Changes in nutrient ratios drive changes in pelagic and benthic assemblages, and benthic-pelagic coupling in Puget Sound: A compelling hypothesis linking water quality and the benthos.

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Introduction:

Analyses of Ecology's long-term monitoring data indicate that changes in the cycling of organic material might occur that could affect phytoplankton, micro-zooplankton, and benthic communities.

The long-term change has potential implications for marine food web structure, energy transfer, particle export, and higher trophic levels such as fish. A testable hypothesis is presented combining observations about the significance of energy flow through the microbial food web that determines the outcome of energy available for higher trophic levels.

Water Column

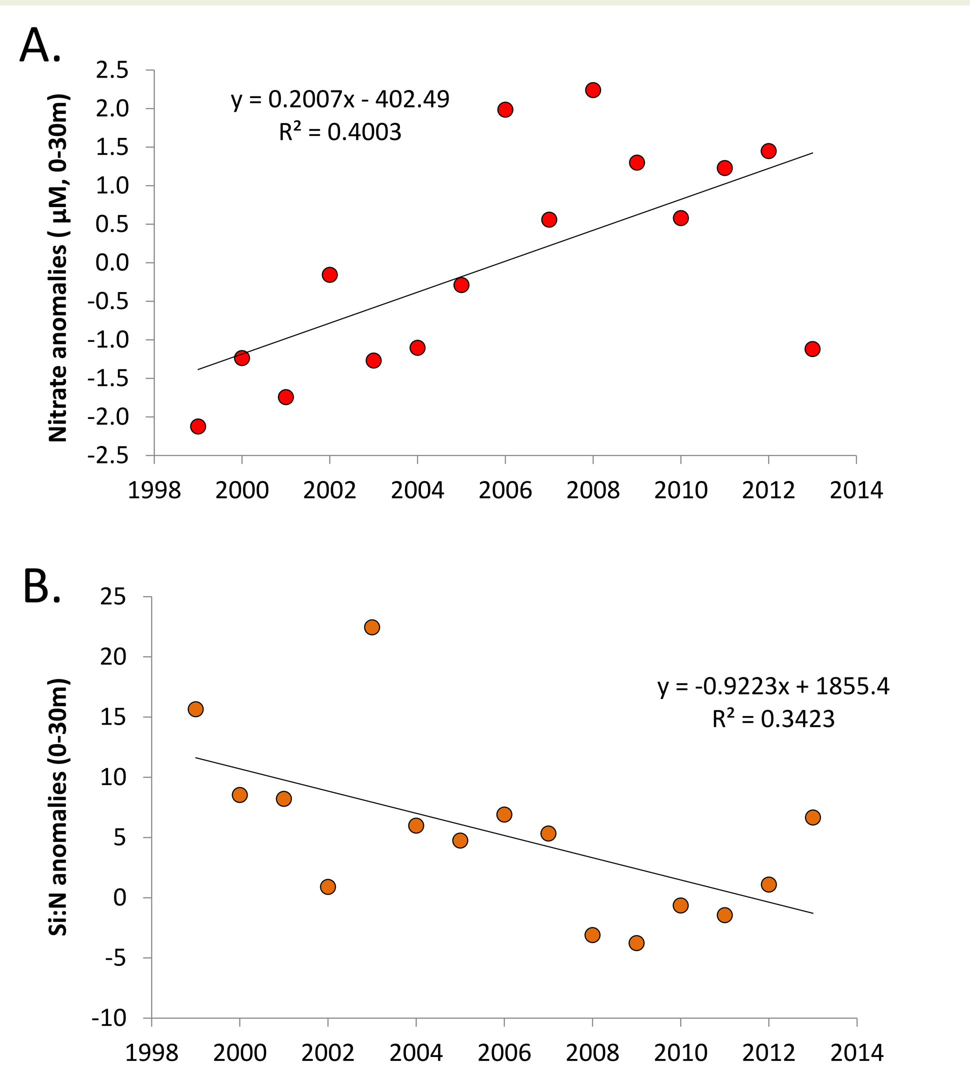


Fig. 1. Inter-annual changes in (A) nitrate and (B) the ratio of silicate to dissolved inorganic nitrogen (Si:DIN) appear to be a result of disproportional nitrogen additions to the system. From 1999 to 2013, inter-annual patterns of nitrate (A) steadily increased in the surface waters. As a result, the ratio of silicate to dissolved inorganic nitrogen (Si:DIN) decreased. Yearly anomalies were calculated by the difference between expected (site-specific seasonal baseline) and observed median water-column concentrations at 0, 10, and 30m. Anomalies from 17 stations were averaged over the year and station network (17 core stations) (see map Fig. 3).

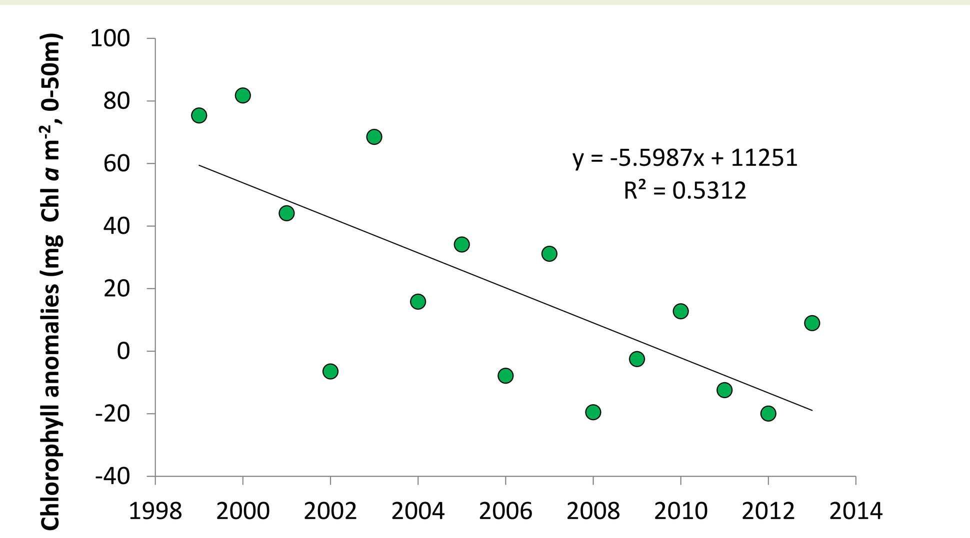
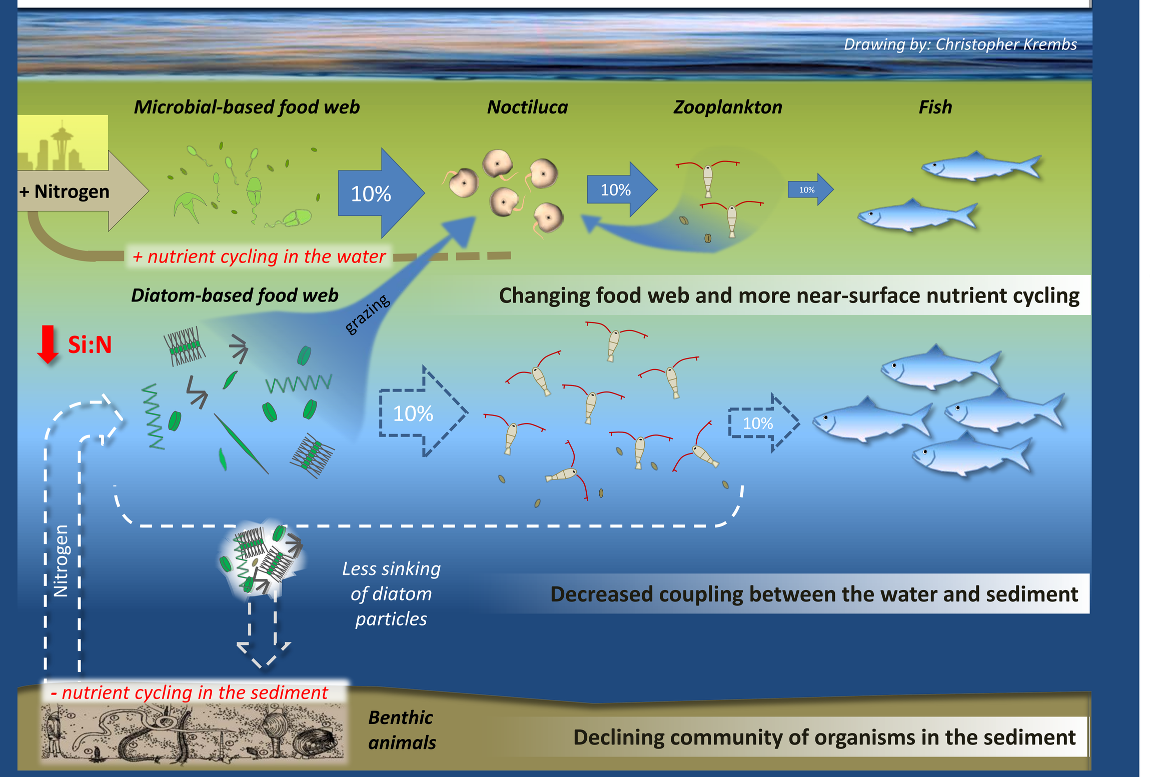


Fig. 2. Declining phytoplankton biomass in Puget Sound.
The inter-annual decline in subsurface phytoplankton biomass suggests a reduced supply in organic material for the marine food web. The trend is based on site and seasonal anomalies and calculated as in Fig. 1.

Fig. 9 Hypothesis: Changes in the Marine Food Web and Energy Transfer in Puget Sound



Hypothesis:
Nitrogen additions to Puget Sound cause nutrient ratios Si:N:P to change and indirectly might create a larger energy transfer through the microbial food web by promoting conditions for increased micro-zooplankton grazing. This has consequences for overall phytoplankton species composition, biogeochemical cycles, higher trophic levels food availability, and benthic-pelagic coupling.

EOPS, Aerial photography 6-17-2013

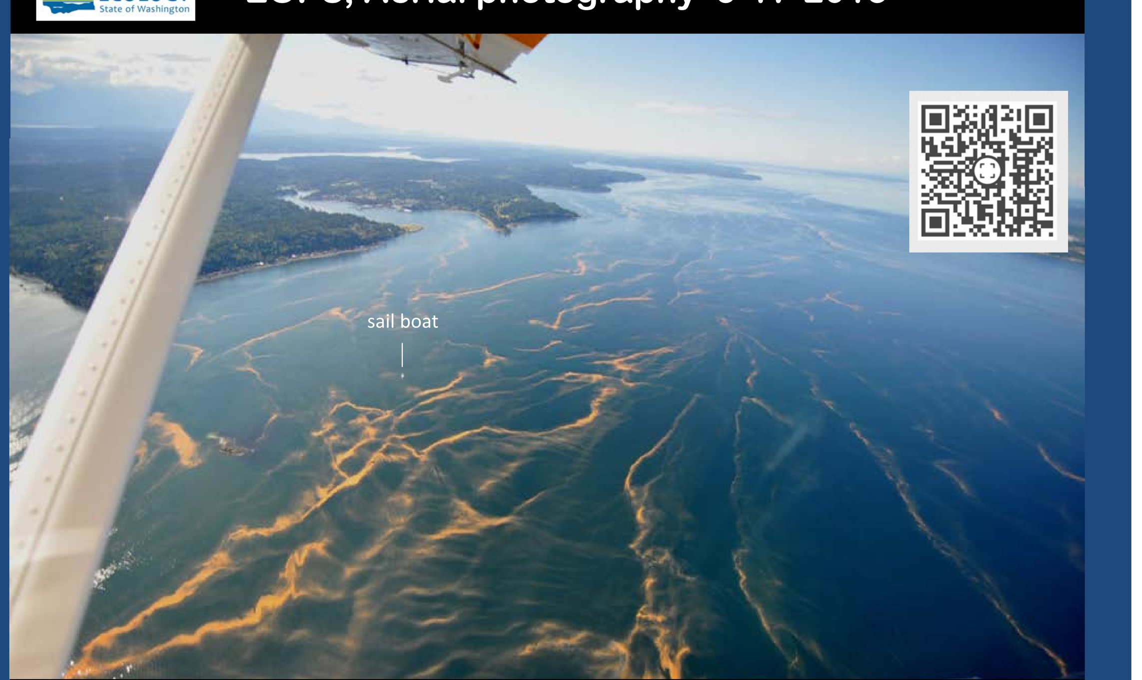


Fig. 5. ***Noctiluca*** **bloom at surface in very long bands.** Location: Between Bainbridge Island and Elliott Bay (Central Basin), 5:27 PM. Ecology, Publication No. 13-03-075.

Results and Discussion:

Long-term increases in nitrogen concentrations (Fig. 1 A) and shifting nutrient ratios (Fig. 1 B) suggest human nitrogen inputs to Puget Sound. Yet, decreasing phytoplankton biomass (Fig. 2) in our monitoring network (Fig. 3) suggests large-scale changes in lower trophic levels of the pelagic food web that match a decline in the marine benthos (Fig. 4 A, B).

• Monitoring of lower food web dynamics remains a knowledge gap in Puget Sound and is indispensable to connect water quality to the marine food web!

Human pollution causes nutrient imbalances (Fig. 1 B) and plays a role in the shift from diatom to dinoflagellate assemblages [1]. Large blooms of the dinoflagellate *Noctiluca* (Fig. 5) in our station network [2] are consistent with the increases in nitrogen (Fig. 1A). In contrast, a decrease in subsurface phytoplankton biomass (Fig. 6), particularly in the late summer (Fig. 7), contradicts nitrogen trends.

• Could long-term observations indicate that food web dynamics alter nitrogen concentrations in the water?

A negative correlation between nitrate and phytoplankton biomass* implies that phytoplankton can control nitrate levels in Puget Sound. Therefore, mechanisms that control phytoplankton biomass could increase nitrogen concentrations.

• We present several observations that could indicate changes in the microbial food web in Puget Sound.

Micro-zooplankton grazers (<200µm) control phytoplankton biomass in Dabob Bay, Hood Canal [3] and can consume the diatom biomass once per day [4]. We confirm that phytoplankton biomass and ammonium track one another following blooms (Fig. 7). We propose that findings in Dabob Bay might apply to the larger Puget Sound region.

• A shift from a copepod- to a micro-zooplankton-dominated food web can reduce the energy flow to higher trophic levels (more trophic levels) and reduce carbon export to depth.

Abundant flagellate blooms in Puget Sound [2] (Fig. 5) and *Noctiluca* have been implicated in coastal eutrophication [5]. *Noctiluca* feeds on diatoms, copepod eggs, fecal pellets [5].

• The export of organic material from a micro-grazer-dominated food web retains nutrients near the surface [6]. It differs from the organic-carbon-rich, and fast-sinking fecal pellets of a copepod-dominated food web.

Evidence of a potentially reduced carbon export to depth comes from Ecology's long-term benthic monitoring program. Puget Sound-wide decreases in benthic endo- and epi-benthic detritivores can't be tied to pollutants (Fig. 4).

• We suggest a potential connection between the changes in the pelagic and benthic food webs.

We hypothesize a transition from diatom- towards a flagellates-dominated microbial food web, caused by nutrient imbalances (Fig. 9). *Noctiluca* could reinforce the process by exerting grazing pressure on diatoms while competing with copepods for resources.

• Reduced phytoplankton biomass and strong micro-zooplankton grazing could explain the nitrogen increase via increased top-down grazing control on

* (data from Fig. 1A, correlated with Fig. 2, significant negative correlation, Spearman rank corr. coef.)

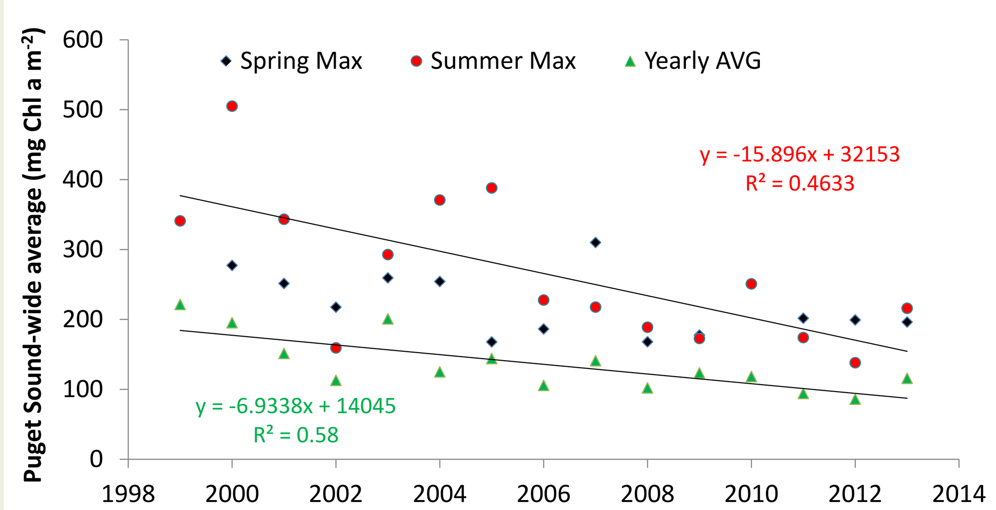


Fig. 6. Changes in the relative importance of spring and late-summer phytoplankton blooms. Long-term trends in chlorophyll a standing stock (0-50m) are decreasing (green). The decrease is predominantly driven by a decline in the late-summer phytoplankton bloom (red), yet spring blooms are unchanged (black). Data were calculated as in Fig. 1.

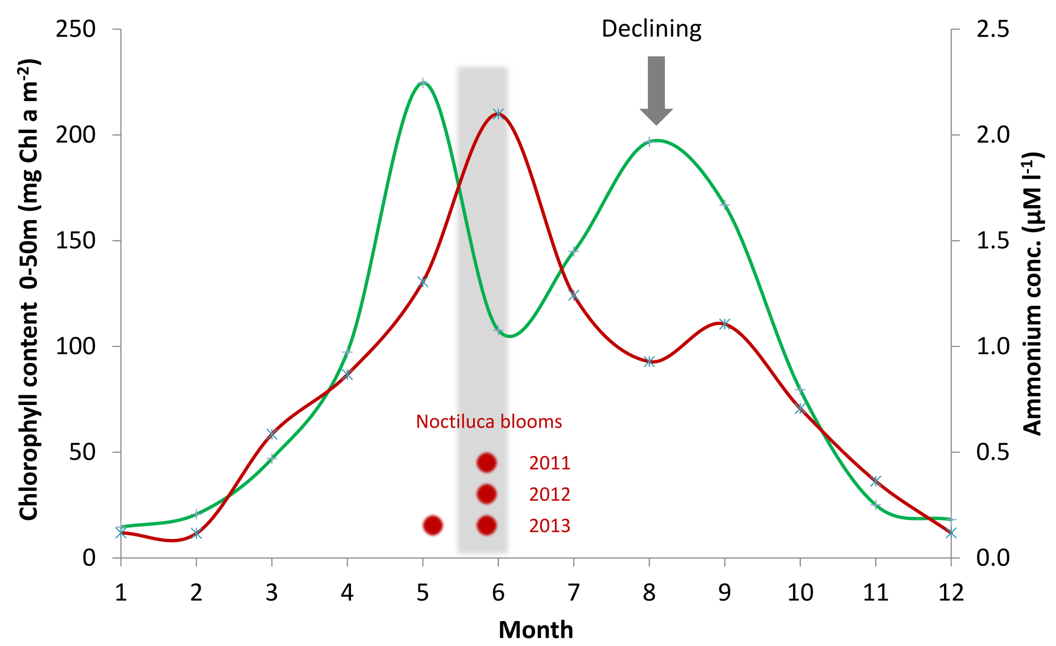


Fig. 7. Seasonal patterns of subsurface phytoplankton, ammonium, and *Noctiluca.*
Seasonal patterns of chlorophyll a (green line) and ammonium (red line) concentration across Puget Sound give insight into the seasonal coupling of the microbial food web. Both chlorophyll a and ammonium are proxies for algal standing stock and ammonium excretion by phytoplankton grazers. Two seasonal phytoplankton peaks (spring and late-summer bloom) are followed by peaks in ammonium. Seasonal data are based on 10-year Puget Sound-wide averages over the period 1999 to 2008. Data were spatially (0, 10, 30m depth) aggregated at 17 monthly-sampled stations.

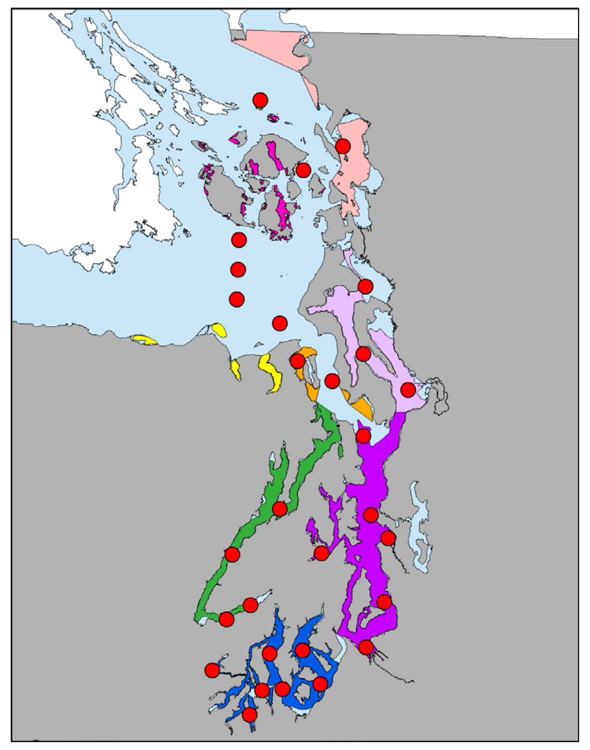


Fig. 3. Marine long-term monitoring locations in the greater Puget Sound area (southern Salish Sea). Red dots depict monthly-visited water-column stations. Colored regions illustrate benthic monitoring regions sampled using a random sampling design.

Benthos

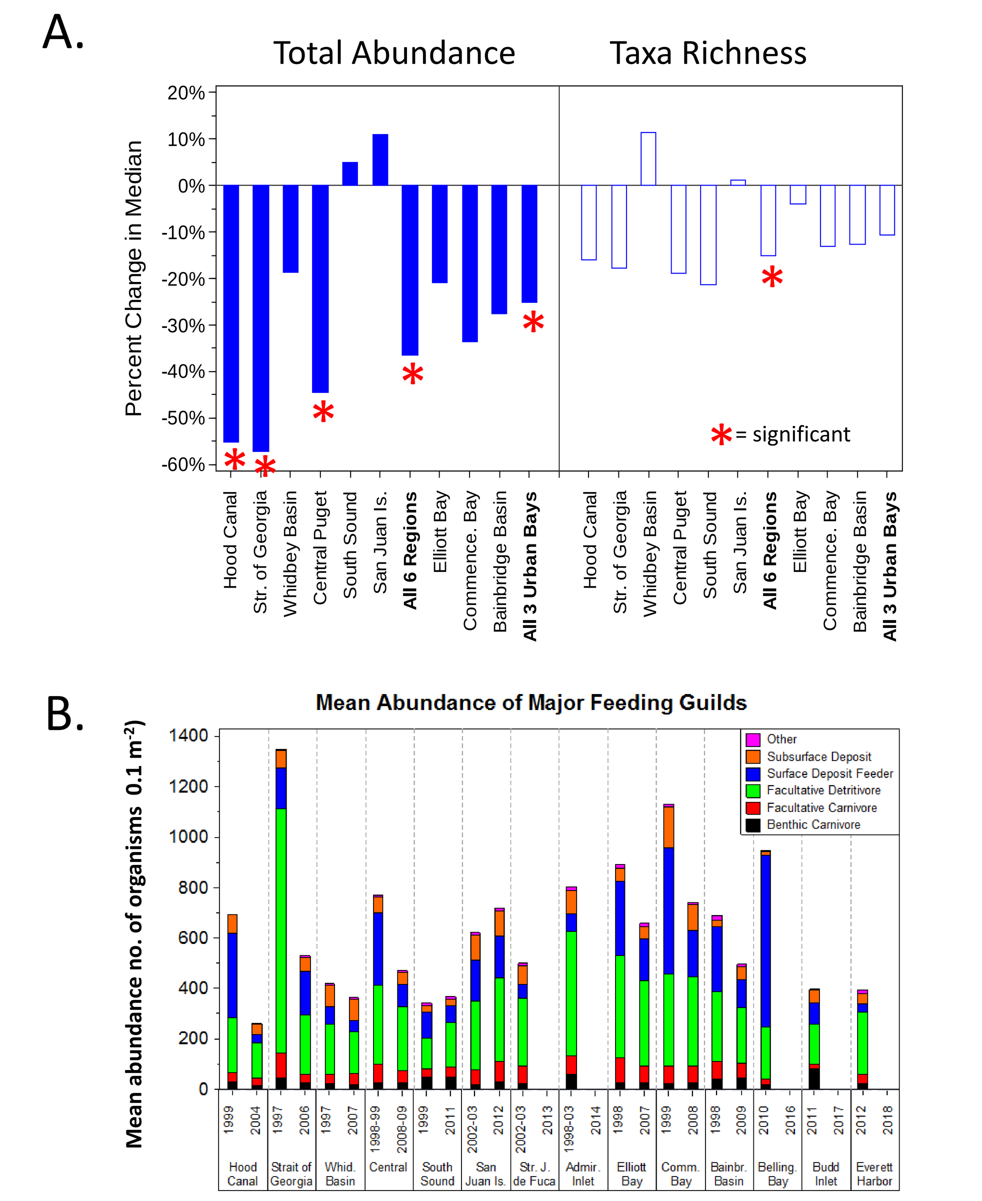


Fig. 4. (A) Changes in benthic macro-invertebrate total abundance and taxa richness (both 0.1 m^{-2}) of 6 geographic regions and 3 urban bays of Puget Sound sampled approximately a decade apart in time. Asterisks indicate statistically significant changes (Kruskal-Wallis test, α = 0.05). **(B) Functional feeding guild [7] composition of benthic assemblages in 8 geographic regions (left side of graphic) and 6 urban bays (right).** Paired baseline and resample results are given for the 6 resampled regions and 3 resampled urban bays. Sample sizes are approximately 40 for each region and 30 for each urban bay.

References:

[1] Dongyan Liu et al., 2013
[2] EOPS 2011-2013
[3] Leising et al., 2005
[4] Verity et al., 1996a; Nejstgaard et al., 1997; Landry et al., 2000a; Calbet, 2001; Suzuki et al., 2002
[5] Dodge, 1982; Fukuyo et al., 1990; Hallegraeff, 1991; Taylor et al., 1995; Steidinger & Tangen, 1996
[6] Kiørboe, 2003
[7] Macdonald et al., 2012