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Long-term studies of profundal zoomacrobenthos in Sweden's great lakes: implications of biotic interactions

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Time-series analysis of zoobenthos in Sweden's great lakes showed that the predominant macroinvertebrates seemed to exhibit long-term population trends. Though the causal mechanisms are not known, it is suggested that food availability and competitive interactions may be important factors. For example, *P. affinis* density and biomass were significantly correlated (positively) with variables representing food quality and quantity. During years with high abundances of amphipods, interactions between the predominant zoobenthic components may be important structuring forces. Profundal populations of Oligochaeta and *Pisidium* spp. in Lake Vänern exhibited long-term oscillations "in phase" with *Pontoporeia* (r=+0.85 and r=+0.90, respectively). In contrast, the abundances of *P. affinis* and Chironomidae in Lake Mälaren were "out of phase" with one another (r=–0.80). Differences in foraging behavior may be an important mechanism lowering encounter rates and exploitative interactions between coexisting populations. It is suggested that meteorological cycles may influence pelagic production and allochthonous inputs (food availability), and, with time-lags, affect zoobenthic populations. However, interactions between the predominant zoobenthic populations, such as competition for food (exploitative) and physical disturbance (interference), may be equally important in forming the long-term trends.

1. Introduction

Recently, marine and terrestrial ecologists have shown that many species exhibit long-term cyclic population fluctuations (e.g. Garsd & Howard 1981, Gray & Christie 1983, Rose et al. 1986, Edwards & Coull 1987). Though the data sets used are often limited in the number of observations, such cyclic phenomena appear to occur in response to long-term hydrographic cycles with, for the most part, known physical explanations (sensu Gray & Christie 1983). In their literature review, Gray & Christie (1983) concluded that hydrographic conditions (viz. salinity and temperature) had cycles of 3 to 4 yr., 6 to 7 yr., 10 to 12 yr., 18 to 20 yr., and 100 yr., with direct physical causes.

Gray & Christie (1983) reviewed the significance of hydrographic cycles as a factor structuring aquatic communities. With regard to profundal communities, it was suggested that cyclic patterns of autochthonous algal production (growth and production altered by changes in temperature regimes) subsequently affect the benthos, resulting in a similar, but time-delayed, response of the dominant opportunistic populations. Interactions at population/community levels, however, may presumably act antagonistically or synergistically in structuring the zoobenthos. Such interactions should result in some population trends being "in phase", whereas others may be "out of phase" with the dominating hydrographic cycle.

In long-term ecological monitoring programs, predictability is a central assumption of the variables chosen to describe a community or ecosystem. Thus, knowledge of the quantitative significance of meteorological cycles in structuring populations (variation) in space and time, creating endemic cycling phenomena, is important for interpretation of long-term ecological data sets. Ideally, prediction of monitored variables should be based on a complete understanding of the intricate ecological interactions governing the dynamics of populations and communities, as change in the biocenosis, whether at the population or community level(s), can only be inferred if observations lie significantly outside a predicted range. When the causes of variation are not completely understood, however, forecasting of events is still possible on a purely statistical basis (e.g. using historical demography).

This paper deals with a time-series analysis of *Pontoporeia affinis* Lindström and other macrobenthic animals in Sweden's great lakes, and the potential importance (correlative) of biotic interactions in structuring zoobenthos communities. *P. affinis* is a "glacial relict" species which often predominates in the profundal zoomacrobenthos of Sweden's great lakes (Ahl & Wiederholm 1988) and many parts of the Baltic Sea (e.g. Andersin et al. 1978). In the lakes reviewed in this paper, *P. affinis* constitutes (numerically) 62% (Vänern), 50% (Vättern), and 42% (Mälaren) of the profundal macroinvertebrate communities. Together with the Oligochaeta, these two groups constitute ca. 90% of the overall total zoomacrobenthos densities.

2. Materials and methods

Long-term ecological monitoring of Sweden's great lakes has been in progress for many years. To date, Lake Vänern has been investigated for 15 yr. (1973–1987), Lake Vättern for 11 yr. (1977–1987), and Lake Mälaren for 19 yr. (1969–1987). The sampling sites, variables analyzed, and techniques used have been described in many previous papers (e.g. Ahl & Wiederholm 1988 and references cited therein).

Briefly, zoobenthos samples were collected using an Ekman sampler (256 cm^2), passed through a sieve with a 0.6 mm mesh and preserved in 70% ethanol. The samples were sorted against a black background, at 10× magnification, and the species were identified and counted. In Lakes Vänern and Vättern profundal zoobenthos sampling was performed on a biannual basis (May and August sampling), with 5 (Vänern) and 9 (Vättern) replicate samples collected per site and date. In Lake Mälaren sampling was restricted to autumn (September–October), with 5 replicate samples collected per site.

3. Results and discussion

The population dynamics of *Pontoporeia affinis* in Sweden's great lakes seemed to exhibit long-term population oscillations. Fig. 1 shows untransformed and transformed (3 yr. moving average) data plots of *P. affinis* in Lakes Vänern, Vättern, and Mälaren (Johnson & Wiederholm unpubl.). In order to identify a true 10 yr. cycle, it is necessary to have a minimum of 20 yr. of observations. Nevertheless, it appears that Lakes Vänern and Mälaren (studied for 15 and 19 yr., respectively) have a 8–12 yr. oscillation (Fig. 1a & 1c). In other words, the amphipods in these lakes may be influenced by the well-documented "solar or sunspot cycle". This cycle can be accurately predicted (Ottestad 1979), and has been traced back to 647 B.C. (Schove 1965). Though

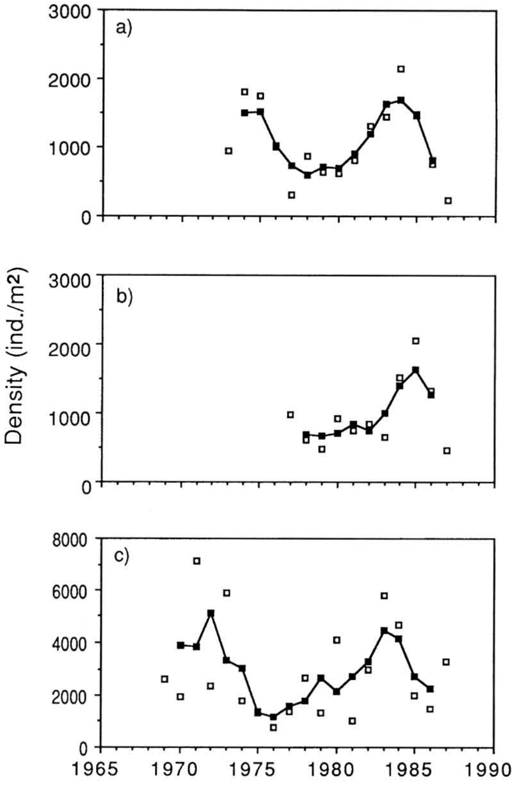

Fig. 1. Time-series plots of untransformed (annual mean) and transformed (3 yr. moving average) densities of *Pontoporeia affinis* for lakes (a) Vänern, (b) Vättern, and (c) Mälaren (overall means for 30 m and 50 m sites). Open = untransformed data; filled = transformed data.

the zoobenthos in Lake Vättern has been monitored for only 11 yr., it is nonetheless interesting to note that the densities appear to be "in phase" with those in Vänern (Fig. 1b). Lakes Vänern and Vättern are situated close to one another, and are characterized as deep, nutrient-poor systems. Generally, *Pontoporeia* densities in Sweden's great lakes were high during the early 1970's, low densities were recorded around 1980, and the numbers then usually increased, reaching highs in the mid-1980's.

Food availability is undoubtedly an important factor for the profundal zoobenthos. For example, in a literature review Morgan et al. (1980) concluded that food quantity and quality are the main factors limiting secondary production. Further study is required to determine whether the food resource is the forcing function behind the population trends in Sweden's great lakes, as suggested by Gray & Christie (1983) for marine systems. Using least squares regression, however, it was found, that *P. affinis* density and biomass were related significantly ($P \leq 0.05$) with variables representing food. For example, amphipod density and biomass were positively related with variables that represented food quantity, either directly (median total algal biovolume and maximum Bacillariophyceae biovolume; usually the spring diatom bloom, with the response in amphipod density showing a one year lag) or indirectly (chlorophyll *a*, total phosphorus).

If the profundal food resource, originating from autochthonous or allochthonous production, is limiting either spatially or temporally, density-dependent factors may be governing the population dynamics. Johnson & Wiederholm (1989) present correlative evidence that *P. affinis* growth is strongly (negatively) influenced by conspecific density. The 0^+ and 1^+ generations (animals ca. 6 mo. and 18 mo. old, respectively) showed similar growth patterns, viz. mean body length usually decreased as amphipod abundance increased, indicating the importance of density-dependent factors. Though the mechanism is not fully understood, it was postulated by Johnson & Wiederholm (1989) that conspecific competition for food may be important. Regression has shown *Pontoporeia* growth (increase in body length of 0^+ and 1^+ generations) to be strongly correlated with median total algal biovolumes (R^2=0.41, P=0.0192 and R^2=0.43, P=0.0154 for 0^+ and 1^+ generations, respectively). In Lake Mälaren and Lake Vänern, *P. affinis* density (at t+1 yr.) is strongly correlated (R^2=0.78, P=0.0001; Lake Vänern) with the maximum Bacillariophyceae biovolume, usually the spring bloom (Johnson & Wiederholm unpubl.). Indeed, as the adult body length of *Pontoporeia* is positively correlated with fecundity (Winnell & White 1984), it was argued by Johnson & Wiederholm (1989) that factors which affect 1^+ body length and abundance (i.e. reproducing amphipods) should directly affect subsequent recruitment. If predation and other factors which affect *P. affinis* mortality are excluded, years with high food

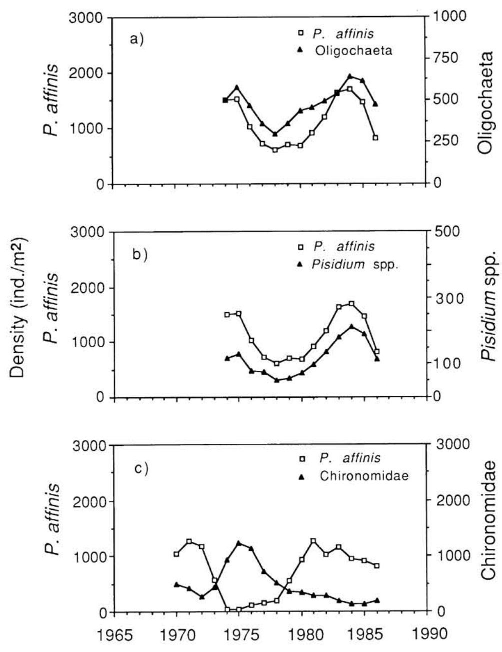

Fig. 2. Time-series plots (3 yr. moving average) of *Pontoporeia affinis* and (a) Oligochaeta and (b) *Pisidium* spp. of Lake Vänern, and (c) Chironomidae of Lake Mälaren (means for 30 m sites).

availability (e.g. strong vernal Bacillariophyceae blooms) may:

1) increase overall survival (recruitment success) of 0^+ generations, resulting in strong year classes and
2) increase the fitness and potential reproductive capacity (greater mean length and higher lipid content) of the 1^+ generation.

Interactions between macroinvertebrates may be important in structuring profundal communities. Fig. 2 shows time-series plots of the predominating macrobenthic animals in Lakes Vänern and Mälaren (Johnson & Wiederholm unpubl.). The Oligochaeta and *Pisidium* spp. of Lake Vänern exhibited long-term population fluctuations (with periods of ca. 8 yr.) which are "in phase" with *P. affinis* density (Fig. 3a & 3b). Cross-correlation plots showed that both of these groups were strongly (positively) correlated with amphipod abundance (Oligochaeta, $r=+0.85$, $P<0.001$, and *Pisidium* spp., $r=+0.90$, $P<0.001$). In contrast, the Chironomidae of Lake Mälaren (Fig. 3c) were "out of phase" with *P. affinis* ($r=-0.80$, $P<0.001$). These findings suggest that the components of the profundal zoomacrobenthos are not necessarily reacting to the same environmental (biotic or abiotic) stimuli.

The patterns observed may result from different foraging behaviors. For example, both Oligochaeta and *Pisidium* are subsurface deposit feeders, whereas *P. affinis* and Chironomidae are usually classified as surficial deposit feeders. The subsurface feeding behaviors of oligochaetes and *Pisidium* should result in lower encounter rates (*i.e.* decrease exploitative interactions) between these two groups and *Pontoporeia*. Similarities in foraging behavior between *P. affinis* and Chironomidae, on the other hand, may lead to periods of exploitative interactions, if food is limiting either spatially or temporally. The increase in chironomid abundance coincident with low amphipod densities suggests competitive release. Interference may be an equally important, if not a dominating, mechanism structuring profundal communities when amphipods occur in high abundances (cf. Elmgren et al. 1986). Elmgren et al. (1986) showed that high amphipod abundance adversely affected *Macoma* recruitment. Similarly, high *P. affinis* densities may deleteriously affect the fitness of established chironomid populations and/or recruitment success of juveniles (first and second instars). For instance, high amphipod densities may result in greater mortality of eggs or young larvae (e.g. plausible mechanisms being predation, either specific or nonspecific, and/or indirect physical disturbance).

4. Conclusion

Meteorological cycles may be setting the scene (e.g. through oscillations in food availability), but biotic interactions between predominant profundal zoobenthos populations may be equally important in explaining density oscillations. Though the mechanism is unclear, it is postulated that food may be an important structuring variable. High densities of amphipods will alter food availability (and sediment physico-chemical properties) in two ways:

1) directly through sediment ingestion and stripping of nutrients (i.e. decreasing sediment food quality and quantity) and
2) indirectly through fecal pellet production, i.e. the greater particle size of fecal pellets may render them inaccessible for reingestion by amphipods, chironomids and other surficial deposit feeders, presumably resulting in periods when food is limiting.

Further study is required of the importance of food (on both temporal and spatial scales), the time-lags involved in sediment regeneration following intensive grazing by profundal detritivores, and the potential importance of competitive interactions as community-structuring variables.

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