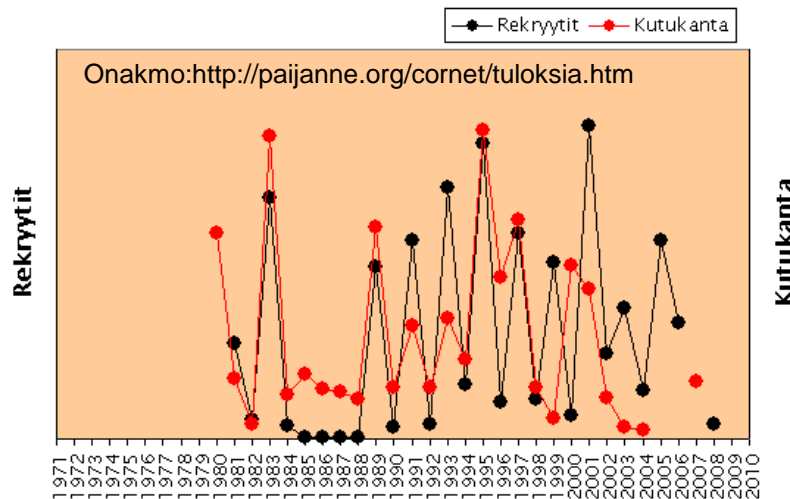
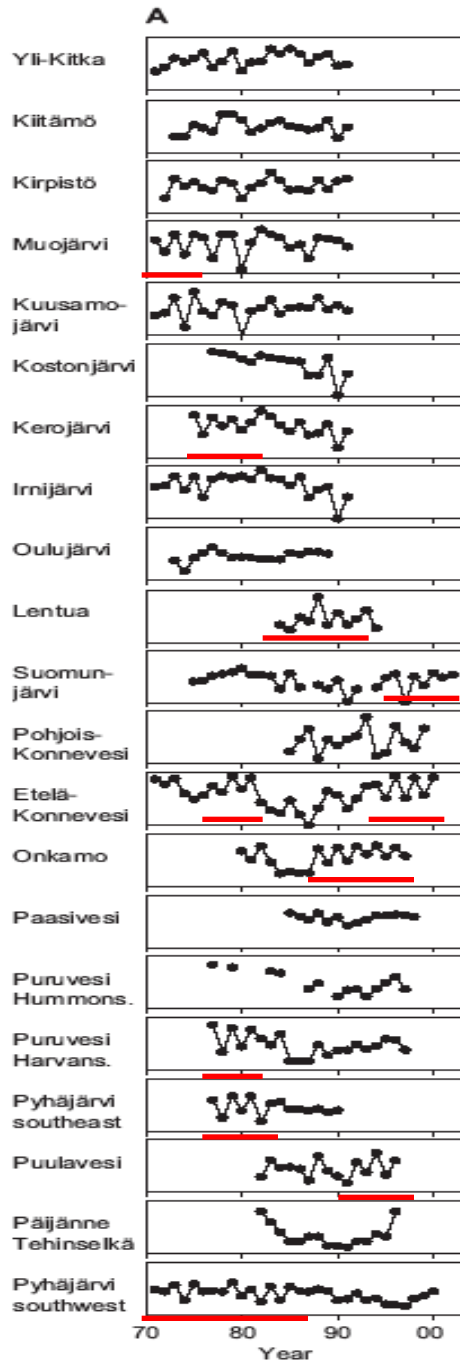


Typical variability: 2-y cycle

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 c in recruitment



Typical variability: Recessions

KONNEVESI

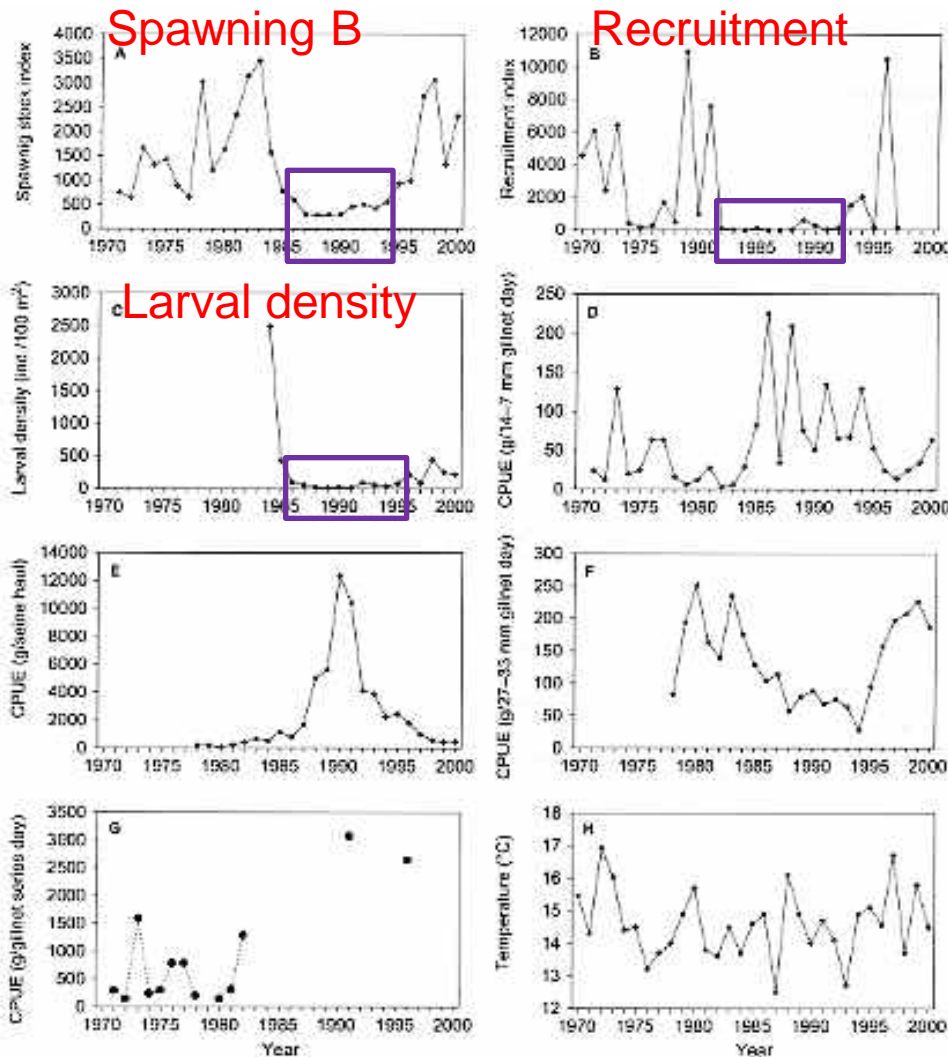
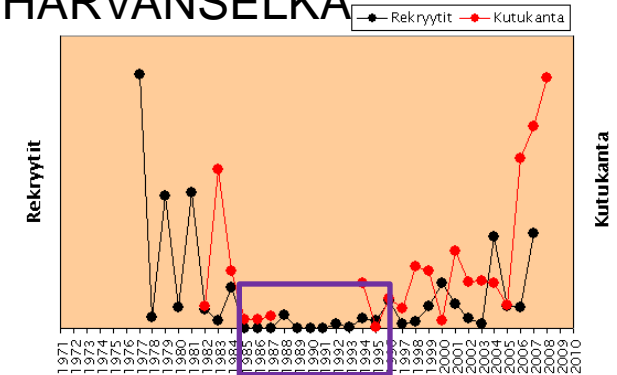
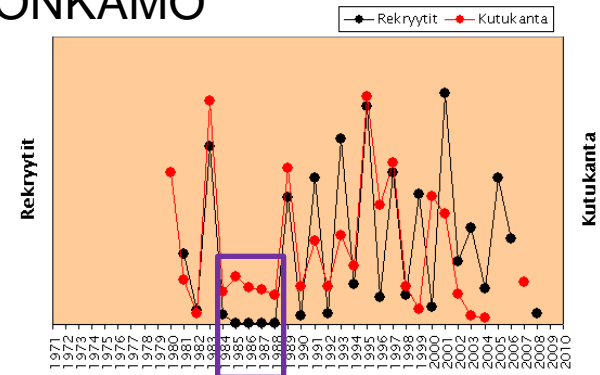


Fig. 1. The most important time series analyzed from 1971 to 2000. — A: index of vendace spawning stock. — B: index of vendace recruits. — C: vendace larval density one week after ice-off. — D: index of small perch (CPUE (g) of perch in 14–17 mm gill nets from knot to knot. — E: CPUE (g) of perch in seine. — F: index of big perch (CPUE (g) of perch in 27–33 mm gill nets). — G: CPUE of perch in test fishing (g per gill net series day) (Puttonen & Valkeajärvi 2000). — H: mean temperature from June to August.

HARVANSELKÄ



ONKAMO



Valkeajärvi & Marjomäki 2004

Typical variability: Spatial synchrony

 Marjomäki et al. 2004

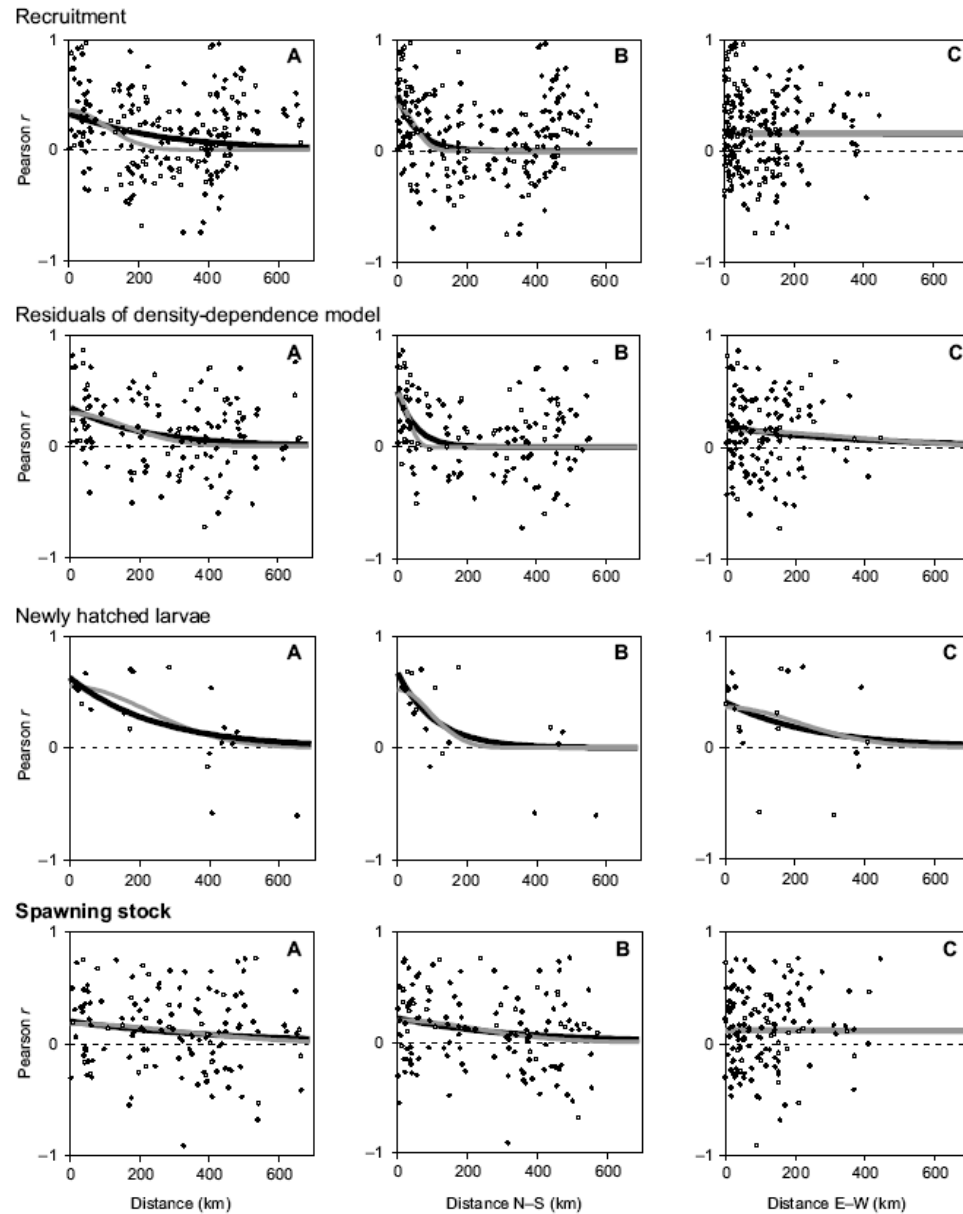


Fig. 3. Correlation of recruitment, residuals of the density dependence model, newly hatched larvae and spawning stock, between pairs of vendace stocks versus (A) distance, (B) north-south and (C) east-west vector of distance between the stocks. Fits of the models $r_{ij} = r_0 \exp(-Dv^{-1})$ (black curve) and $r_{ij} = r_0 \exp[-0.5(Dv^{-1})^2]$ (grey curve).

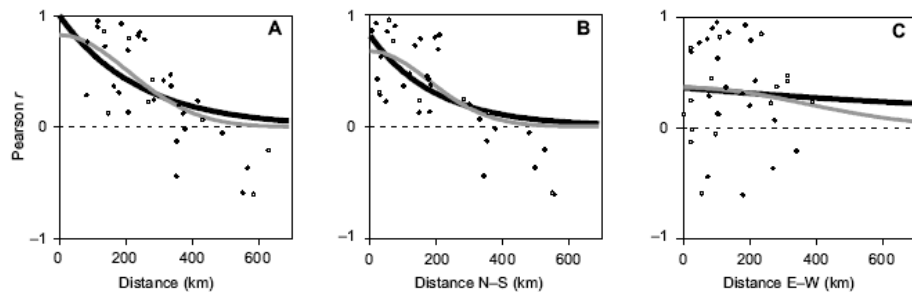


Fig. 5. Correlation between mean temperature during four week period after the local ice break date at pairs of weather stations versus (A) distance, (B) north-south and (C) east-west vector of distance between the stations. Curves as in Fig. 3.

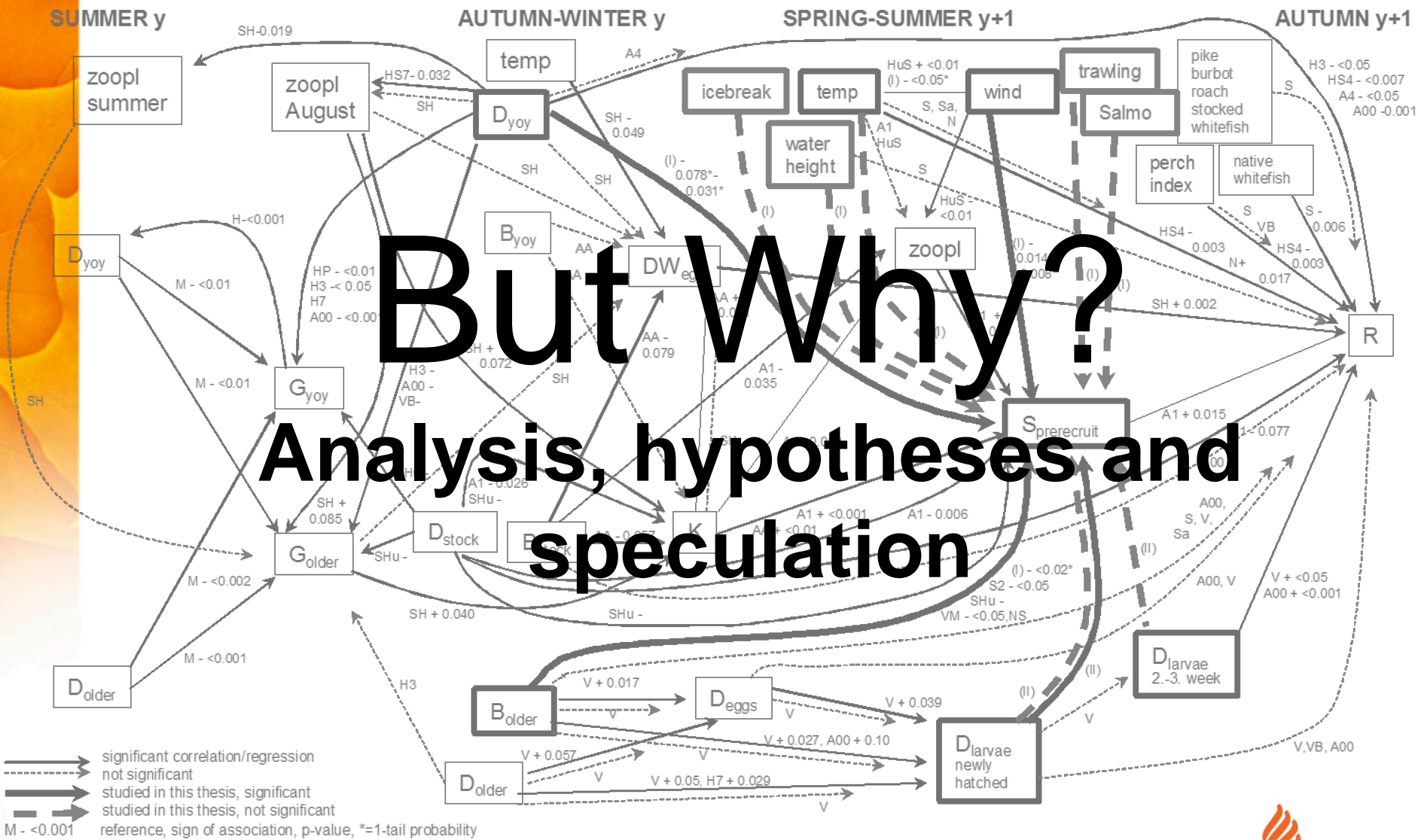


FIGURE 3 A selection of analysed associations between factors potentially linked to recruitment of vendace in field data. In boxes: B=biomass, D=density, DW=dry weight, G=growth, K=condition, S_{perecruit}=survival, temp=temperature, zoopl=zooplankton. References: A1= Auvinen 1988, A4= Auvinen 1994, AA=Auvinen & Auvinen 1994, A00=Auvinen et al. 2000, H3=Helminen et al. 1993a H7=Helminen et al. (1997) HP=Hamrin & Persson 1986, HS4=Helminen & Sarvala 1994, HS7= Helminen & Sarvala 1997, HuS= Huusko & Sutela 1998b, M=Marjomäki & Kirjasniemi 1995, N=Nyberg et al. 2001, S=Salojärvi 1991a, S2=Salojärvi 1991b, Sa=Salonen (1998), SHu=Salmi & Huusko 1995a & b, SH=Salvala & Helminen 1995, V= Viljanen 1988b, VB=Valkeajärvi & Bagge 1995, VM= Valtonen & Marjomäki 1988.

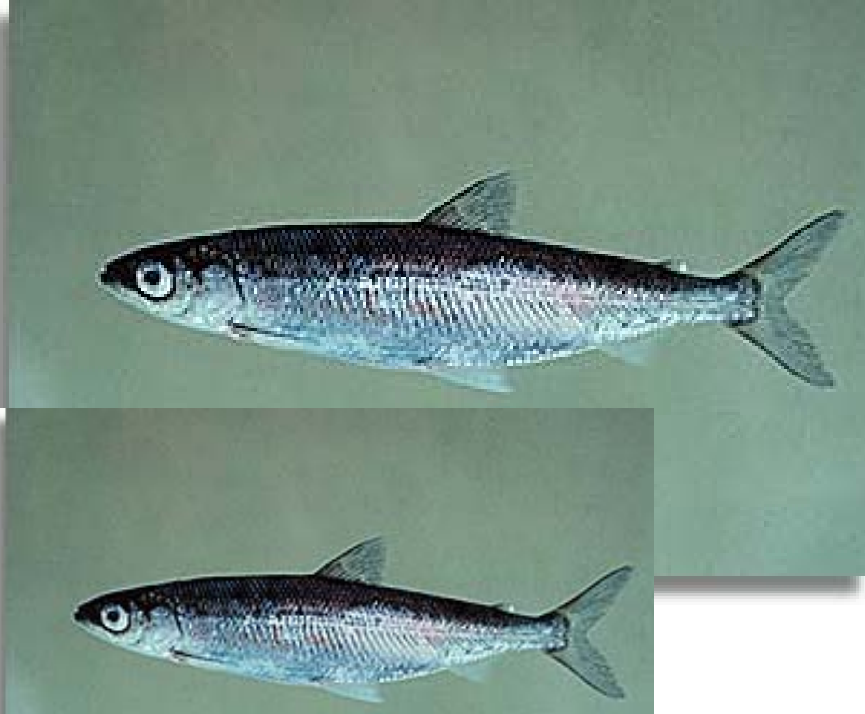
Marjomäki, T. J. 2003: Recruitment variability in vendace, (*Coregonus albula* (L.)), and its consequences for vendace harvesting. *Jyväskylä Studies in Biological and Environmental Science* 127: 1-66.

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

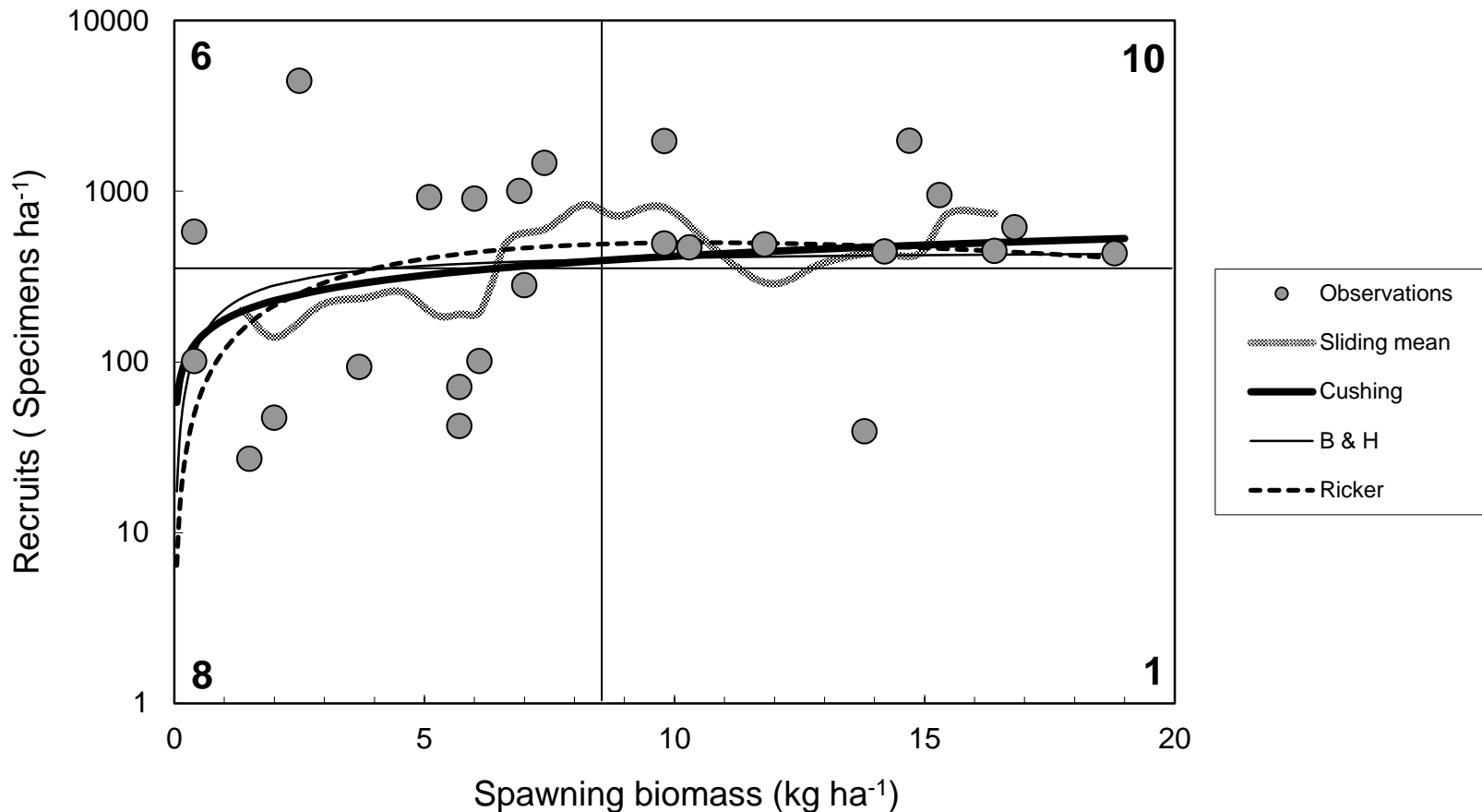
Consequences of **natural mortality**

- Predation mortality size dependent



Density dependent compensatory regulation: SB->R

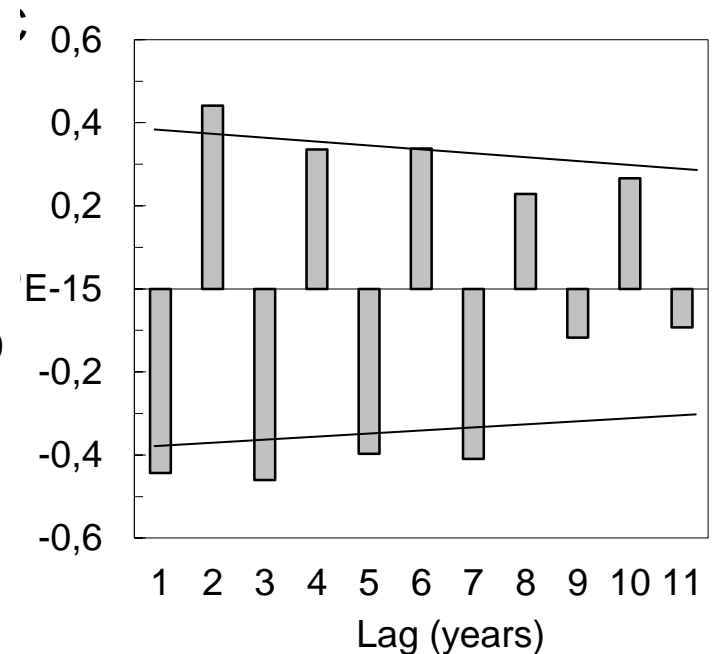
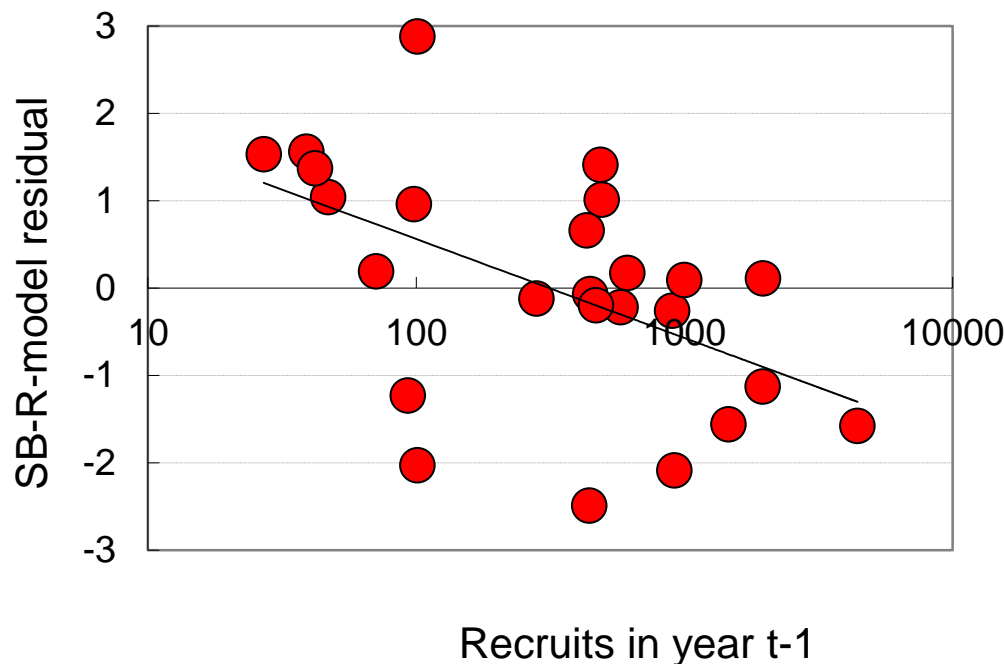
Strong compensation



Lake Puula (Marjomäki et al. 2014)

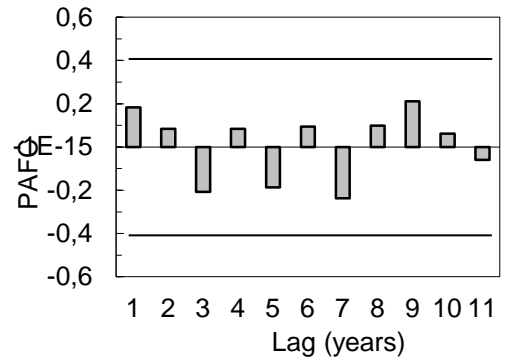
Density dependent compensatory regulation: Previous R->R

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



Density dependent compensatory regulation:

- Combining the compensatory effects of SB and prev. R \rightarrow 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:

Popul Ecol (2014) 56:513–526

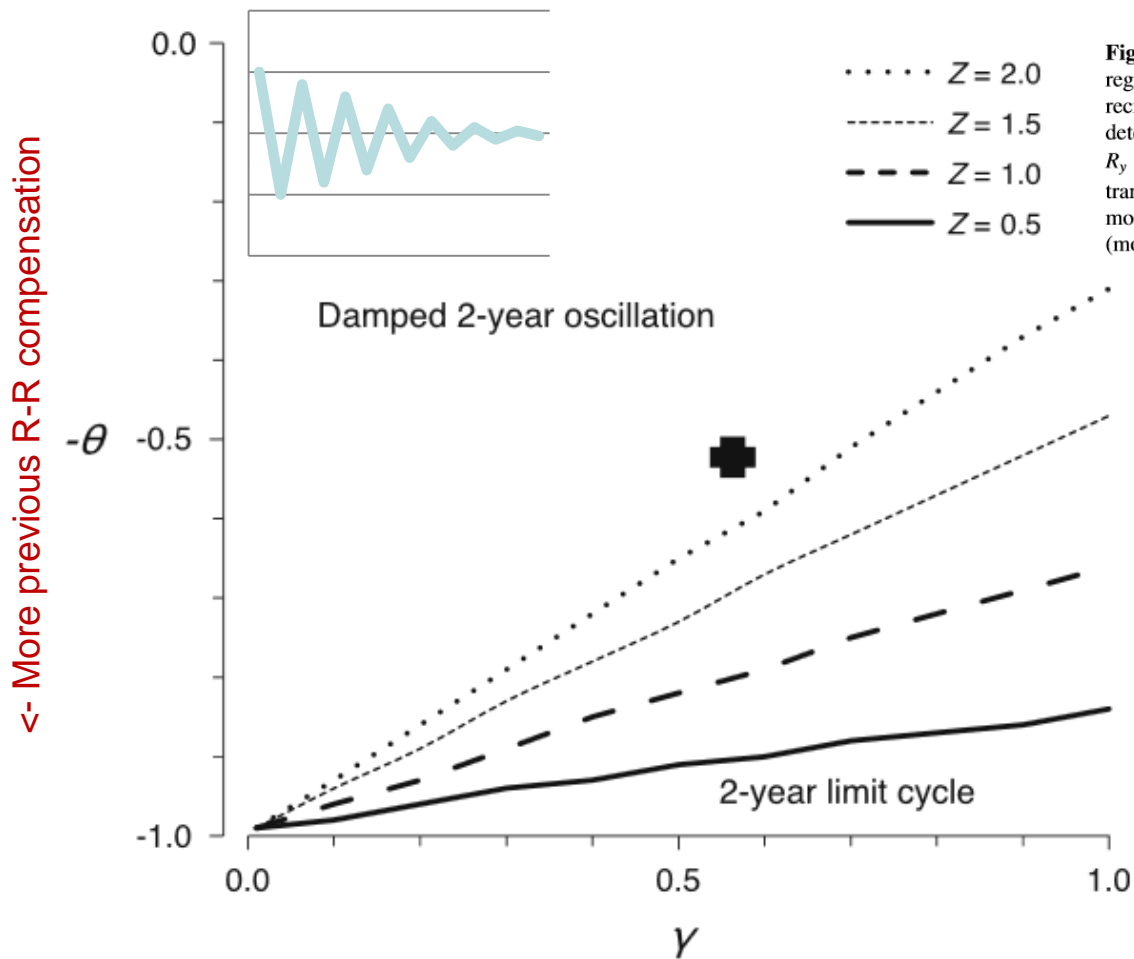
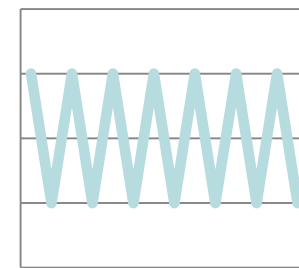


Fig. 7 The transition lines in parameter space $(\gamma, -\theta)$ between the regimes of damped 2-year oscillations and 2-year limit cycles for the recruitment time series simulated with the artificially perturbed deterministic population model incorporating recruitment function $R_y = \alpha S B_{y-1}^y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

← More previous R-R compensation

Less adult survival →

Less SB-R compensation →



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)



<http://www.comicvine.com/forums/battles-7/the-joker-vs-punisher-and-or-cyclops-1547721/>



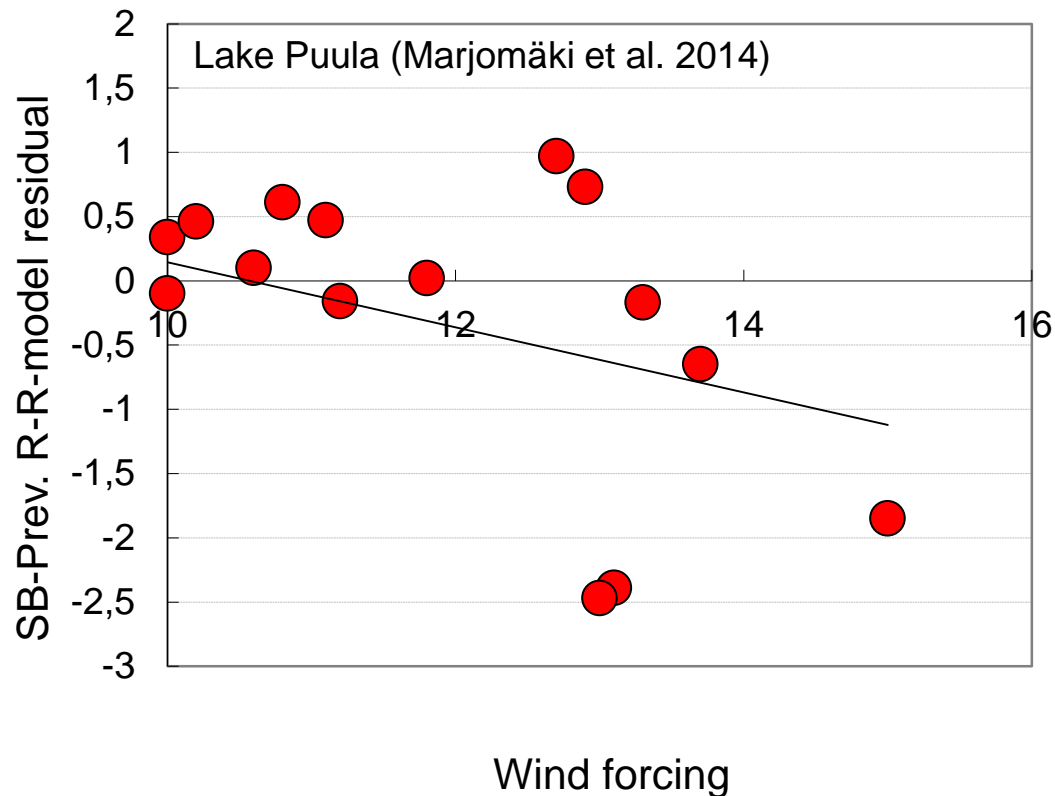
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Density independent factors

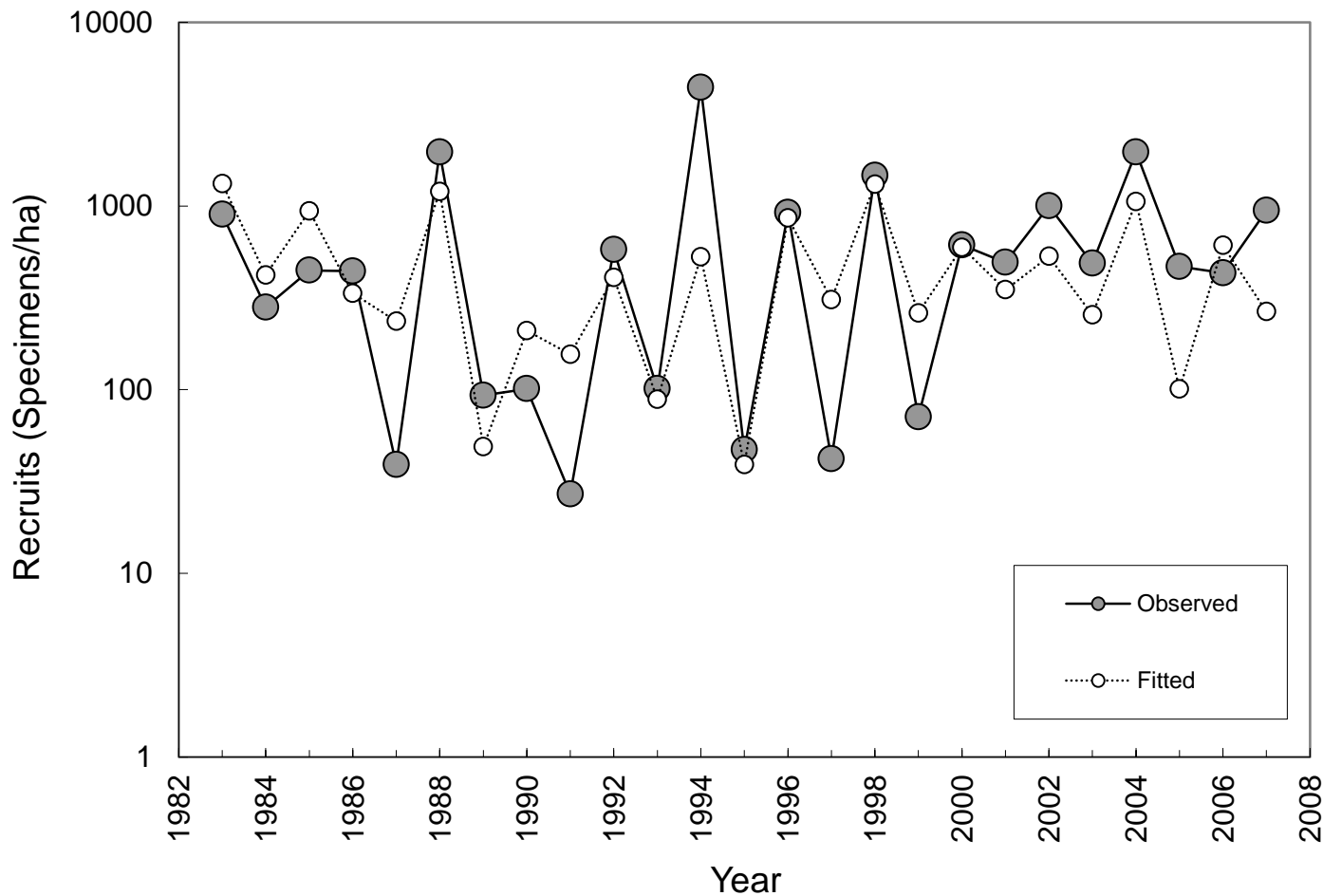


Density independent factors

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



Final model fit



Density independent factors

- Predators?
 - E.g. perch + Temperature

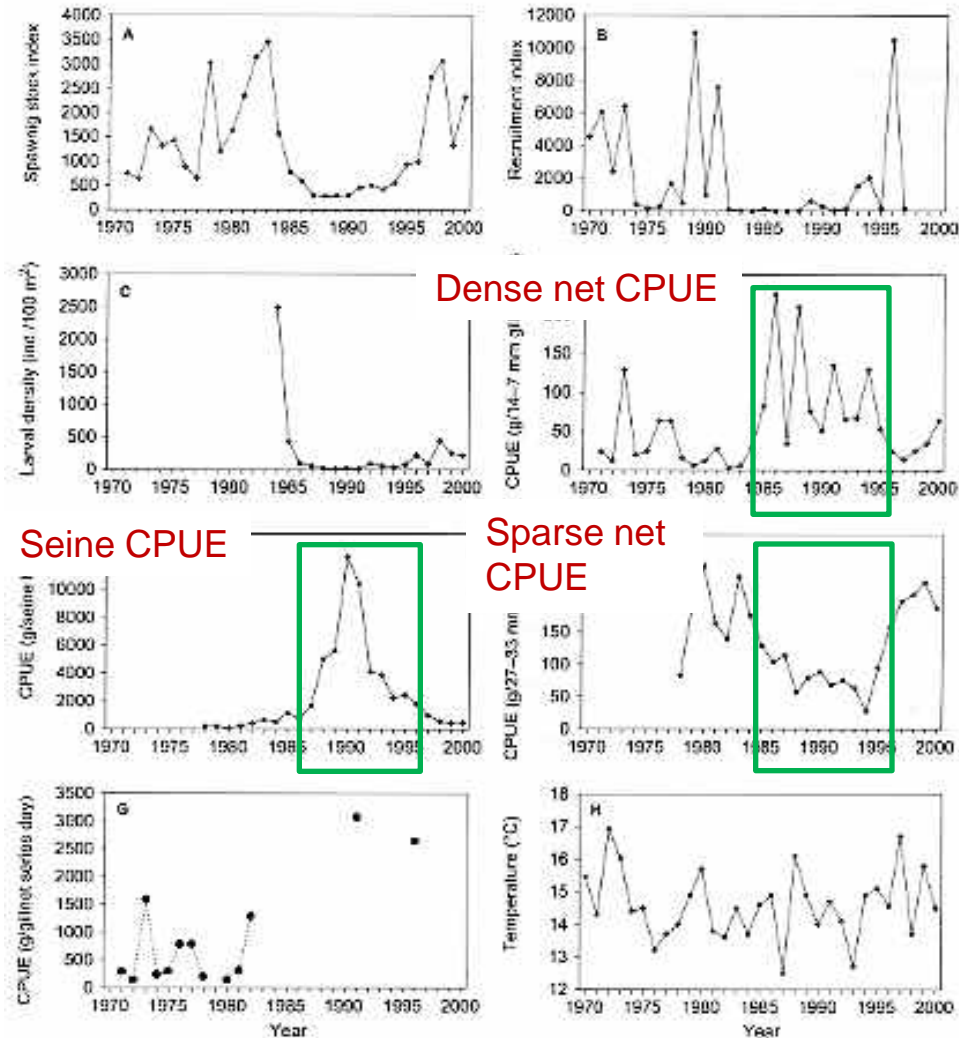


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Analysis summary

Compensation

- Growth
- Natural mortality?
- Reproductive success

Depensation

Unpredictable environmental factors

- E.g. Wind
- E.g. Perch (mostly temperature related)
 - Recessions?



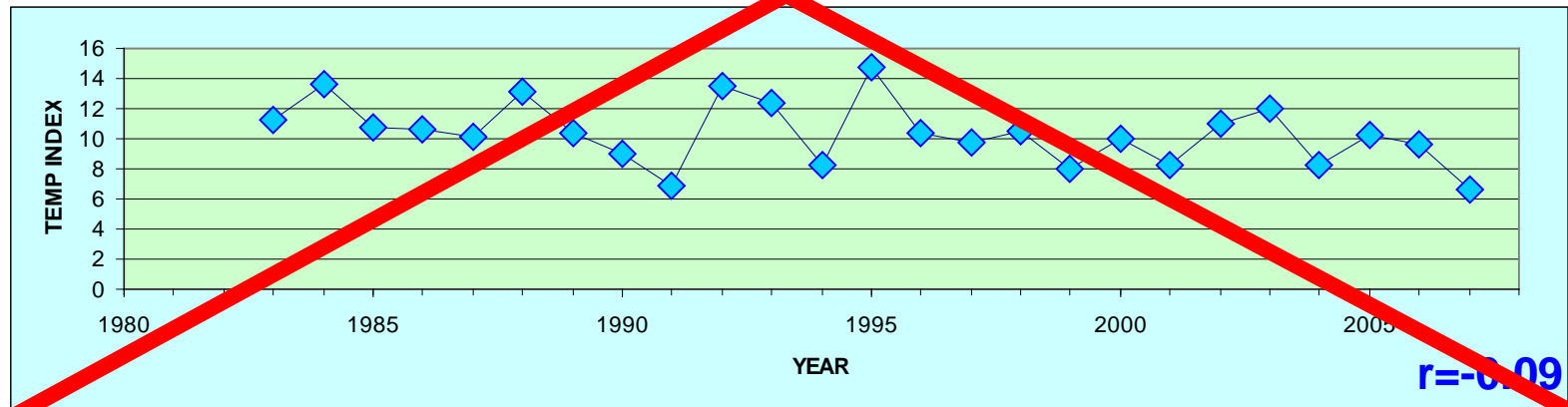
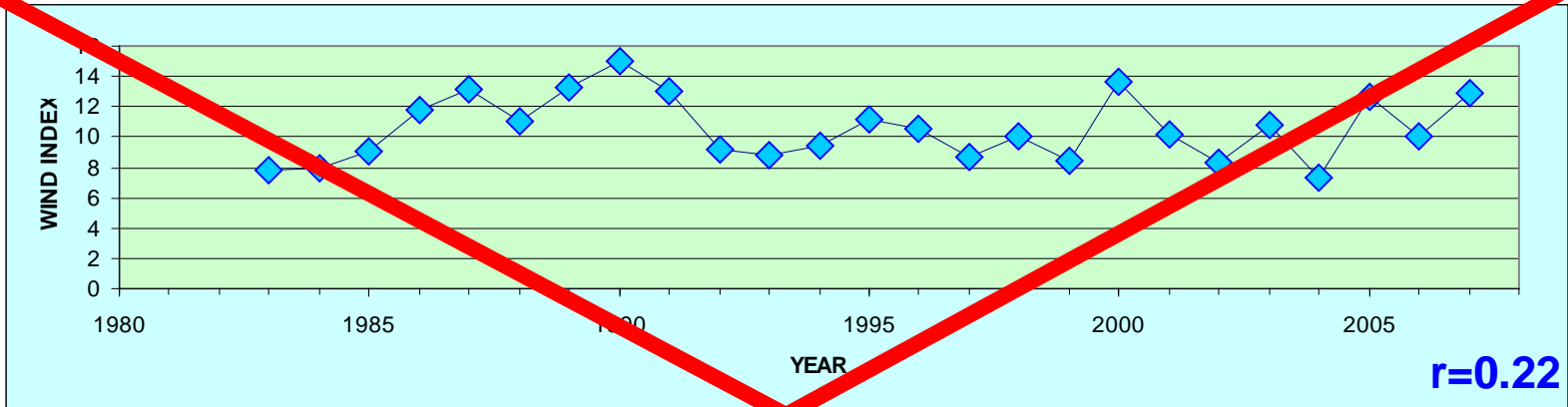
BUT WHY?

Facts and fiction about
2-y cycles



Why 2-y cycles

NOT Independent external force (Elton 1924)



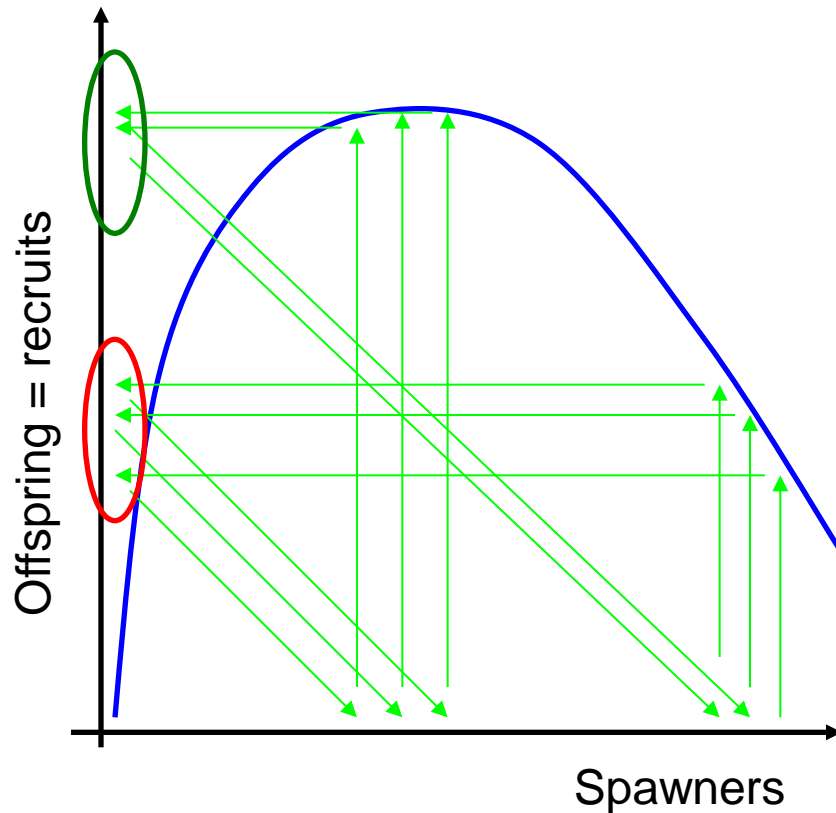
Why 2-y cycles

- **NOT induced by strong SB-R relationship**
 - Over-compensation (Ricker 1954)
 - Generation cycle (Townsend 1990)



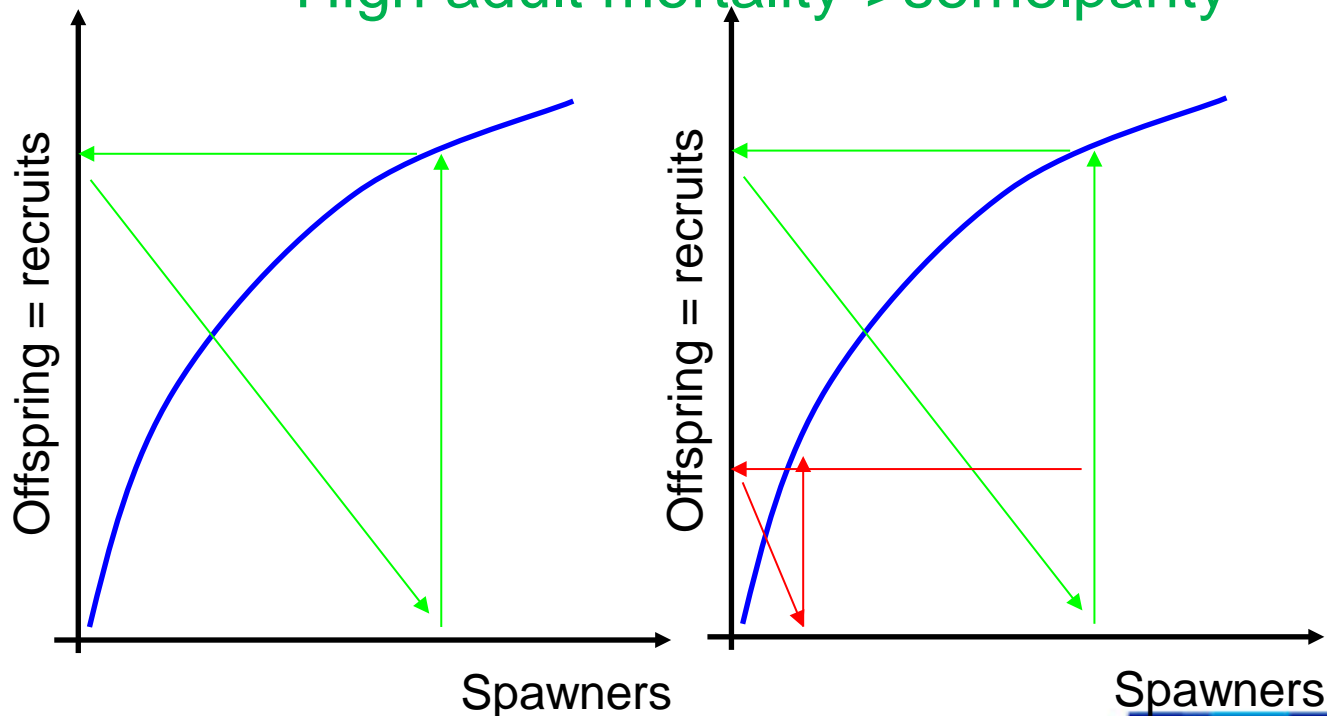
Why 2-y cycles

- 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

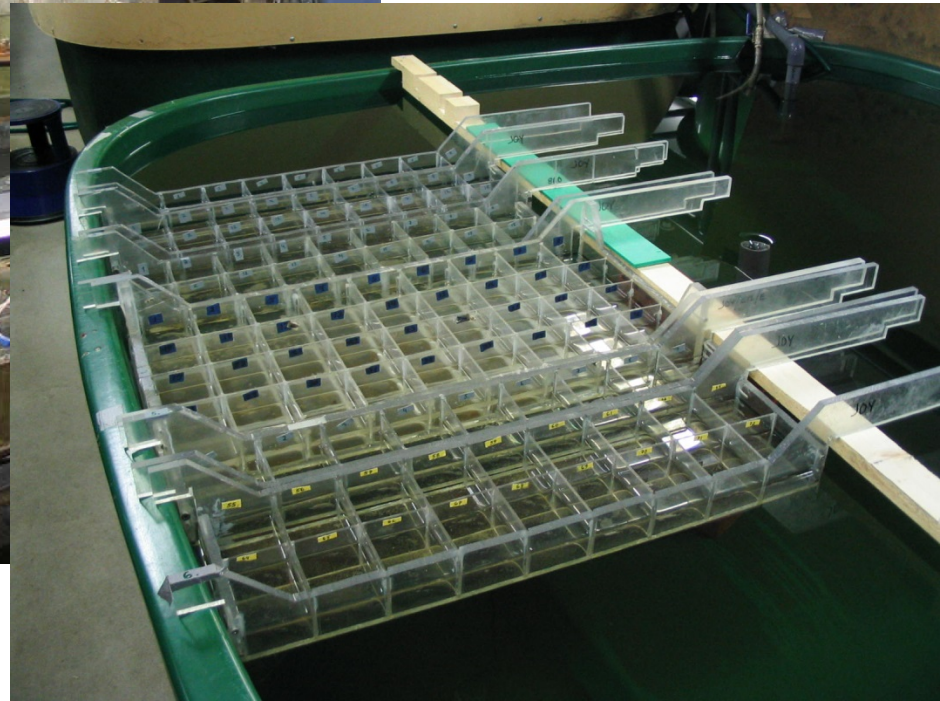


Why 2-y cycles

- **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:

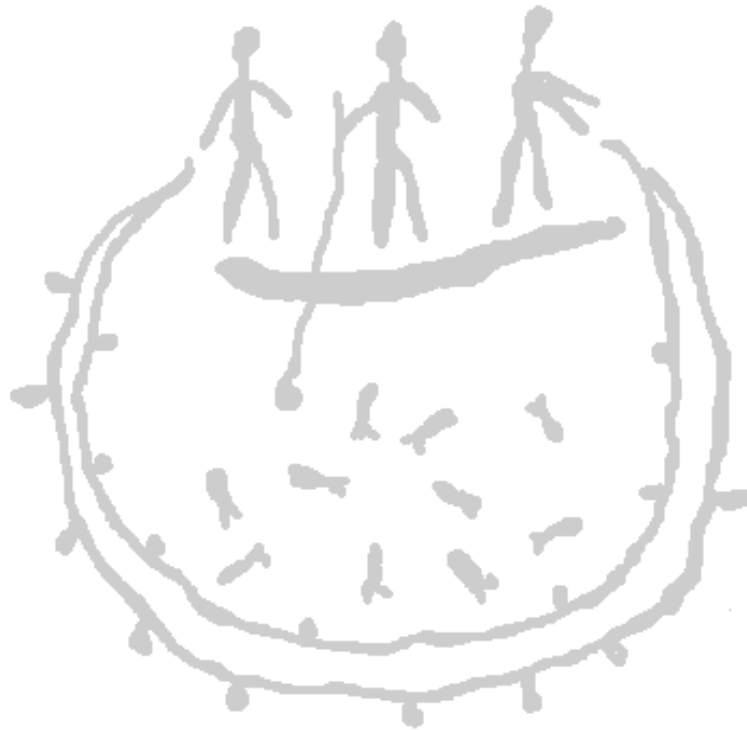
- Several potential parallel forces
 - Cannibalism
 - Future food resources
 - Competition->Sub-population effect->egg/larval quality
 - Generation cycling in special cases

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?



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