

REPRODUCTION AND SIZE DISTRIBUTION OF PELAGIC  
CHAETOGNATHA IN THE NORTHERN CALIFORNIA CURRENT

by

AUDREY G. LILLIE

A THESIS

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was only collected from one transect and in one summer season. *Pseudosagitta lyra* had very low reproductive indices and a very large interquartile range of body lengths. Finally, *Parasagitta elegans* was the most abundant species in this region. Its reproductive index was relatively high and had the largest overall range in body lengths. This study verified seasonal and regional patterns in chaetognath life history that demonstrate these individuals' responsiveness to environmental variability, confirming their use as bioindicators of ecosystem productivity and food web dynamics.

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## Introduction

The oceans are estimated to host over two million species and over 90% of all species on Earth, most of which are microscopic and smaller (Mora et al., 2011). Many of these miniscule organisms are plankton, life forms that are small enough to be carried by tides and currents and are unable to swim with or against these forces. There are multiple ways to categorize these individuals: by their relative sizes, abilities, life cycles, or types. However, a fundamental division of plankton is whether an organism is a type of zooplankton (consumers) or phytoplankton (primary producers) (Suthers et al., 2019).

The range of organisms within heterotrophic zooplankton includes pelagic species from phyla like Mollusca (sea snails), Arthropoda (krill, isopods, ostracods), worms of multiple phyla, Cnidaria, Ctenophora, Chordata, and others (Suthers et al., 2019). Some zooplankton live in the water column for their entire life cycle while others do not. For example, larvae from larger animals often live their early lives in the dynamics of the currents, rather than on or near the sea floor (Suthers et al., 2019). These organisms consume others to survive—often eating other zooplankton or phytoplankton. Plankton play a fundamental role in ocean ecosystems and food webs and are indeed the foundation of the marine food web across the globe (Frederiksen et al., 2006). The energy-rich compounds from phytoplankton's photosynthesis are passed onto the zooplankton that consume the phytoplankton, and then are subsequently transferred to each additional level of the food pyramid.

The efficiency of the energy transfer that begins with plankton can help us understand the productivity and health of various ecosystems as well as the influence of plankton on the global carbon cycle (Poulton et al., 2006). Marine plankton play crucial roles in the cycles and sinks of nutrients other than carbon as well, especially in the context of worldwide environmental

concerns, a changing climate, and a threatened marine biosphere (Falkowski, 1994).

Phytoplankton utilize nutrients such as phosphorus and nitrogen to photosynthesize and produce organic matter—which in turn are consumed by zooplankton and larger animals (Johnson, 1957). These nutrients are eventually discarded in the form of feces or reintroduced into the food chain through decomposition and are recycled back into the ocean to repeat the same process. Plankton are the basic fuel in almost every food chain in the sea, by one path or the next, and—as a result—effectively support the diets of roughly 3 billion people in coastal communities that rely on seafood for their primary protein (Hoegh-Guldberg et al., 2019).

### *Phylum Chaetognatha*

Phylum Chaetognatha, commonly known as arrow worms or chaetognaths, are a type of fragile gelatinous marine plankton that play a large role in the marine food web due to their roles as both predators and prey (Choo et al., 2022; Patuła et al., 2023). They are the second most abundant type of zooplankton, following copepods, and can have huge effects on copepod populations as copepod predators (Saito, 2001; Venkataraman & Raghunathan, 2015).

Chaetognaths are translucent and slender, range from 2 mm to 120 mm long, and are often characterized as “bristle worms” because of the grasping bilateral spines on the ventral sides of their heads used in prey capture and consumption (Jenner, 2007).

Chaetognath reproductive biology is tightly linked to environmental conditions, including nutrient concentrations, which makes them indicator species of food web dynamics, population dynamics of their own and larger consumers, and nutrient concentrations of local waters (Stone, 2023). Tracking their reproductive status, therefore, can be used to help interpret population dynamics. Little, however, is known about their speciation and reproduction in the regions like

the Northern California Current (NCC) due to the misconception that gelatinous plankton are less important in the grand scheme of oceanic organisms (Hays et al., 2018). Compiling information about various aspects of Chaetognatha life history is a necessary first step in understanding their role in the marine ecosystems off the California, Oregon, and Washington coasts.

### *Body Plan and Species*

Morphology of chaetognaths has simplified over evolutionary time, resulting in few morphological characteristics which, while used to identify species, often makes it more difficult (Gasmi et al., 2014). Morphological features used to differentiate species include fin number and size, presence of tail fins, and ovary/body size ratio (Tokioka, 1965). As of 2015, there are 132 species identified globally, with upwards of 27 taxonomically validated species living in the northern Pacific Ocean (Bieri, 1959; Stone, 2023). Kozloff (1974) listed four species in the Puget Sound and British Columbia: *Parasagitta elegans* (Verrill, 1873), *Eukrohnia hamata* (Möbius, 1875), *Sagitta decipiens* (Fowler, 1905), and *Sagitta lyra* (Krohn, 1853), with *S. elegans* thought to be the most common. Tokioka (1965) divided the genus *Sagitta* into multiple genera including *Parasagitta*; the main difference between the two lies in intestinal morphology. Kozloff (1974) distinguished *Parasagitta elegans* from others in the North Pacific by the position and size of its two lateral fins. This species is found in many waters of the northern hemisphere, from about 40°N to the Arctic, and is the most abundant species in the upper 200 m of the Pacific Ocean (Terazaki & Miller, 1986; Bieri, 1991).

## *Environmental Effects & Life Cycle Dynamics*

The large masses of water called gyres that circulate within oceans tend to maintain relatively small ranges of environmental factors such as temperature, dissolved oxygen (DO), and salinity, which keeps various animal populations somewhat separate due to their various physiological tolerances (Stone, 2023). For example, the southern boundary of the Pacific Subarctic Water Mass at 40°–41°N has been documented as the southern boundary of *P. elegans* (Bieri, 1959). Similarly in the Southern Hemisphere, there are differences in the abundance and sizes of *E. hamata* within the Antarctic Circumpolar Current (ACC) and south of its southern border, which separates the warmer, eastward flowing ACC in the north, and the colder westward-flowing Coastal Current in the south (Terazaki et al., 2013).

Without the ability to confirm speciation using methods like DNA Barcoding (Bucklin et al., 2011), understanding the biological responses of different cohorts of chaetognaths is the first step in comprehending their ecological role in the NCC. Pauly et al. (2021) showed that chaetognath body length increased with decreasing sea surface temperature, a result of metabolic rate (i.e., O<sub>2</sub> consumption). Grigor et al. (2017) also noted that, in colder regions where resource availability comes in pulses, *E. hamata* and *P. elegans* typically have longer life spans (at least two years), which allows for larger adults due to the extension of growth periods. Conversely, chaetognath life cycles are often shorter and sometimes completed in one season in temperate and tropical waters (Russell 1932; Pauly et al., 2021).

Large sizes in chaetognaths reflect higher feeding rates and growth, and many population changes reflect those of other zooplankton (Stone, 2023). Upwelling of cold water increases zooplankton abundance due to the influx of nutrient availability (Purushothaman et al., 2021). Chaetognaths are secondary consumers, preying on zooplankton like copepods (Baier & Purcell,

1997). Class Copepoda consumes phytoplankton, which rely on sunlight and nutrients like nitrogen and phosphorus, therefore making the predators of copepods tertiary reliant on the sun (Keppel et al., 1991; Ho et al., 2025). Some research also suggests that chaetognaths feed on fine particulate and DO matter, a process that would indicate a direct link between chaetognath feeding and nutrient concentrations (Casanova et al., 2012).

### *The Northern California Current*

The Northern California Current (NCC) is the cold eastern boundary current system of the North Pacific Gyre that extends from northern California to southern British Columbia (~25°N to 50°N) (Hickey, 1979). Its circulation is influenced by seasonal winds: during the spring and summer months, southward winds drive coastal upwelling, bringing cold, nutrient-rich water from deep oceanic waters to the surface (Huyer, 1983). Upwelling supports high primary production including dense phytoplankton blooms (Yoder et al., 1984). Fall and winter months have opposite dynamics: northward winds force downwelling, resulting in lower surface nutrients and biological productivity.

The NCC supports diverse marine organisms of all sizes, a food web supported by oceanic drivers (Briseño-Avena et al., 2020). Upwelling intensity, freshwater input, and other factors impact species distribution, recruitment success, and other food web dynamics (Hickey, 2008).

In addition to nutrient-rich upwelling and significant freshwater inputs, the Pacific Northwest region and surrounding coasts have a broad continental shelf, and a high density of shelf-break canyons, which help to intensify upwelling and enhance the retention of upwelled nutrients (Davis et al., 2014). Currents and circulations in the water that can be the consequences of canyons, tides, and downwelling tend to retain nutrients brought to the system by upwelling

and river runoff. Shelves act as a sort of buffer between coasts and the open ocean, sometimes resulting in pronounced nutrient levels, but other times have less DO from agricultural and wastewater release (Diaz & Rosenberg, 2008). Retention time of high-nutrient waters in the region can have significant consequences in the ocean. Nutrient fluxes support primary productivity, which may in turn support higher trophic levels but may also result in algal blooms (Brokaw et al., 2024). Together, these oceanographic and biological processes make the NCC an ecologically and economically valuable system.

### *Reproduction and Seasonal Patterns*

Chaetognaths are hermaphrodites, meaning they possess both male and female organs. Each individual has a pair of testes near the tail with sperm stored in seminal vesicles, and a pair of ovaries that develop eggs closer to the middle region of the body (Terazaki and Miller, 1982). Hermaphroditism alone allows flexibility in reproduction when a sexual partner is not available.

Fertilization is typically internal. During copulation, sperm (in the form of spermatophores, or sperm packets) is deposited at another individual's seminal receptacle, a tube along the length of the ovary (Alvariño, 1990). It was once thought that sperm was extruded to the water and that movement of ciliary epithelia at the opening of the oviducts concentrated the sperm toward the other chaetognath's ovaries. However, this was later refuted: not all chaetognaths have ciliary epithelia. Instead, spermatophores are deposited directly into a partner's body, which also improves efficiency. During incubation, chaetognath eggs surpass the larval stage and emerge from the incubating parent as juveniles, which reduces vulnerability to predation (Stone, 2023). Species sometimes have varying hatching strategies. *P. elegans* releases buoyant eggs directly into the water, whereas other species retain them for some time in the fins of adults (Alvariño, 1968; Kotori, 1975). Reproductive measurements serve as both demographic

metrics and a basis for understanding an individual's nutritional state and health, indicated by gonad index (gonad size: body size). Well-fed chaetognaths will allocate more resources to gonads, presumably leading to increased reproductive output (Alvariño, 1968). Conversely, less nutrient availability will lead to decreased gonad growth, and lower reproductive output.

Chaetognatha reproductive cycles are seasonally synchronized with nutrient availability, DO, temperature, and other water conditions that increase prey for juveniles (Alvariño, 1990; Pauly et al., 2021; Stone, 2023). In addition to Grigor et al. (2017) which found that in cold Arctic waters *P. elegans* and *E. hamata* had life spans that lasted two or more years, Ramírez et al. (2017) found that *P. elegans* produced a brood between summer and autumn, during peak production and in waters near the surface. Newborns were continuously observed from July to February. In wintertime, the species exhibited vertical migration to live in meso-pelagic waters alongside *E. hamata*, and neither grew, nor reproduced, during the season. Some species, like Southern Ocean-inhabiting *E. hamata* and *Parasagitta gazelle*, are characterized by spawning in deeper ocean waters, followed by an juveniles' upward vertical migration during development, then a return to deeper layers to reproduce once again (Samemoto, 1987; Øresland, 1990).

Overall, abundance of chaetognaths has been observed to be highest in the summer (Zo, 1973; Terazaki & Miller, 1986; Wu et al., 2014; Stone 2023). In Nova Scotia, *Parasagitta elegans* generally employs two seasonal periods of egg development, in spring and autumn (Zo, 1973). However, the number of autumn-hatching individuals is noted to be much fewer than the number of those born in the spring. The fall hatchlings' growth halted during the winter months until warmer temperatures and increased food levels drove further maturation. At Ocean Station P in the subarctic Pacific, total numbers of *P. elegans* in summer months were approximately 5 times those of fall and winter—increasing sharply in May and June, and staying decently constant

from November to April, possibly due to low mortality rates (Terazaki & Miller, 1986). In a South Carolina estuary, spring and summer months also exhibited populations dominated by juveniles, whereas adults oftentimes dominated other parts of the year (Stone, 2023). In the South China Sea, chaetognath abundance was highest in warmer summer months as well (Wu et al., 2014).

### *Study Objectives*

The primary objectives of this study were to track fluctuations and proportions of body size and reproductive indices of sexually immature and mature chaetognaths, measured by body and ovarian dimensions, within samples from different times of the year. These demographic proportions may provide insight into recruitment success, population structure, and growth rate. By contributing to the study of northeast Pacific Chaetognatha and providing insight into their reproductive and population patterns in the context of environmental factors and a changing climate, this work aims to fill critical knowledge gaps about how these organisms function as indicators of ecosystem productivity and resilience in one of the world's most economically important coastal regions. Through analysis of reproductive patterns and body size distributions across seasons, this study will elucidate the life cycle strategies of chaetognaths in the NCC and their sensitivity to the oceanographic variability that characterizes this system.

Chaetognath body morphology is an indicator of ecosystem health, productivity, and oceanographic conditions in the face of climate change via nutrient pulses. In the context of the Northern California Current—a highly productive yet dynamic ecosystem susceptible to warming and changing upwelling patterns—understanding chaetognath speciation, life cycles, and reproductive responses is crucial for assessing how this region's food webs may shift under future climate scenarios.

## Methods

### *Biseasonal Transect Collection*

We collected samples aboard four research cruises off the Oregon and Washington coasts in the summers (2022-07-20 to 2022-07-28 and 2023-08-10 to 2023-08-18) and winters (2022-03-03 to 2022-03-11 and 2023-02-17 to 2023-02-26) of 2022 and 2023. Cruise transects extended east of six ports starting at the southernmost Rogue River (RR, 42.5008433°N), followed by Heceta Head (HH, 43.98962077°N), Newport Hydrographic (NH, 44.6509198°N), Cape Meares (CM, 45.47994333°N), Columbia River (CR, 46.16872126°N), and Grays Harbor (GH, 47.10287132 °N) in mid-Washington (Figure 1). In the winter of 2023, sampling from Cape Meares and Rogue River was cancelled due to storms. Each transect consisted of either 4, 5, or 6 stations. Samples were collected at fixed locations primarily during the day, using a coupled Multiple Opening-Closing Net and Environmental Sampling System (MOCNESS; 333- $\mu$ m mesh) in the upper 25 m of the water column that could be controlled from a remote system. After nets were recovered, chaetognaths were selected by hand for photographing, then placed into storage for future use. At each station, data from a Conductivity, Temperature, and Depth Sensor (CTD) was taken from surface to the bottom or to 100 m surface depth for deeper sites. Data included measurements of temperature, salinity, oxygen, chlorophyll-*a* fluorescence, and pH.

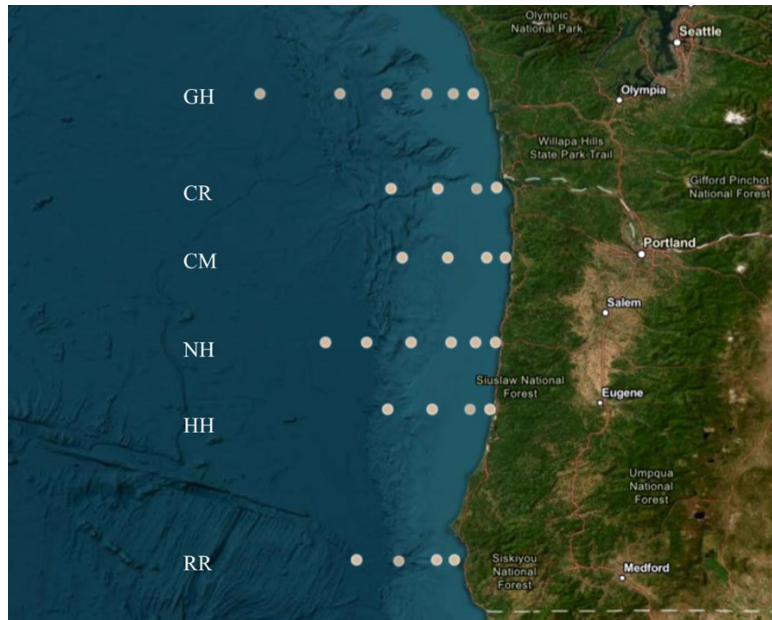


Figure 1: Map of cruise transects and study stations (Esri)

Study region was off the coasts of Oregon and Washington, USA. Study stations shown as dots, transect acronyms in white.

### *Photography, Image Analysis, & Morphometric Data*

Photographs were taken with a Nikon D850 DSLR. Individuals were laid into dishes with minimal overlap, and their tails were straightened as well as tools would allow. Several images were taken of the specimens in each petri dish alongside a small ruler for scale, and each was labeled with subsample information. ImageJ3 1.8.0 software (Abràmoff et al., 2004) was used to take digital measurements of each chaetognath. Using the segmented line tool, body length and width measurements were taken with the highest possible accuracy (Figure 2). Occasionally, there was damage to the body during collection, primarily in the tail region. Such individuals were eliminated from the sample pool. The freehand selection tool was used to measure the elliptical ovaries. Measurements were saved as .csv files, and copies of the images with measurement boundaries displayed on top of them were saved as .tif files.

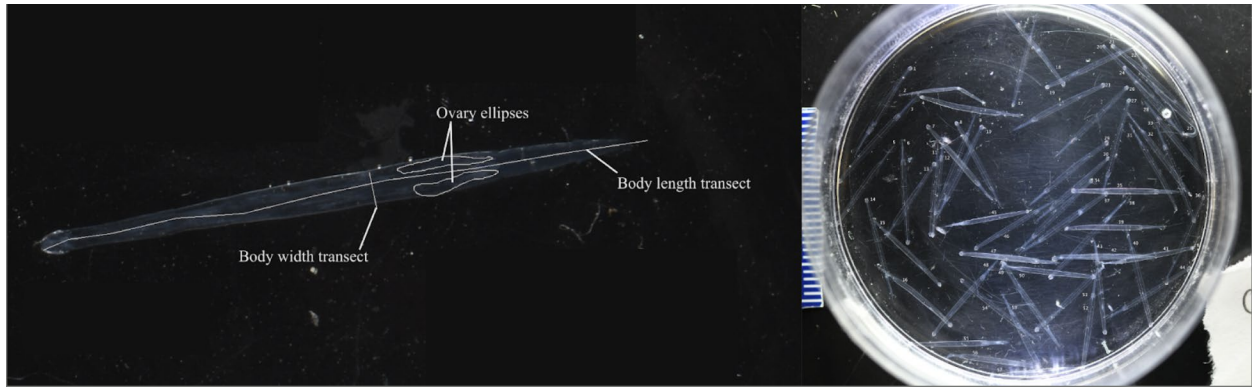


Figure 2: Measurement process on ImageJ software

Body length measured as a transect from anterior tip (head) to posterior tip (tail), body width measured at the visually widest part of the organism's midsection. Ovaries measured as ellipses.

### *Data Analysis*

All data were originally compiled into Google Sheets and Microsoft Excel (16.84), where all simple quartile and proportional measurements were performed. Morphometric data analysis and graphing was done in R 4.5.1 and RStudio 2025.5.0.496. ArcGIS (ESRI) was used to map the transect study locations. Body ellipse area was measured using the equation:

$$A = \pi (\text{body length} \div 2) (\text{body width} \div 2) \quad (1)$$

Reproductive index was measured as the ratio between each individual's average ovary ellipse area ( $\text{mm}^2$ ) and body area ( $\text{mm}^2$ ). The use of area as the metric for this ratio stood in lieu of a volume-based measurement to avoid organ volume overestimation. Previous categorizations of chaetognath reproductive maturity have used the fraction denoting how far the gonad extends over the body's length, so the use of area instead may give us additional confidence in reproductive index ratio estimations (Alvariño, 1967).

### *Statistical Methods*

Welch's t-test was used to compare seasonal differences between body lengths, body widths, body ellipse areas, ovary areas, and body area to ovary area ratios. One-way ANOVA tests and posthoc Bonferroni-corrected pairwise tests were used to compare differences across transects of body length and reproductive index. Pairwise comparisons using a Wilcoxon rank sum test and Benjamini-Hochberg (BH) p-value adjustment method were used for comparing body length and reproductive index among identified species to adjust for unequal group sizes, which otherwise violated normal t-test assumptions. Two-way ANOVA tests and post-hoc analysis using estimated marginal means (EMMS) were used to compare transect location, shelf position, and their interactions with body length and reproductive index.

Lab members previously identified a portion of collected individuals to the species level. The same data analyses were done on these individuals. For measurements regarding reproductive index, most were completed using only the specimens that had present ovaries. For the stated analyses that were done using individuals without any ovaries, and their reproductive index was listed as '0.0.'

To identify zones of upwelling, we used chlorophyll-*a* fluorescence measurements as a proxy for likely upwelling along with shelf position due to mechanisms of water retention that keep water masses containing phytoplankton-fueling nutrients on the continental shelf. Analysis of fluorescence versus seafloor depth indicated that the continental shelf lay at seafloor depths of 250 m and less, while samples taken deeper than 250 m were designated as past the shelf break.

## Results

### Surface Temperatures

A

2022		Summer		Winter	
Depth (m)	Mean temp (°C)	Standard Error	Mean temp (°C)	Standard Error	
5	13.425	2.888	12.659	0.512	
25	12.005	2.595	9.014	0.478	
100	7.905	0.589	8.593	0.434	

B

2023		Summer		Winter	
Depth (m)	Mean temp (°C)	Standard Error	Mean temp (°C)	Standard Error	
5	15.460	3.471	8.960	0.475	
25	13.595	3.653	9.090	0.388	
100	8.298	0.496	8.664	0.573	

C

2023-2023		Summer		Winter	
Depth (m)	Mean temp (°C)	Standard Error	Mean temp (°C)	Standard Error	
5	14.480	3.336	8.976	0.492	
25	11.049	3.043	9.046	0.440	
100	8.350	0.612	8.622	0.540	

Table 1: Average temperatures per season and year

Mean temperature (°C) and standard error listed for summer and winter of both 2022 and 2023, plus the averages of both years for both seasons. Water profile data were taken at various sea floor depths, as denoted in the table (5 m, 25 m, 100 m).

Transect	Summer			Winter		
	Mean temp (°C)	Standard Error	n	Mean temp (°C)	Standard Error	n
GH	15.0	1.96	271	8.54	0.415	333
CR	13.1	3.80	253	8.76	0.468	341
CM	14.1	3.45	220	9.05	0.269	245
NH	13.7	4.20	441	9.21	0.292	503
HH	13.9	2.29	131	9.34	0.461	335
RR	12.9	2.42	287	9.26	0.467	299

Table 2: Average surface water temperature by transect and season

Transect latitudes decrease as listed (GH to RR). Temperatures taken from 5 m surface depth. Mean temperature (°C), standard error in temperature, and number of samples listed for each season on each transect.

Transect	On-Shelf		Off-Shelf	
	Mean temp (°C)	Standard Deviation	Mean temp (°C)	Standard Deviation
GH	11.5	3.14	11.4	4.11
CR	9.51	2.13	12.3	3.99
CM	10.5	12.3	12.5	4.14
NH	9.41	1.18	13.4	4.25
HH	10.0	1.76	12.2	3.10
RR	9.71	1.22	12.0	2.75

Table 3: Average temperatures on each transect on and off the continental shelf

Transect latitudes decrease as listed (GH to RR). Temperatures taken from 5 m surface depth. Mean temperature (°C), standard error in temperature, and number of samples listed for each season on each transect. Samples on the continental shelf are denoted at those in the water column at seafloor depths less than 250 m, where those past the shelf break are denoted as > 250 m seafloor depth.

Average water temperature at 5 m depth across all stations in summer months was  $14.48 \pm 3.34^\circ\text{C}$  and during winter months  $8.99 \pm 0.49^\circ\text{C}$  (Table 1). The summer of 2023 had a large marine heat wave, connected to that year's developing El Niño climate (Table 1; Forgrave et al., 2025). Average water temperature varied minimally among transects with no consistent

relationship with latitude. Temperatures were more variable in summer months with an overall decreasing trend from north to south. The opposite effect was seen in winter months, so the northernmost transect, GH, had the greatest temperature range, while the southernmost, RR, had the least (Table 2). Surface temperatures on the shelf (< 250 m bathymetric depth) were altogether lower than temperatures off the shelf at every transect (Forgrave et al., 2025; Table 3).

## Species

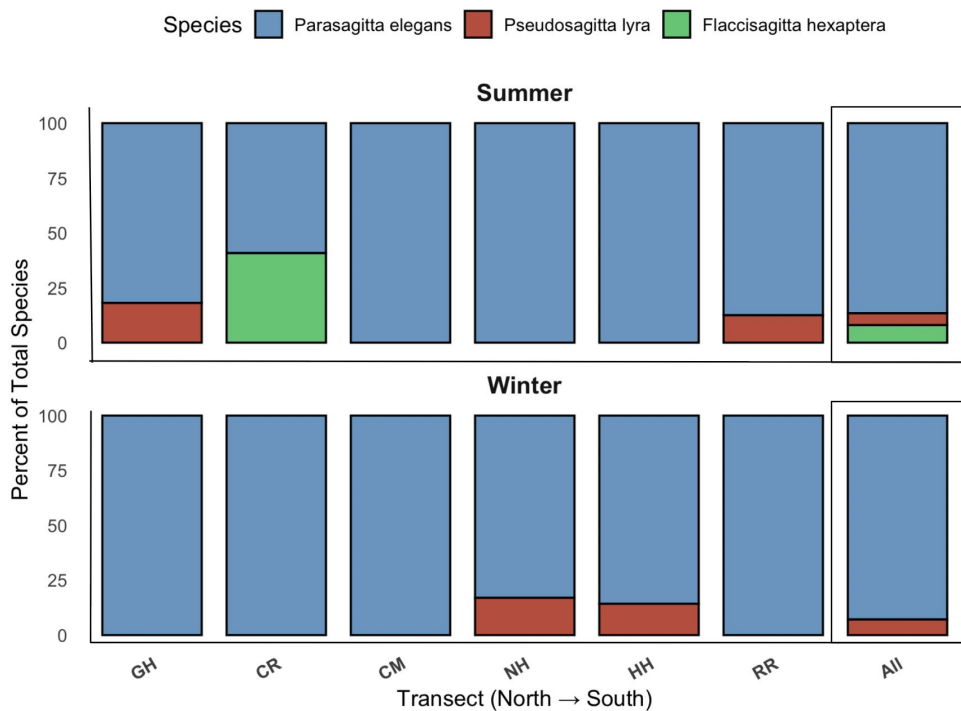


Figure 3: Species distribution across transects and seasons

Percentages of each species from total species count separated by season (summer vs winter) and by transect of collection, the latter of which decrease in latitude from left to right (GH to RR).

Average species distributions for each season listed in the final seventh column on the right.

Species and their denoted colors as the following: *Parasagitta elegans* = blue, *Pseudosagitta lyra* = red, *Flaccisagitta hexaptera* = green.

Of 3660 total specimens, 1638 were visually identified to species. *Parasagitta elegans* represented 89.7% of the identified individuals, followed by *Pseudosagitta lyra* (6.2%) and

*Flaccisagitta hexaptera* (4.1%). *F. hexaptera* was the least common, only appearing in one summer population on transect CR (Figure 3). *P. lyra* appeared in all transects except for CM and CR and appeared in both winter and summer seasons. *P. elegans* was the most prominent species on every transect and season.

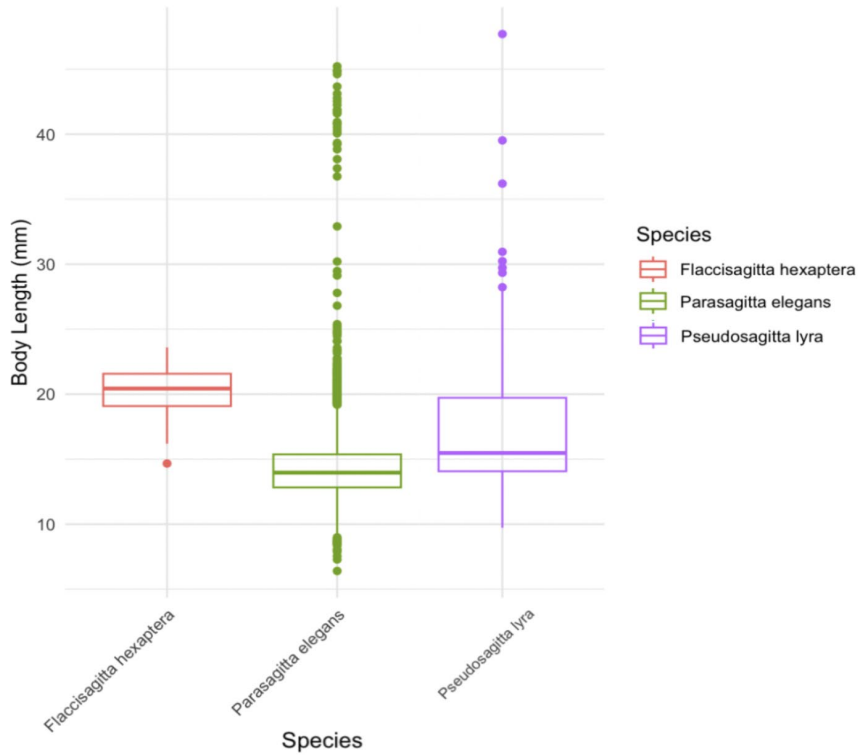


Figure 4: Body length variation between species

Species colored as the following: *Parasagitta elegans* = green (middle), *Pseudosagitta lyra* = purple (right), *Flaccisagitta hexaptera* = red (left). Measurements taken from the entire subset of identified individuals with no regard to season or region.

Factor	df	Sum Sq	Mean Sq	F-value	PR (>F)
Species	2	2846	948.6	40.96	<2 x 10 <sup>-16</sup>
Residuals	1558	36077	23.2		

Table 4: 1-way ANOVA for body lengths among species

Degrees of freedom (df), sum of squares, mean square, f-statistic and p-value measured to identify how much body lengths varied between species. Measurements taken from the entire subset of identified individuals with no regard to season or region.

Species	<i>Flaccisagitta hexaptera</i>	<i>Parasagitta elegans</i>
<i>Parasagitta elegans</i>	$< 2 \times 10^{-16}$	
<i>Pseudosagitta lyra</i>	$2.1 \times 10^{-06}$	$8.7 \times 10^{-10}$

Table 5: Pairwise comparisons of body lengths among species

Comparisons done using t-tests with pooled standard deviations for identification of how unique each species' body length was in relation to one another. Measurements were taken from the entire subset of identified individuals with no regard for season or region of collection.

Mean body length differed between species (Figure 4, Table 4:  $F_{4, 1558} = 40.96$ ,  $p < 0.0001$ ). Wilcoxon pairwise t-tests with Benjamini-Hochberg correction identified statistically significant comparisons between every species' mean body length (all  $p < 0.05$ ) except for *P. lyra* ( $p = 0.058$ ) (Table 5). *F. hexaptera* exhibited the highest median body length, followed by *P. lyra* and *P. elegans*. However, *P. elegans*, the most common species, had a large range of body lengths, from 1.1 mm (the smallest of all measured specimens) to  $> 45$  mm (Figure 3). *P. lyra* had fewer outliers but the largest interquartile range and largest range between minimum and maximum. Its largest outlier had the greatest length of all specimens, reaching 47.7 mm in body length.

Factor	df	Sum Sq	Mean Sq	F-value	PR (>F)
Species	2	0.0218	0.007283	9.257	$4.55 \times 10^{-06}$
Residuals	1554	1.2226	0.000787		

Table 6: 1-way ANOVA regarding reproductive indices per species of those identified.

Degrees of freedom (df), sum of squares, mean square, f-statistic and p-value for identification how much reproductive index varied between species. Measurements taken from the entire subset of identified individuals with no regard to season or region.

Species	<i>Flaccisagitta hexaptera</i>	<i>Parasagitta elegans</i>
<i>Parasagitta elegans</i>	$7.2 \times 10^{-05}$	
<i>Pseudosagitta lyra</i>	$4.3 \times 10^{-06}$	$7.0 \times 10^{-05}$

Table 7: Pairwise comparisons of reproductive indices among species.

Comparisons done using t-tests with pooled standard deviations to identify how unique each species' reproductive index was in relation to one another. Measurements were taken from the entire subset of identified individuals with no regard for season or region of collection.

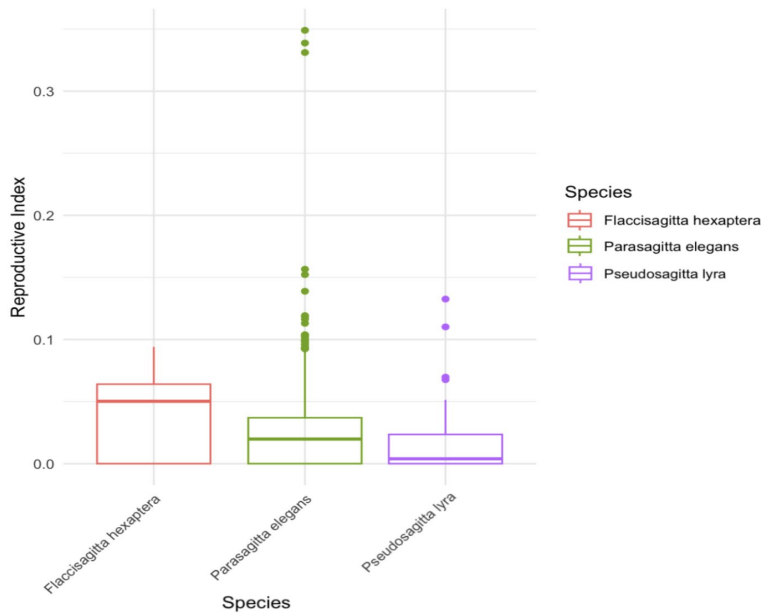


Figure 5: Reproductive indices per species.

Measurements taken from the entire subset of identified individuals with no regard to season or region. Species colored and placed as the following: *Parasagitta elegans* = green (middle), *Pseudosagitta lyra* = purple (right), *Flaccisagitta hexaptera* = red (left).

There were significant differences in reproductive index among species (Figure 5, Table 6:  $F_3, 1554 = 9.257, p < 0.0001$ ). *F. hexaptera* exhibited the highest mean reproductive index ( $0.37 \pm 0.002$  SE), followed by *P. elegans* ( $0.24 \pm 0.001$  SE), then *P. lyra* ( $0.030 \pm 0.024$  SE). Wilcoxon pairwise t-tests (applied due to unequal group sizes violating t-test assumptions) revealed significant differences between several species' pairs (Table 7). *F. hexaptera* differed significantly from both *P. elegans* and *P. lyra* ( $p < 0.0001$  for both). *F. hexaptera* had the largest

median reproductive index, followed by *P. elegans* and then *P. lyra*. Both *P. elegans* and *P. lyra* had high outliers. Outliers of *P. lyra* ranged from 0.02 to 0.14, and outliers of *P. elegans* had a range from 0.09 to over 0.35.

## Morphology

### *Seasonal & Regional Patterns in Body Size*

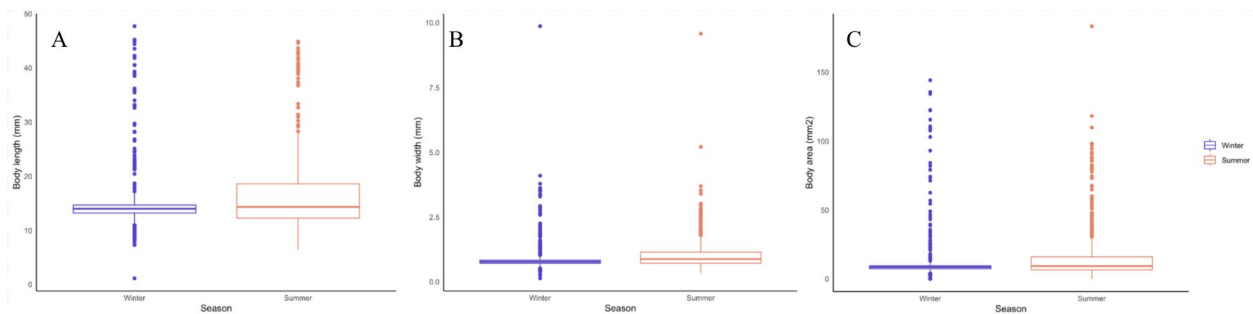


Figure 6: Sizes of individuals compared between seasons

Individuals collected in summer months are colored in orange, and those from winter months are blue. a) denotes body lengths, b) denotes body widths, and c) body ellipse areas ( $p < 0.0001$  for all). Summer individuals were larger in all three measures.

Across all specimens, chaetognath body size as measured by length, width, and ellipse area was larger in summer than in winter (Figure 6: a.  $t = 10.161$ ,  $df = 2339.1$ ,  $p < 0.0001$ ; b.  $t = 12.588$ ,  $df = 2618.2$ ,  $p < 0.0001$ ; c.  $t = 9.2823$ ,  $df = 2844.2$ ,  $p < 0.0001$ ). Those collected in summer months tended to have longer body lengths (mean = 15.664 mm) and widths (mean = 0.982 mm) with larger body ellipse areas (mean = 12.977 mm<sup>2</sup>) while the population collected in winter months had shorter lengths (mean = 14.099 mm) and widths (mean = 0.799 mm) with smaller body areas (mean = 9.272 mm<sup>2</sup>). All had exceptional statistical robustness with summer individuals averaging approximately 11% longer, 23% wider, and 40% greater in body area. The 95% confidence intervals for these differences in means (Figure 6: a. 1.263 — 1.867 mm; b.

0.154 — 0.211 mm; c. 2.922 – 4.488 mm<sup>2</sup>) all indicate small but consistent seasonal variation in body size. Absolute differences in mean measurements between seasons were relatively small (1.6 mm in length, 0.18 mm in width, 3.7 mm<sup>2</sup> in area), but the narrow confidence intervals and large sample sizes demonstrate a robust seasonal pattern across the study region in both 2022 and 2023. Additionally, of all individuals collected in winter months, 83.8% had body lengths less than 15 mm, while in summer months only 56.6% were less than 15 mm long.

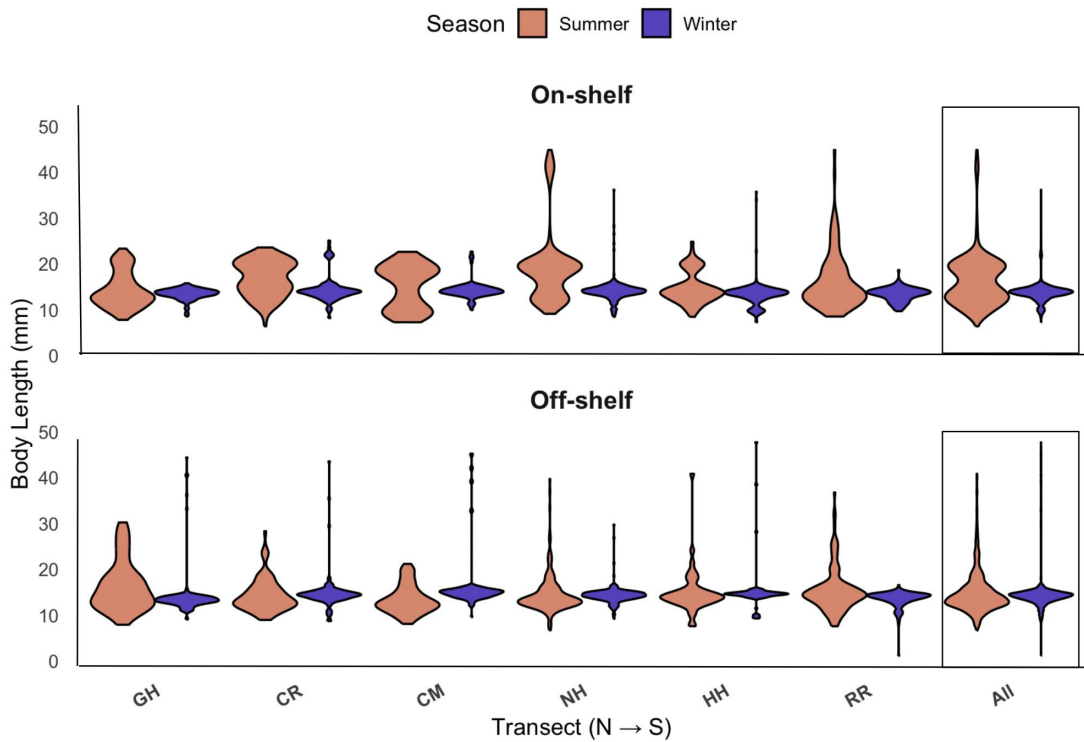


Figure 7: Mean body length variation by transect, season, and collection location

Collection location determined by on-shelf or off-shelf location (on shelf = 250 m or less, off shelf break > 250 m sea floor depth). Measurements separated by season (summer is orange, winter is purple) and by transect, the latter of which decrease in latitude from left to right (GH to RR). A final seventh category shows the average body lengths of all specimens from on the shelf and all specimens from off the shelf break.

<b>Factor</b>	<b>df</b>	<b>Sum Sq</b>	<b>Mean Sq</b>	<b>F-value</b>	<b>PR (&gt;F)</b>
Transect	5	1000	200.05	10.09	$2 \times 10^{-10}$
Residuals	3514	64499	18.35		

Table 8: 1-way ANOVA for body length among transects

Degrees of freedom (df), sum of squares, mean square, f-statistic, and p-value to determine how much of an impact transect location has on body length. Measurements taken from the entire set of individuals with no regard for season or region of collection.

<b>Transect</b>	<b>GH</b>	<b>CR</b>	<b>CM</b>	<b>NH</b>	<b>HH</b>
<b>CR</b>	0.00222				
<b>CM</b>	0.07055	1.00000			
<b>NH</b>	$4.2 \times 10^{-7}$	1.00000	0.58960		
<b>HH</b>	1.00000	0.00052	0.01932	$1.1 \times 10^{-7}$	
<b>RR</b>	1.00000	0.22691	1.00000	0.00088	0.95157

Table 9: Pairwise comparisons of body length differences among transects

Comparisons done using posthoc Bonferroni-corrected pairwise t-tests to determine how unique body length was between each transect, comparing one to another. Measurements were taken from the entire set of individuals with no regard for season or region of collection.

There was a significant effect of transect on mean body length (Figure 7, Table 8:  $F_{5, 3514} = 10.9$ ,  $p < 0.0001$ ). To identify which transects differed, a post-hoc pairwise t-test with Bonferroni correction located several statistically significant comparisons (Table 9). Body lengths were significantly different between transects CR and GH ( $p = 0.0022$ ), GH and NH ( $p < 0.0001$ ), CR and HH ( $p = 0.00052$ ), and CM and HH ( $p = 0.019$ ), HH and NH ( $p < 0.0001$ ). Other transect comparisons were not significant after correction. Mean body lengths also differ across transects seasonally. GH still showed a considerably low mean body length in winter months and had one of the smallest three mean body lengths in summer months (Figure 7). Transect NH had the highest mean body lengths of all transects in summer months. These results indicate that body size distributions were not uniform across the six transects.

## Effect of Continental Shelf Break

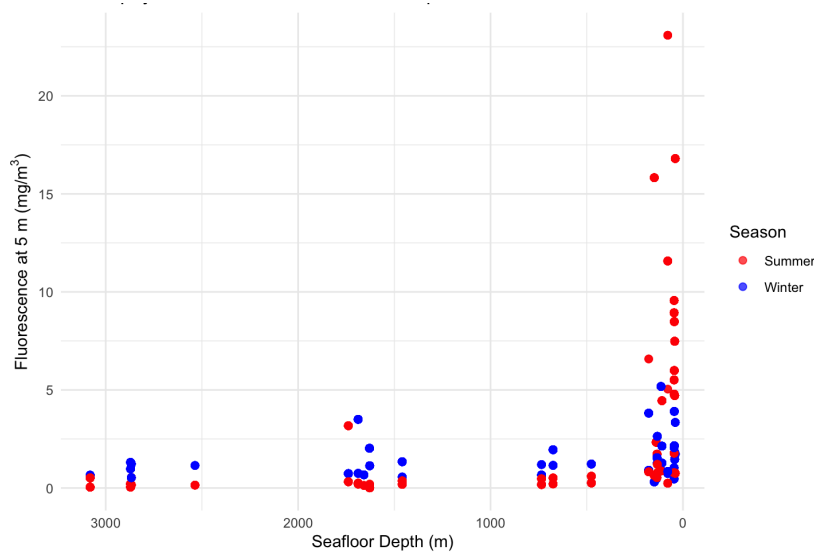


Figure 8: Chlorophyll-a fluorescence compared to seafloor depth

Fluorescence measurements taken from 5 m surface depth. Compared between seasons, summer measurements in red and winter measurements in blue. Specimens designated as on the continental shelf were taken at seafloor depths of 250 m or less, where those from off the continental shelf break were taken at seafloor depths over 250 m.

Measurements of surface chlorophyll-*a* fluorescence were high up to a sea floor depth of 250 m, and then declined where the sea floor was > 250 m. In the summer months, fluorescence was considerably higher than in winter months where the seafloor was 250 m deep or less, but winter and summer fluorescence levels differed minimally at off-shelf stations with higher depths (Figure 8). Using seafloor depth as an indication of the continental shelf break, there were indications that chaetognath morphology has a relationship to the plankton's proximity to the coast.

<b>Factor</b>	<b>df</b>	<b>Sum Sq</b>	<b>Mean Sq</b>	<b>F-value</b>	<b>PR (&gt;F)</b>
Transect	5	992	198.46	11.012	1.54 x 10 <sup>-10</sup>
Shelf Position	1	144	144.39	8.012	0.00467
Transect: Shelf Position	5	1127	225.49	12.511	4.62 x 10 <sup>-10</sup>
Residuals	3507	63205	18.02		

Table 10: 2-way ANOVA comparing transect location and shelf position to mean chaetognath body length

A two-way ANOVA test identified degrees of freedom (df), sum of squares, mean square, f-value, and p-value to determine the relationship between transect and shelf position on chaetognath body length.

<b>Transect</b>	<b>Estimate (mm): Contrast (On-Shelf – Off-Shelf)</b>	<b>Standard Error (mm)</b>	<b>df</b>	<b>t.ratio</b>	<b>p-value</b>
GH	- 0.692	0.370	3507	-1.873	0.0612
CR	1.011	0.369	3507	2.743	0.0061
CM	-0.452	0.400	3507	-1.130	0.2586
NH	1.939	0.280	3507	6.930	<0.0001
HH	-1.387	0.445	3507	-3.119	0.0018
RR	0.258	0.362	3507	0.715	0.4747

Table 11: Comparisons of shelf position on mean body length per transect

Post-hoc analysis was done using estimated marginal means (EMMs) to evaluate the effect of shelf position on body length, separated by transect. Estimates between on-shelf and off-shelf samples of mean body length are shown by standard error in difference in body length estimate, t-statistic, degrees of freedom (df), and p-value to determine the role of these two variables on body length.

There were significant effects of transect location, shelf position, and their interactions on mean chaetognath body length (Figure 7, Table 10). Shelf position had a significant effect on body length, and the interaction between transect and shelf position was also significant. These results indicate that the effect of shelf position on body area varied strongly between transects. Post-hoc analysis (EMMs) showed transect-specific differences in how much shelf position affected body length (Table 11). Transect CR exhibited significantly larger specimens on-shelf

compared to offshore of the shelf break (estimate = 1.011 mm). Transect NH showed an even more pronounced on-shelf increase to body size (estimate = 1.939 mm). However, the transect HH showed significantly smaller specimens on-shelf than off-shelf (estimate = -1.387 mm).

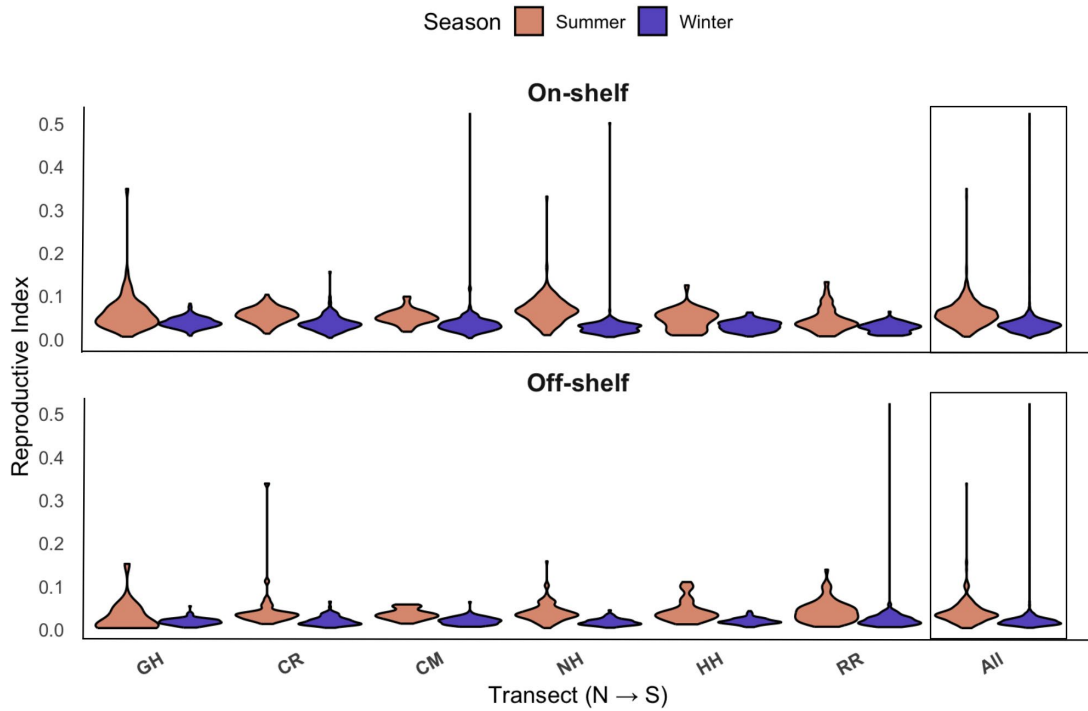


Figure 9: Mean reproductive index variation by transect, season, and collection location

Collection location determined by on-shelf or off-shelf location of collection (on shelf = 250 m or less, off-shelf > 250 m sea floor depth). Measurements separated by season (summer is orange, winter is purple) and by transect, the latter of which decrease in latitude from left to right (GH to RR). A final seventh category shows the average body lengths of all specimens, separated by on-shelf and off-shelf.

<b>Factor</b>	<b>df</b>	<b>Sum Sq</b>	<b>Mean Sq</b>	<b>F-value</b>	<b>PR (&gt;F)</b>
Transect	5	0.0147	0.00294	3.033	0.00985
Shelf Position	1	0.1339	0.13385	137.928	<2 x 10 <sup>-16</sup>
Transect: Shelf Position	5	0.03622	0.00723	7.455	6x 10 <sup>-07</sup>
Residuals	2281	2.2136	0.00097		

Table 12: 2-way ANOVA comparing transect location and shelf position to mean reproductive index

A two-way ANOVA test identified degrees of freedom (df), sum of squares, mean square, f-value, and p-value to determine the relationship between transect and shelf position on chaetognath reproductive index.

<b>Transect</b>	<b>Estimate (mm): Contrast (On-Shelf – Off-Shelf)</b>	<b>Standard Error (mm)</b>	<b>df</b>	<b>t.ratio</b>	<b>p-value</b>
GH	0.026706	0.00343	2281	7.778	<0.0001
CR	0.016046	0.00357	2281	4.494	<0.0001
CM	0.021029	0.00356	2281	5.910	<0.0001
NH	0.018361	0.00246	2281	7.457	<0.0001
HH	0.007626	0.00383	2281	1.992	0.0465
RR	0.000104	0.00357	2281	0.029	0.9767

Table 13: Comparisons of shelf position on mean reproductive index per transect

Post-hoc analysis was done using estimated marginal means (EMMs) to evaluate the effect of shelf position on body length, separated by transect. Estimates between on-shelf and off-shelf mean reproductive index are shown by standard error in difference in body length estimate, t-statistic, degrees of freedom (df), and p-value to determine the role of these two variables on reproductive index.

There were also significant effects of transect location, shelf position, and their interaction on chaetognath reproductive index (Figure 9, Table 12). Shelf position had a significant effect on body length, as did the interaction between transect and shelf position, showing that the effect of shelf position on body area varied strongly between transects. Post-hoc analysis (EMMs) showed transect-specific differences in how much shelf position affected reproductive index for almost every single transect (Table 13). All transects except RR exhibited significantly larger reproductive indices on-shelf compared to off the shelf break. RR showed

significantly smaller reproductive indices on-shelf than off-shelf (difference estimate = 0.000104 mm). Chlorophyll-*a* fluorescence measurements on transect RR did not show a pattern consistent with other transects, most of which showed higher fluorescence closer to shore (Forgrave et al. 2025).

### *Seasonal & Regional Patterns in Reproduction*

Of 3660 individuals, 2324 (63.48%) had at least one detectable ovary. Of 2057 individuals collected in the wintertime, 1521 (73.94%) had at least one ovary. Of 1603 individuals collected in the summer months, 803 (50.09%) had at least one ovary.

Average ovary ellipse area from specimens collected in summer months was consistently larger across data quartiles and had higher maximum areas compared to those collected in winter months. A two-sample t-test confirmed that the difference was significant ( $t = 14.072$ ,  $df = 879.72$ ,  $p < 0.0001$ ). The mean ovary ellipse area was nearly three times greater in the summer (mean =  $0.775 \text{ mm}^2$ ) than in the winter (mean =  $0.261 \text{ mm}^2$ ). The 95% confidence interval for this difference in means was  $0.585 - 0.442 \text{ mm}^2$ , indicating a robust seasonal effect. When the same tests were done on the dataset that included all specimens with no ovaries present (reproductive index of zero), results showed the same effect ( $t = 9.1632$ ,  $df = 879.72$ ,  $p < 0.0001$ ) with a summer mean of  $0.388 \text{ mm}^2$ , winter mean of  $0.193 \text{ mm}^2$ , and 95% confidence interval of  $0.237 - 0.153 \text{ mm}^2$ .

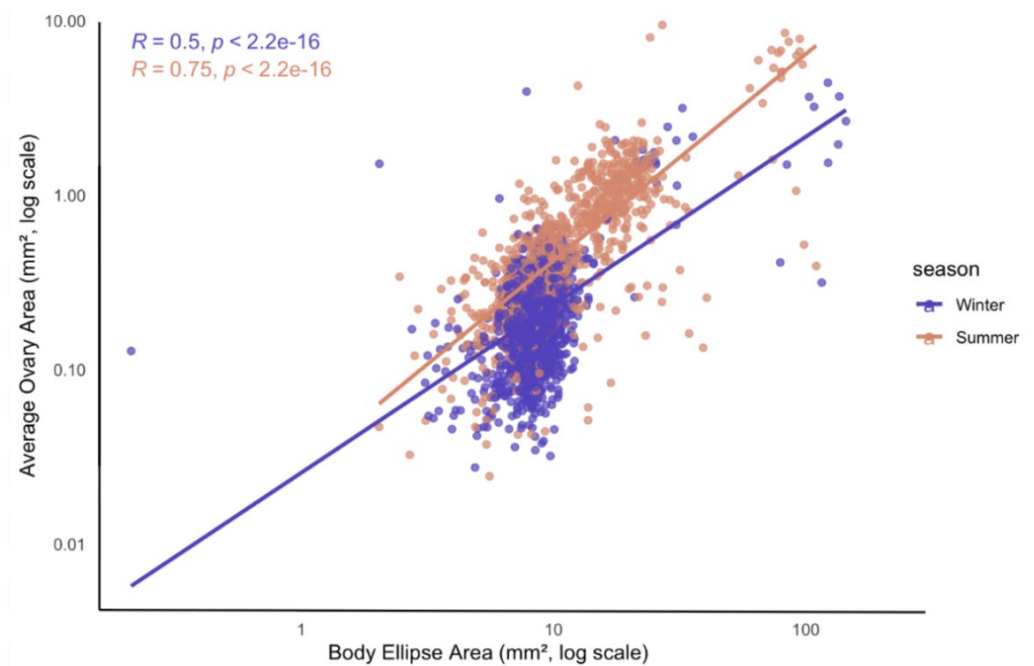


Figure 10: Reproductive index compared between collection season

Log-transformed relationships between body ellipse areas and ovary ellipse areas (reproductive index).  $R = 0.75$  for summer collections (orange) and  $r = 0.5$  for winter collections (purple) ( $p < 0.0001$ ).

Another two-sample t-test revealed a statistically significant difference in reproductive index between seasons (Figure 10:  $t = 16.984$ ,  $df = 1517.8$ ,  $p < 0.0001$ ). Chaetognaths collected in the summer (mean = 0.0510) had larger reproductive indices on average than those measured in the winter (mean = 0.0280). The 95% confidence interval for this difference in means was 0.0204 to 0.0258, showing a small but consistent seasonal variation in body length. The correlation coefficient between body area and ovary area from those collected in summer seasons was  $r = 0.75$ , and  $r = 0.5$  for winter collections.

<b>Factor</b>	<b>df</b>	<b>Sum Sq</b>	<b>Mean Sq</b>	<b>F-value</b>	<b>PR (&gt;F)</b>
Transect	5	0.0147	0.002943	2.824	0.0151
Residuals	2287	2.3837	0.001042		

Table 14: 1-way ANOVA for reproductive index per transect.

Degrees of freedom (df), sum of squares, mean square, f-statistic, and p-value to determine how much of an impact transect location has on reproductive index. Measurements taken from the entire set of individuals with no regard for season or region of collection.

<b>Transect</b>	<b>GH</b>	<b>CR</b>	<b>CM</b>	<b>NH</b>	<b>HH</b>
<b>CR</b>	1.000				
<b>CM</b>	1.000	1.000			
<b>NH</b>	1.000	1.000	1.000		
<b>HH</b>	0.634	0.036	1.000	0.085	
<b>RR</b>	1.000	0.197	1.000	0.487	1.000

Table 15: Results from Pairwise T-test regarding reproductive index differences between transects.

Comparisons done using posthoc Bonferroni-corrected pairwise t-tests to determine how unique reproductive index was between each transect, comparing one to another. Measurements were taken from the entire set of individuals with no regard for season or region of collection.

An ANOVA test indicated that the mean reproductive index also differed among transects. Results indicated an effect of transect on body length (Figure 9, Table 14:  $F_{5, 2287} = 2.824$ ,  $p = 0.0151$ ). Post-hoc pairwise t-tests with Bonferri correction identified statistically significant comparisons between transects HH and CR (Table 15:  $p = 0.036$ ).

## Discussion

This study clarified strong environmental and taxonomic relationships among body size, reproductive investment, and oceanographic conditions of the Northern California Current (NCC). Pronounced seasonal patterns in chaetognath growth and reproductive output demonstrated that the individuals in this region are responsive to environmental variability, confirming their use as bioindicators of ecosystem productivity and food web dynamics.

### Species

Of the species that have already been identified, there were significant differences between measurements of both body length and reproductive index, an indication that the NCC hosts chaetognaths with many diverse forms and life history strategies. The species identifications within our subset of individuals agreed with those that have been identified in this Pacific Northwest region by previous studies, like Kozloff (1974).

*Flaccisagitta hexaptera* exhibited the highest median reproductive index ( $n = 67$ ), suggesting that this species allocates a relatively large proportion of body resources to reproduction in comparison to other species. This could represent a strategy suited to variable environments where rapid reproduction maximizes fitness. *F. hexaptera* only appeared in samples taken at the station nearest the coast on transect CR in summer months, indicating that its presence in this region is uncommon and possibly seasonal. This species has been noted in samples solely on the shelf in other regions, which aligns with our findings (Noblezada & Campos, 2008). *F. hexaptera*'s large body size and huge reproductive index are significantly different from both *Parasagitta elegans* and *Pseudosagitta lyra*.

*Pseudosagitta lyra* had a low mean reproductive index over a large sample size ( $n = 102$ ). This species was collected in both winter and summer months and was found on the majority of transects. These results indicate that this species either has a reproductive index unique to its species, or it reproduces at seasons or times that were not part of our sampling process.

*Parasagitta elegans* exhibited an intermediate mean reproductive index. We made the conclusion that this species' overall life history patterns align with the aspects that this study has commented on, based on its large sample size ( $n = 1469$ ). *P. elegans* is by far the most abundant chaetognath in the Northern California Current. Not only did it dominate every single transect but dominated both seasons as well. Its high mean reproductive index reflects the prominent patterns of what this study has concluded.

### **Seasonal Patterns in Body Size**

There were distinct seasonal differences in the patterns of Phylum Chaetognatha collected from the NCC. More individuals were collected in winter months even though more samples were taken in summer months. The region from which specimens were collected ( $> 25\text{m}$  depth from sea surface) exhibited much higher temperatures in the summer than in the winter, showing that even though upwelling is known to bring cooler temperatures from the deep ocean, it may not be enough to offset surface temperatures. This could have been influenced by especially high summer temperatures in 2023 due to that year's impressive heat wave and warrants additional years for study. This negative correlation between abundance and surface water temperatures contradicts other studies that claim abundance is associated with higher water temperatures (Terazaki & Miller, 1986; Wu et al., 2014).

The specimens collected in summer months were altogether larger than those collected in winter months as seen in all morphometric measures, confirming other studies that state that chaetognath body length increases with decreasing temperatures (Pauly et al., 2021). This discrepancy could be an indication of an overwintering period and the seasonality of chaetognath life cycles (Terazaki & Miller, 1986; Samemoto, 1987; Øresland, 1990; Stone, 2023), and is more likely an effect of the nutrients provided from seasonal upwelling rather than cooler water temperatures.

Larger chaetognath body size in summer suggests an increase in nutrient availability in the summer months, likely driven by coastal upwelling (Purushothaman et al., 2021). The coastlines adjacent to the NCC experience prominent seasonal upwelling dynamics from spring through summer, bringing deep, cold, nutrient-rich waters from the deep ocean to the surface. With an increase in nutrients and sunlight, primary producers exhibit an increase in biomass, leading to cascading effects throughout the food web. As carnivores feeding on copepods and other zooplankton, chaetognaths are responsive to these pulses in productivity. Larger body sizes in summer suggest that these individuals have experienced accelerated growth rates compared to those collected in the winter, indicating enhanced feeding conditions and the potential ability to grow into larger adult sizes before reaching reproductive maturity (Pauly et al., 2021). Based on the smaller proportions of body sizes in winter months, and a rise in average body size in the upwelling season, it is likely that the chaetognaths in this region have a life span around one year.

## Regional Patterns in Body Size

There was not a direct relationship between chaetognath body length and latitude. However, individuals collected at different transects did show several statistically significant variations from one another in body length. The northernmost transect GH, 47.10° N, yielded measures that were significantly different than CR and NH, suggesting that it may have a distinct size-structured community. The mean size of GH individuals was smaller than all other transects, especially in winter months. Temperatures at transect GH were lower than all other transects in winter months, but higher than all other transects in summer months, which indicates that there is a reduction of upwelling in this region. The cohort of chaetognaths living in this region may be able to tolerate drastic seasonal temperature variations more than others.

Transect HH, 43.99° N, was distinct from CR, CM, and NH in chaetognath morphology, suggesting that it may also be unique ecologically or oceanographically. After Bonferroni correction, other adjacent transects did not stand out as significantly different, suggesting more gradual transitions between cohorts, if any. Elevated body lengths during summer months at NH, lower lengths at GH, and the uniqueness of HH suggest that latitudinal ranges in upwelling intensity or prey communities' structure chaetognath growth patterns. At the very least, these results illustrate that body size distributions were not uniform across the six transects and corroborate that body size varies with region.

The results from this study hint at the presence of distinct subpopulations within the region that have different size structures or ecological responses. If there are separate populations of chaetognaths living within the same region (i.e. transect) and therefore experiencing the same environmental dynamics, differences in their physiological or morphological responses is most likely at the species level. The presence of the northernmost community that is overall smaller

than the rest of the individuals collected, which also withstands the highest temperature variations, indicates the presence of uniquely adapted populations.

The NCC exhibits substantial mesoscale variability upwelling patterns with certain regions experiencing more persistent upwelling or stronger nutrient retention that may concentrate prey and support enhanced chaetognath growth. Statistical significance in body length across transects may be an indication of these upwelling patterns and surface retention patterns, corroborating previous studies (Purushothaman et al., 2021; Brokaw et al., 2024). Phenotypic variation may be driven by some of these changing environmental gradients like temperature, where cooler northern waters are known to have slower developing, but larger, cohorts of chaetognaths (Grigor et al., 2017). Different communities exhibiting unique life history stages may also be localized in different regions. It is also possible that these groups of individuals belong to different species.

The significant effects of shelf position on body size and reproductive index further provide evidence that regions of upwelling shape chaetognath life history. There is a sharp decline in chlorophyll-*a* fluorescence concentrations where the seafloor is deeper than 250 m, confirming that the shelf break represents a distinct boundary in primary productivity (Yoder et al., 1984). This boundary would have cascading effects through the food web, influencing chaetognath populations as well as those of their prey and predators.

At multiple transects (CR, NH, GH, CM, HH for reproduction, CR and NH for body size), on-shelf populations exhibited larger body sizes and reproductive indices than off-shelf populations. This pattern strongly suggests that waters on the shelf provide more favorable feeding environments, most likely due to the elevated prey densities associated with upwelling-driven productivity. The on-shelf advantage was particularly pronounced at transect NH, where

specimens average 1.9 mm longer on-shelf—a difference representing approximately 13% of mean body length. There was a notable exception at transect HH, where off-shelf individuals were larger in both body area and length. This discrepancy merits further investigation: the reversal may reflect local hydrographic features or species composition, but in one case or the next requires more sampling.

It may be beneficial for further work to compare chaetognath morphological metrics to specific upwelling indices, nutrient levels, and water temperatures to clarify exactly what biological effects upwelling has on these organisms.

### **Seasonal Patterns in Reproductive Status**

There was a much larger proportion of individuals collected in winter months that had one or more ovaries than in the summer months, indicating a higher presence of mature individuals in winter months, and in turn more individuals that were spent or had yet to grow an ovary in summer months. However, a larger proportion of small (<15 mm length) chaetognaths existed in winter months than in summer months. The indication is that there is a brood of chaetognaths in late summer/fall months. It also alludes to the possibility that chaetognaths mature at sizes that are not their maximum, which corroborates other studies that consider this idea (Pauly et al., 2021; Stone, 2023).

Additionally, a nearly three-fold increase in average ovary area and two-fold increase in summer average reproductive indices demonstrate that chaetognaths allocate surplus energy from increased feeding ability not only to physiological body size, but also to reproductive investment. This aligns with life history rules that claim that organisms in productive environments would invest more in reproduction (Alvariño, 1990). The higher proportion of individuals with visible

ovaries during winter months but with substantially smaller ovary sizes suggests a strategy of maintaining a state of readiness to reproduce beginning shortly after hatching and modulating reproductive output in response to food availability. This could indicate a reproductive response that could be quickly initiated if water conditions improve. Further studies should incorporate specimens from various depths in the water column as well as seasons outside of what have been studied in this paper to provide a comprehensive understanding of how these organisms function in the water column over the cycle of a year.

## Conclusions

This work aimed to add to the understanding of phylum Chaetognatha and its life history patterns in the Northern California Current, as one of the few papers regarding these individuals in this ecosystem.

We found that chaetognaths are bioindicators of ecosystem productivity. Because they are consumers of other organisms that rely on phytoplankton, chaetognaths' reproductive investment and body size have an indirect yet positive relationship with nutrient concentrations in their local ecosystems. For this reason, chaetognath body morphology may also be an indication of upwelling. In the NCC, the continental shelf break is a distinct boundary for levels of primary productivity as indicated by chlorophyll-*a* fluorescence, especially in summer months during the upwelling season. In the region between the shelf break and coastline, water masses and the nutrients within them are retained due to river flows and other near-coast circulations—these retained nutrients provide favorable feeding environments for chaetognaths and many other organisms in the marine food web.

In summer months chaetognath specimens were overall larger and their reproductive index ratios are bigger, both likely a result of high nutrient concentrations in the water from upwelling. In wintertime, average body sizes of specimens were much smaller, yet a higher proportion of individuals had grown at least one ovary. The most sensible conclusion for these data is a general life cycle in which chaetognaths hatch when nutrients in the water column are at their highest concentrations—during or soon after upwelling—hatching primarily in late spring and early summer. Chaetognath maturity, shown by ovary presence, seems to occur early in their life cycles and at a fraction of their maximum sizes, even with water nutrient levels may be relatively low. Until the next upwelling season, chaetognaths do not grow very much in body size for their

first six to eight months of life, living in a sort of dormancy while unable to consistently feed. When the late spring upwelling season brings a large flux of nutrients to the region, these organisms invest energy from food into both their body and gonad sizes, successfully growing into their adult sizes to successfully reproduce so their young may start the cycle once again.

This research also explored the idea that there is some regional population structure in the NCC, some of which may have unique environmental tolerances. Results show that populations from different regions have significant differences in morphological features, but with no distinct pattern.

Of species that had already been identified from this dataset, there were significant differences in body length and reproductive index. The species *Parasagitta elegans* was the most abundant in this region and is most likely to conform to the patterns that this research has set. *Pseudosagitta lyra* and *Flaccisagitta hexaptera* were present in this region as well. *F. hexaptera* had the highest reproductive index, indicating that it dedicates the most energy to its gonad growth compared to the others. *P. lyra*, on the other hand, had an impressively low reproductive index—indicating that either this species may reproduce in species that we did not sample, or overall has a different reproductive strategy than the phylum patterns.

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