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NOTE

# Asynchronous shifts in the demographics of two wave-swept kelp species (Laminariales) after nearly four decades

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## Abstract

Kelp forests are among the most abundant and productive marine ecosystems but are under threat from climate change and other anthropogenic stressors. Although knowledge is growing about how the abundance and distribution of kelp forests are changing, much less is known about the "non-lethal" effects that global change is having on the performance and health of kelp populations in areas where they persist. Here we assessed the age distribution of two common stipitate kelp species, *Laminaria setchelli* and *Pterygophora californica*, at Wizard Islet in Barkley Sound, British Columbia, Canada, and compared these data to historical demographic data collected by De Wreede (1984) and Klinger and DeWreede (1988) from the same site between 1981 and 1983. We observed that *L. setchelli* populations in 2020 were younger and less evenly aged than the same populations sampled nearly four decades prior, while the *P. californica* population was composed of older individuals on average than at the historical time point. Although the drivers of these demographic changes remain unclear, Barkley Sound has experienced substantial changes in the physical and biological environment over the past decade that could be responsible for these patterns. Given that the size of an individual and its probability of reproduction increases with age, shifting demographics may impact the reproductive output of each population, potentially altering the competitive relationships between co-occurring species. Changes in size distribution may also influence ecosystem-level processes such as habitat complexity or productivity.

KEYWORDS
age structure, global change, historical ecology, kelp forests, population ecology

Marine forests formed by kelp (order Laminariales) are among the most productive (Pessarrodona et al., 2022) and widespread coastal marine ecosystems, covering more than one-third of the world's coastlines (Fragkopoulou et al., 2022; Jayathilake, 2021). However, kelp forests are threatened across much of their distribution as warming waters, changes in trophic structure, and other human-induced pressures drive declines in some places (Wernberg et al., 2019, 2024). Although a growing body of research has shown how kelp abundance is changing across much of the planet (e.g., Krumhansl et al., 2016; Wernberg et al., 2019), we have a limited understanding of how global change is impacting other aspects of performance. Environmental

**Abbreviations:** SCUBA, self-contained underwater breathing apparatus; SSWD, seastar wasting disease.

change may alter key population-level characteristics—for example, impacting growth, competitive ability, or reproductive success—which could then influence ecosystem-level processes such as productivity and habitat complexity.

In British Columbia, Canada, recent work indicates that kelp forests have faced threats from both ocean warming (Starko et al., 2022, 2024) and increases in sea urchin abundance (Burt et al., 2018; Schultz et al., 2016; Starko et al., 2022). While some kelp forests have remained stable in the face of these stressors (Mora-Soto et al., 2024; Starko et al., 2024), region-specific declines have occurred in places where these drivers have become too intense (Burt et al., 2018; Gendall, 2022; Schultz et al., 2016; Starko et al., 2019, 2022, 2024). In Barkley Sound, an area historically rich in kelp, increased sea surface temperatures and sea urchin numbers have severely impacted kelp forests, resulting in a significant decrease in the extent of kelp forest ecosystems coinciding with a large marine heatwave between 2014 and 2017 (Starko et al., 2022). This marine heatwave was associated both with unprecedented heat and with the seastar wasting disease (SSWD) epidemic that effectively removed a key benthic predator, the sunflower star (*Pycnopodia helianthoides*), from the ecosystem (Harvell et al., 2019). The loss of the sunflower star, in turn, facilitated a boom in the abundance of kelp-grazing urchins (Burt et al., 2018; McPherson et al., 2021; Starko et al., 2022).

Although recent work has shed light on how the distribution and abundance of kelp forest ecosystems are changing in British Columbia (e.g., Gendall, 2022; Mora-Soto et al., 2024; Starko et al., 2024), knowledge of population-level characteristics other than abundance is severely lacking. Changes in age distribution, for example, might be expected to coincide with changes in the environment (Boizard, 2007; De Wreede, 1984, 1986; Klinger & DeWreede, 1988), as the strength of stressors or sources of disturbance change. These changes might influence population-level reproductive output (Klinger, 1985) or the average size of individuals (DeWreede, 1986; Klinger & DeWreede, 1988), potentially altering ecosystem function. Some perennial kelp species form growth rings, which, much like tree rings, can be used to age individual kelps (Boizard, 2007; DeWreede, 1986; Klinger & DeWreede, 1988). In Barkley Sound, British Columbia, strong seasonal patterns of growth make this method of aging reliable (De Wreede, 1984; Klinger & DeWreede, 1988). This approach was used to determine the demographic structure of two stipitate kelp species (*Laminaria setchellii*, *Pterygophora californica*) in Barkley Sound during the 1980s (De Wreede, 1984; Klinger & DeWreede, 1988), revealing that environmental disturbance was a key driver of age structure.

In this study, we resampled age distributions of these two co-occurring kelp species on Wizard Islet, in Barkley Sound, to determine whether population-level demographics have changed after nearly 4 decades. These populations were originally sampled two to three times each by the original surveyors between 1981 and 1982 for *Laminaria setchellii* and between 1981 and 1983 for *Pterygophora californica*. By resampling these two species, we were able to determine whether any changes in age structure were consistent across the two species or alternatively showed opposite patterns. We reached out to the original authors to determine the exact location of these initial collections (to within ~100 m), and where possible, we followed the identical methods of the original studies. All sites were subtidal, and collections were done using SCUBA in June 2020. To account for the error in the exact location of sampling, we conducted two dives, spaced ~100 m apart along the stretch of shore indicated by the original authors (R. DeWreede & T. Klinger, pers. comm., 2000), and considered these collection dives as replicates. During each dive, vertical swaths were identified haphazardly and then systematically sampled (i.e., every plant collected along the swath) until ~15–20 individuals were collected. These swaths were repeated until sufficient sampling had occurred. In total, 146 individuals of *L. setchelli* and 167 individuals of *P. californica* were collected for age determination. Although the original methods described collecting kelp from 1 to 4 m depth, our collections were largely from 1 to 3 m depth due to an absence of kelp below this depth and an abundance of sea urchins, likely reflecting the recent change in the abundance of urchins at this site (Watson et al., 2021) and other parts of the broader region (Starko et al., 2022, 2024).

To analyze stipe rings, stipes were hand-cut into at least three cross- and/or transverse sections taken from 5 to 10 cm above the holdfast. Although sections were first checked in the lab to ensure aging was possible, sections were photographed under a dissecting microscope (with strong backlighting, Figures S1 and S2) and later used for aging. In any case of uncertainty in ring count, both the greatest and lowest number of rings possible were recorded as "minimum" and "maximum" ages. All individuals had rings counted by two to three people independently to determine this range. Using best judgment, we also assigned a "most likely" age. Together, this range of ages allowed us to assess whether any pattern might be explained by observer bias associated with interpreting ring counts. Historical stipe ring counts were extracted from the publications of De Wreede (1984) and Klinger and DeWreede (1988) using GraphClick (Arizona Software, 2010). Data are available at https://doi.org/10.6084/m9.figshare.27923565.v1. We conducted Wilcoxon tests to determine whether samples were drawn from the same distribution, and we also tested for differences in variance across each age distribution using Levene's tests. All statistical analyses were performed in R.

The age structure of both species differed between historical and resampled data. Samples of *Pterygophora californica* in 2020 were generally older than those in the 1980s: Mean age increased from 4.7 to 6.3 years (De Wreede, 1984). In contrast, *Laminaria setchellii* exhibited the reverse trend, with a younger mean age in 2020 than in 1981–1982, decreasing from 8.3 to 5.2 years (Klinger & DeWreede, 1988). These findings highlight species-specific responses within the same habitat. Variance was significantly greater in the historical dataset for *L. setchellii* (Levene's Test: $W = 123.38$, $df = 1, 546$, $p < 0.001$) but not *P. californica* (Levene's Test: $W = 1.0254$, $df = 1, 759$, $p = 0.3116$). We compared data from 2020 to each historical year independently and observed consistent results (Tables S1 and S2, Figure S3).

We determined that observer bias could not explain this change in age distributions. Regardless of whether the maximum, minimum, or most likely ring count was used, we observed the same patterns of significance (Table S1). Furthermore, age structures were mostly consistent across the two collection dives at Wizard Islet with slight but statistically significant differences in mean ages across dives for *Laminaria setchellii* (Wilcoxon Test: $W = 1647.5$; df = 1, 144; $p = 0.002$) but not *Pterygophora californica* (Wilcoxon Test: $W = 2966$; df = 1, 165, $p = 0.105$; Figure S4).

Multiple drivers may be responsible for these observed changes in age structure. Long-term monitoring data from Wizard Islet has revealed that sea urchin populations have increased at the site since the late 1980s (Watson et al., 2021). This likely explains why the original surveyors were able to sample deeper than we were. Watson et al. (2021) also hypothesized that decreases in storm intensity may have facilitated the vertical migration of urchins at this site. Deeper kelp may be less disturbed by waves during storms, potentially explaining the shift to younger ages in *Laminaria setchellii*. However, it is not clear why this would have had the opposite effect on *Pterygophora californica*. High sea surface temperatures recorded between 2014 and 2016 may have also played a role in driving these patterns. Thermal stress could have reduced recruitment or increased mortality of certain age classes, possibly explaining the younger age structures observed in *L. setchellii* (Schiel & Foster, 2006). Why this impact would be restricted to *L. setchellii*, however, remains unclear given the similar thermal tolerances of the two species (Muth et al., 2019). Interestingly, the most common age class for *L. setchellii* was between 4 and 5 years old, which would suggest these individuals recruited toward the end of the 2014–2016 marine heatwave (Figure 1).

Regardless of the underlying mechanism, the age structure of kelp forests could play a crucial role in their ecology, impacting both the resilience and functionality of these ecosystems. Mature kelp forests create complex habitats that support a diverse array of marine species (Steneck et al., 2002; Teagle et al., 2017). Larger kelp individuals contribute to structural complexity with their extensive canopies and holdfasts that provide shelter and nursery grounds for fish, invertebrates, and other algae (Steneck et al., 2002). Because age correlates with size in these species (Boizard, 2007; De Wreede, 1984; DeWreede, 1986; Klinger & DeWreede, 1988), changes in the age structure toward younger individuals could reduce the overall canopy height. Moreover, kelp forests that are homogeneous in size could have reduced structural complexity compared to forests with kelp of varying sizes. Older kelp are also capable of greater reproductive output (at least in *Laminaria setchellii*: Klinger, 1985), potentially influencing recruitment dynamics. This could slow the recovery of kelp forests after environmental disturbances or harvesting if recruitment is limited by spore production. Rates of carbon drawdown and sequestration (via cross-shelf transport; Filbee-Dexter et al., 2024) may also vary depending on the age structure of the population. Older individuals tend to have larger stipes (Boizard, 2007; De Wreede, 1984; DeWreede, 1986;

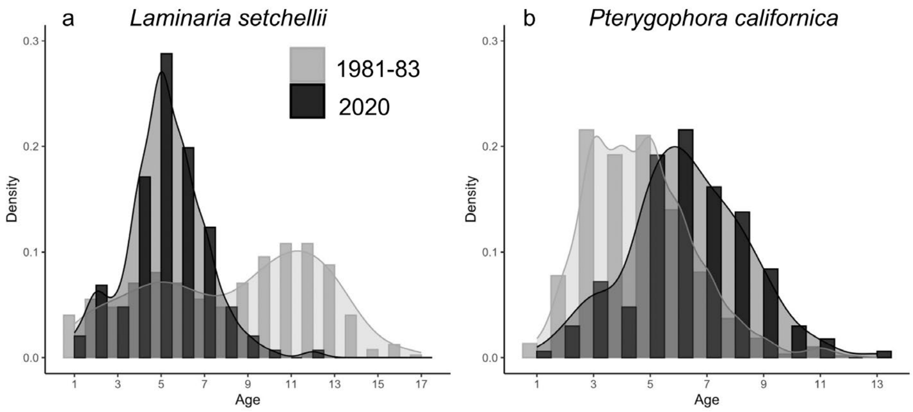

**FIGURE 1** Age distribution of two subtidal stipitate kelp species on Wizard Islet. (a) *Laminaria setchelli* age class distribution for stipes collected at Wizard Rock in 2020 (Modern, $N = 146$) and 1981–1982 (Historic, $N = 398$). (b) *Pterygophora californica* age class distribution for stipes collected at Wizard Rock in 2020 (Modern, $N = 167$) and 1981–1983 (Historic, $N = 594$).

Klinger & DeWreede, 1988), which are likely to decompose far slower than blades in these species (Wickham et al., 2020).

Understanding the future of kelp forests will depend not only on identifying changes in the distribution of these habitats but also on identifying changes in population-level characteristics of habitat-forming species. These changes may be difficult to capture but could have important implications for the functioning of kelp forest ecosystems. Future research efforts should expand on this work to better understand how environmental change and human impacts are altering the age and size distribution of marine habitats around the world.

## AUTHOR CONTRIBUTIONS

**Samuel Starko:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); supervision (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Alyssa Allchurch:** Data curation (equal); formal analysis (equal); writing – original draft (equal); writing – review and editing (equal). **Christopher Neufeld:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); supervision (supporting); writing – review and editing (equal).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** An example of a cross (top) and transverse (bottom) section of *Laminiaria Setchellii* used for aging.

**Figure S2.** Photograph showing overall microscope set-up used to age kelps of both species.

**Figure S3.** Age distribution estimated from each dive in 2020 compared with the historical data from 1981 to 1983.

**Figure S4.** Age distribution of each sample broken down by species. Top: *Laminaria setchellii*; Bottom: *Pterygophora californica*.

**Table S1.** Statistical results for each comparison made between modern and historical datasets.

**Table S2.** Statistical results for each comparison made between the modern dataset and each historical dataset separately.

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