

Responses of the chaetognath, *Sagitta elegans*, and larval Pacific hake, *Merluccius productus*, to spring diatom and copepod blooms in a temperate fjord (Dabob Bay, Washington)

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Abstract

As part of a broader field study examining the potentially deleterious effects of diatoms on planktonic food webs, we examined the abundance, stage composition, diet, and feeding success of the chaetognath, *Sagitta elegans*, and the abundance and morphometric condition of larval Pacific hake, *Merluccius productus*. Our objective was to look for a relationship between spring phytoplankton blooms and planktonic predators, as mediated by their copepod prey, with special reference to possible deleterious effects of diatoms. Zooplankton were collected weekly during February–May and in mid-summer of 2002 and 2003 in Dabob Bay, Washington State, USA. *S. elegans* abundance was high in summer of both years and was higher in spring 2003 than spring 2002. Larval chaetognaths dominated the population in early spring and remained present throughout sampling. *S. elegans* consumed mostly copepods. The abundance of larval *S. elegans* was correlated with the abundance of copepodites, although no relationship between chaetognath feeding success and prey abundance was found. Larval Pacific hake abundance was high (1200 larvae per square meter) in late February and early March of 2002 and 2003 and decreased rapidly in late spring. The morphometric condition of *M. productus* was not significantly related to copepod abundance. These results indicate that any deleterious effects of diatoms on copepod abundance, at the scale seen during spring 2002 and 2003 in Dabob Bay, did not greatly affect the next higher trophic level.

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1. Introduction

The role of diatoms in planktonic food webs has recently come into question. In the classical view of planktonic food webs, seasonal phytoplankton blooms, often dominated by diatoms, provide pulses of food around which many mesozooplankton (e.g., copepods) life histories are based. Phytoplankton blooms lead to an increase in copepod reproduction, which in turn serves as a food source for newly recruited invertebrate and vertebrate predators. In contrast, recent laboratory studies have shown that a diet made up exclusively of diatoms is deleterious to copepod fecundity and egg hatching success, across many combinations of diatom and copepod species (Ban et al., 1997). Most of these studies of diatom–copepod interactions focused on the effect of one diatom species on one copepod species using dinoflagellates as a control diet (Ban et al., 1997; Chaudron, Poulet, Laabir, Ianora, & Miralto, 1996; Ianora, Poulet, & Miralto, 1995; Ianora, Poulet, Miralto, & Grotoli, 1996). Mixed diets weaken but do not remove the negative effect of diatom-dominated diets on egg hatching viability (Lacoste et al., 2001; Starr, Runge, & Therriault, 1999).

Given the potential for deleterious effects of diatoms on copepods, it is important to investigate the possible ramifications to higher trophic levels. The classical model of predator and prey abundance patterns during spring phytoplankton blooms (Fig. 1(a)) may require revision if copepod and copepod predator abundances are reduced by diatoms (Fig. 1(b)). In order to investigate this issue, two of the dominant predators of copepods in Dabob Bay, Washington, USA, the chaetognath, *Sagitta elegans*, and larval Pacific hake, *Merluccius productus*, were chosen, partially due to their contrasting life histories. Fish spawning is generally the result of temporal cues experienced by adults. It has been argued that it is critical to larval fish survival that adult spawning coincides with spring plankton blooms and high prey densities (Cushing, 1967, 1975). In contrast,

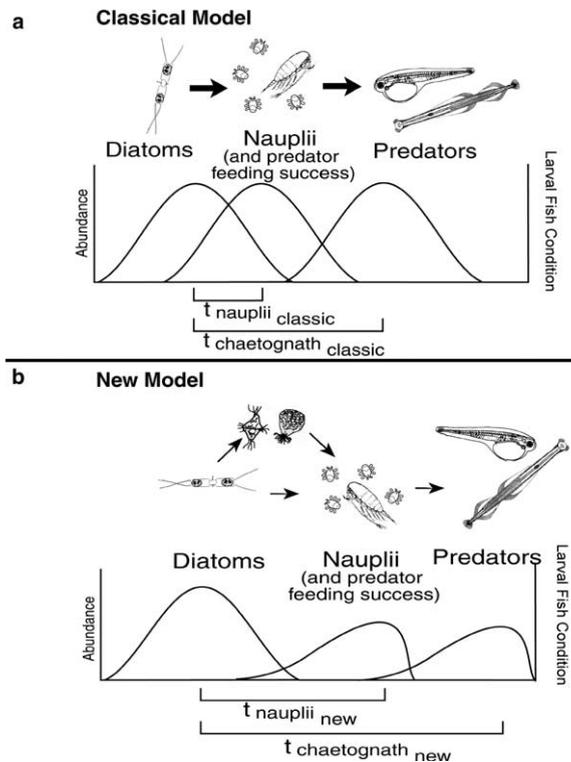


Fig. 1. Classical vs. new model of bloom dynamics. Panel (a): Diatoms serve as the main source of prey to copepods, leading to increased copepod production and subsequent predator feeding success and production. Intervals $t_{nauplii\ classic}$ and $t_{chaetognath\ classic}$ signify periods between the peak of diatom abundance and peaks of nauplius and chaetognath abundance, respectively, during a bloom without deleterious diatom effects. Panel (b): Diatoms are not a sufficient food source or are toxic to copepods, so that copepod production is reduced leading to reduced predator feeding success and production. Intervals $t_{nauplii\ new}$ and $t_{chaetognath\ new}$ signify periods between the peak of diatom abundance and peaks of nauplius and chaetognath abundance, respectively, during a bloom with deleterious diatom effects.

invertebrate predators such as *S. elegans* may be more able to shift the timing of their reproduction with changes in prey abundance. By comparing the effect that changes in copepod prey abundance have on these two predators, one may assess their particular need for abundant prey and the consequences of diatom–copepod interactions to this next trophic level of the food web.

Sagitta elegans is the dominant chaetognath species in the subarctic Pacific (Terazaki, 1998) and specifically in Dabob Bay (Bollens et al., 1992a; King, 1979). It is also an obligate carnivore feeding almost exclusively on copepods and nauplii, making it an extremely important link in the transfer of energy from copepods to higher trophic levels (Terazaki, 1998). *S. elegans* produces one to five or more generations per year (Terazaki, 1998), depending on temperature. Prey availability is also reported to be a determining factor for *S. elegans* distribution and population dynamics, although the nature of the relationship between chaetognaths and their prey is unclear. For instance, several studies note an apparent correlation between the first spring cohort of herbivorous copepods and the maturation and/or egg production of *S. elegans* (King, 1979; Ohman, 1986; Sameoto, 1973; Sullivan, 1980; Zo, 1973), suggesting a dependence upon prey for reproduction. Pearre (1981) compared respiration rate estimates with the caloric content of prey items and noted that larval chaetognaths appeared to consume fewer prey than are needed to meet respiratory demands during December, and they subsequently suffered high mortality rates. However, Sameoto (1973) found no difference in *S. elegans* growth rate between two sites with differing prey levels in the NW Atlantic, and concluded that the chaetognaths did not appear to be food limited. Sullivan (1980) studied the feeding of *S. elegans* in the subarctic Pacific Ocean and did not find a significant relationship between feeding and prey abundances for either juveniles or adults. These studies suggest there is mixed evidence for food limitation among larval and adult chaetognaths.

In Dabob Bay there is spawning of a resident population of *M. productus* that is reproductively isolated from the larger coastal stock (Beamish et al., 1982; Goni, 1988). Starvation may cause death of larval fish directly, or cause it indirectly by inducing weakness and susceptibility to predators. Starvation is considered to be a major cause of mortality for larval fish generally (Ferron & Leggett, 1994). Food limitation can be measured by employing several methods used to determine nutritional condition, e.g., morphometric, histological and biochemical measurements (Ferron & Leggett, 1994). None of these methods have been employed in the study of Pacific hake and the relationship between young Pacific hake and their prey has never been studied in the region.

We examined the feeding success and recruitment of *S. elegans* and the morphometric condition of *M. productus* in the context of the potential for spring diatom blooms to affect deleteriously both copepod populations and higher trophic levels in Dabob Bay (see this issue). The specific objectives of this study were: (1) to analyze the abundance patterns and temporal co-occurrence of larval *M. productus* and various life history stages of *S. elegans* with their prey; (2) to quantify diet and feeding success of *S. elegans*, and morphometric condition of *M. productus* in relation to prey abundance; and (3) to examine the relationship between spring phytoplankton blooms, copepod blooms, and *S. elegans* recruitment.

2. Study site

Dabob Bay, Washington State, USA, is a narrow and deep (approximately 190 m) fjord, separated from Hood Canal by a sill at 120 m depth (Fig. 2). The orientation of the bay, the sill at its mouth, and minimal river inflow affect water exchange in Dabob Bay such that it experiences relatively little horizontal advection (Ebbesmeyer, Barnes, & Langley, 1975). Although advection has been shown to mix copepod populations between inside and outside of the bay during much of the year (Osgood & Frost, 1996), this reduced advection makes Dabob Bay an ideal location for the study of zooplankton populations relative to the more advective environments of many coastal areas.

3. Methods

3.1. Sample collection

Chaetognaths and larval hake were collected weekly from February through April of 2002 and 2003, as well as on two additional dates in mid-July of both years. All samples were collected by vertical opening and

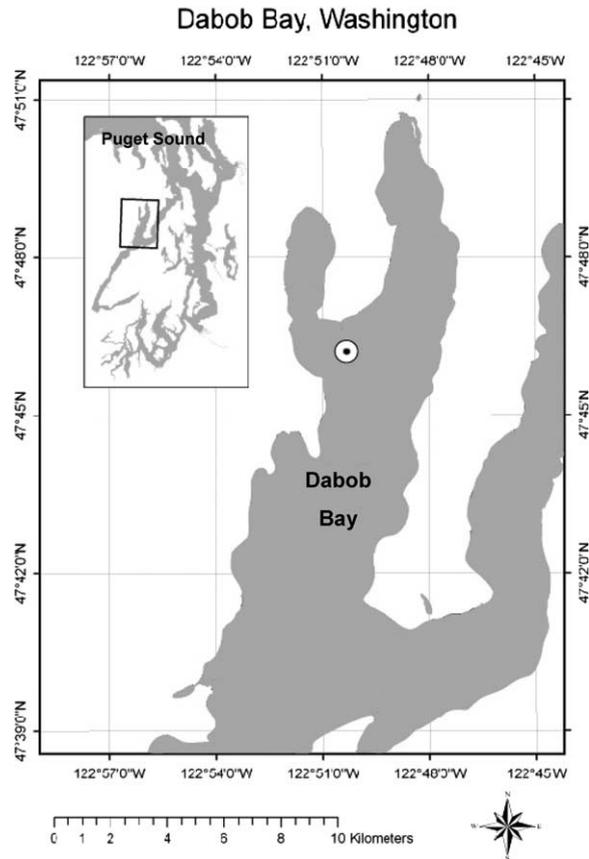


Fig. 2. Site map. Dabob Bay, Washington State, USA.

closing ring net tows (3 replicates) at a single station at 180 m depth (Fig. 2). Chaetognaths and hake larvae were collected at night with a 1 m diameter ring net fitted with 209 μm mesh, and potential prey were collected during the day with an 0.4 m diameter ring net with 73 μm mesh. All nets were towed vertically at 30 m per minute. The water column was sampled in four depth strata in 2002 and five depth strata in 2003. In 2002 depth strata sampled were generally 160–50, 50–25, 25–10, and 10–0 m. In 2003 the deepest stratum was further split into 160–100 and 100–50 m depth strata. These strata were consistent between replicates but not between sampling dates, as they were based in part on the depth of haloclines and chlorophyll concentration. Indeed, these strata were chosen with phytoplankton–copepod interactions in mind (see other papers in this volume), not chaetognaths or larval hake, which were only considered after the fact. All separate depth strata were subsequently integrated into water column totals (see below). The nets were immediately rinsed with seawater from near the surface and all specimens (samples) were preserved in 10% buffered formalin.

3.2. Sample processing

Chaetognaths were sorted from the 209 μm plankton samples in the laboratory. They were then measured for length to the nearest 1 mm, assigned a reproductive stage, and separated by the presence or absence of prey in their guts, as determined by examination through the translucent body wall with a dissecting microscope. Subsamples were taken of the 73 μm mesh samples and all copepodites and copepod nauplii were counted. Copepodites and nauplii were not identified to taxon or stage.

Chaetognath stage classification followed commonly used criteria of ovary development (Russell, 1932; Sameoto, 1973; Zo, 1973). Stage I individuals either lacked ovaries or had marginally detectible development of the ovaries and lacked visible sperm cells in the testes. These chaetognaths are termed larval. Stage II

individuals exhibited signs of development in the testes and well developed ovaries but lacked fully developed ova. Stage III had one or more fully developed ova in the ovaries and were reproductively mature. Stage IV had empty testes and flaccid ovaries and were considered spent. Other methods of staging chaetognaths have been used in which the categories are more detailed (King, 1979; Thomson, 1947). However, in the interest of comparability, we chose the more commonly used method of Russell (1932), with the addition of stage IV for spent animals.

Chaetognaths were grouped by reproductive stage for the purposes of gut content dissections. Stage I chaetognaths were separated from all other stages (i.e., into larval and adult categories) in order to examine differences in prey composition. Twenty-five prey-containing chaetognaths were randomly chosen for dissection from each replicate water column series of samples. The number of chaetognaths dissected from any one depth-specific sample was dependent on the proportion of the total number of chaetognaths (in the entire water column) comprised by that particular sample. Chaetognaths were mounted on a slide with glycerin and dissected using fine insect pins under a dissecting microscope. Prey were identified to coarse taxonomic and developmental stage levels (i.e., copepodite, copepod nauplius, barnacle nauplius, “other”, “remains”, etc.). Only prey heads were counted. If evidence for a prey type was represented only by a body part such as a crustacean limb, that prey was counted as crustacean “remains”, not as an individual. Prey items in the anterior 1/3 of the gut cavity were not counted, as they may be representative of net feeding (Ohman, 1986; Saito & Kiørboe, 2001). *S. elegans* moves ingested prey to the posterior of the gut relatively rapidly and the majority of digestion then occurs there. The time required for ingested prey to move to the posterior portion of the gut cavity has been reported to be 15–30 min at 0 °C (Feigenbaum, 1982). One would expect this time to be shorter at the warmer temperatures present in Dabob Bay. Although our net tows lasted only a few minutes, prey in the foregut may have been the result of net feeding and were therefore not included in our analyses.

All larval fish were sorted from the samples and all Pacific hake were enumerated. Larvae that were newly hatched and lacked many distinguishing characteristics were not included. Samples collected in spring 2002 were sorted in fall 2002 and samples collected in spring 2003 were sorted in the same year. They were then stored in 5% buffered formalin until further analysis in summer 2004. Three sample dates from each year were chosen for analysis of the larvae. These dates were chosen in order to cover the widest possible range of prey availability. In 2002, the fifth, sixth and seventh sample dates were chosen to represent high, medium and low prey availability levels and in 2003 the fourth, fifth and sixth sample dates were chosen and represented low, medium and high prey availability, respectively. Prey availability levels for larval hake were determined by the abundance of copepodites and nauplii in the week previous to dates that fish were collected. Consecutive weekly sampling dates were chosen to ensure similarly sized larvae and to reduce possibly confounding effects of temperature and other unknown temporal variables.

Two food-sensitive and two food-insensitive characters were chosen for measurement of larval hake (Bollens & Sanders, 2004, & references therein). Food-insensitive characters were standard length (SL, from the tip of the snout to the end of the notochord) and eye diameter (ED). Food-sensitive characters were depth of the body at the anus (ABD) and pectoral body depth (PBD, excluding the gut). All post-yolk sac larvae present on the 6 sample dates were analyzed, with the number of fish for any one date ranging from 266 to 555. Images of individual fish were captured using an 0.5 in. Digital Color CCD Camera IV CCAMW and Leica MZ-6 stereomicroscope (0.63× objective). Measurements were then made using Sigma Scan Pro® Image Analysis software.

3.3. Statistical analysis

Comparisons were made between abundances of copepodites, copepod nauplii, all copepods, larval chaetognaths, reproductive chaetognaths, all chaetognaths and chlorophyll density. Nonparametric Spearman rank correlation coefficients were calculated for each of these comparisons, considering the two sampling years both separately and in combination (Zar, 1999). Statistical analyses were run using SPSS 10.0 for Windows. Abundances of these groups were compared with time lags of 0, 1, 2, and 3 weeks between prey and predators. This was done with the expectation that the consequences of increased feeding might be manifest either as increases in maturation of adult chaetognaths or as production of larval chaetognaths over varying lengths of time.

Feeding success of *S. elegans* was assessed using three different measures: (1) the proportion of chaetognaths with prey, (2) the number of prey per dissected chaetognath for each sample date, and (3) the mean number of prey per chaetognath (containing prey or not). Each of these measures of feeding success was determined separately for larval chaetognaths (stage I) and for all other stages (II–IV) of chaetognaths. They then were compared to the abundance of copepodites and nauplii using an analysis of covariance (ANCOVA) (Zar, 1999).

Larval Pacific hake condition was assessed by comparing the regressions of individual, log-transformed, food-sensitive body measurements (ABD, PBD) to food-insensitive body measurements (SL, ED) among fish that experienced high, medium and low food availability. This resulted in four possible metrics for each food level comparison (ABD vs. SL, PBD vs. SL, ABD vs. ED, PBD vs. ED). The size range of larvae included in the analysis was truncated to provide a consistent size range across dates. Analysis of covariance was used to test the significance of differences in slope coefficients and intercepts among dates with high, low and intermediate food availability in the previous week. Separate comparisons were made between high vs. low, high vs. medium, and medium vs. low food levels for 2002, 2003, and for both years combined.

In addition, principal components analysis was used to combine the two food-sensitive and two food-insensitive body measurements, obtaining one food-sensitive and one food-insensitive score for each individual fish (Kachigan, 1991). This analysis was performed using PC-ORD for Windows. Regressions of the food-sensitive principal component on the food-insensitive principal component were then performed. Analysis of covariance was again used to test for homogeneity in the slopes and for possible differences in intercept.

4. Results

4.1. Phytoplankton and copepod bloom dynamics

The spring phytoplankton blooms of both 2002 and 2003 were characterized by two peaks in chlorophyll concentration (Fig. 3). Chlorophyll levels were highest on February 21 and March 28 of 2002 and March 5 and April 9 of 2003. During the early bloom of each year, *Thalassiosira pacifica* and *Thalassiosira aestivalis* were the dominant phytoplankton species (Horner et al., this issue). The second bloom of each year was a

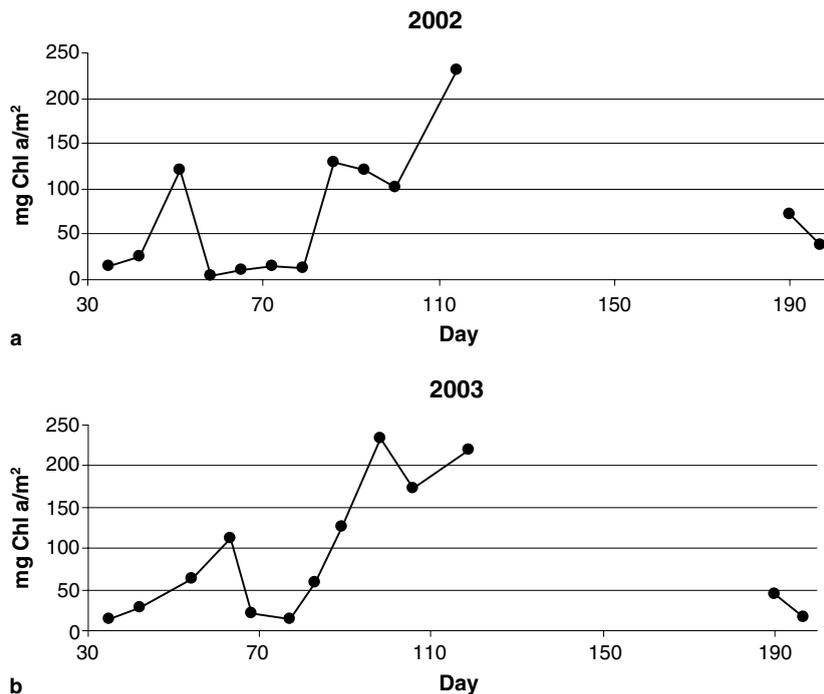


Fig. 3. Depth-integrated chlorophyll *a* in 2002 (a) and 2003 (b), Dabob Bay.

more mixed assemblage, with the genus *Chaetoceros* being dominant, although in 2002 *Phaeocystis* also became dominant (Horner et al., this issue). The abundance of copepodites and nauplii also showed similar patterns during the two years. Copepodite abundance during winter/spring was initially high, followed by two successively smaller peaks, then ended at low levels (Fig. 4). Copepod naupliar density was initially low and then fluctuated in a similar manner as the copepodites. Both copepodites and nauplii were most abundant during summer sampling (Fig. 4).

4.2. Chaetognath abundance and stage composition

The abundance of *S. elegans* was generally higher during spring 2003 than spring 2002 (Fig. 5). During the spring sampling period, chaetognath abundance ranged from 79 to 444 chaetognaths m^{-2} in 2002 and from 117 to 2681 chaetognaths m^{-2} in 2003. Chaetognath abundance was high in July of each year. The high spring abundance of chaetognaths in 2003 was particularly pronounced on the second sampling date, due to a large pulse of larval *S. elegans* presumed to result from production in late 2002 (Figs. 5 and 6).

Larval or stage I *S. elegans* dominated the population early in the year and were present on all sampling dates in both years (Fig. 6). The relative abundance of stage I chaetognaths decreased throughout spring

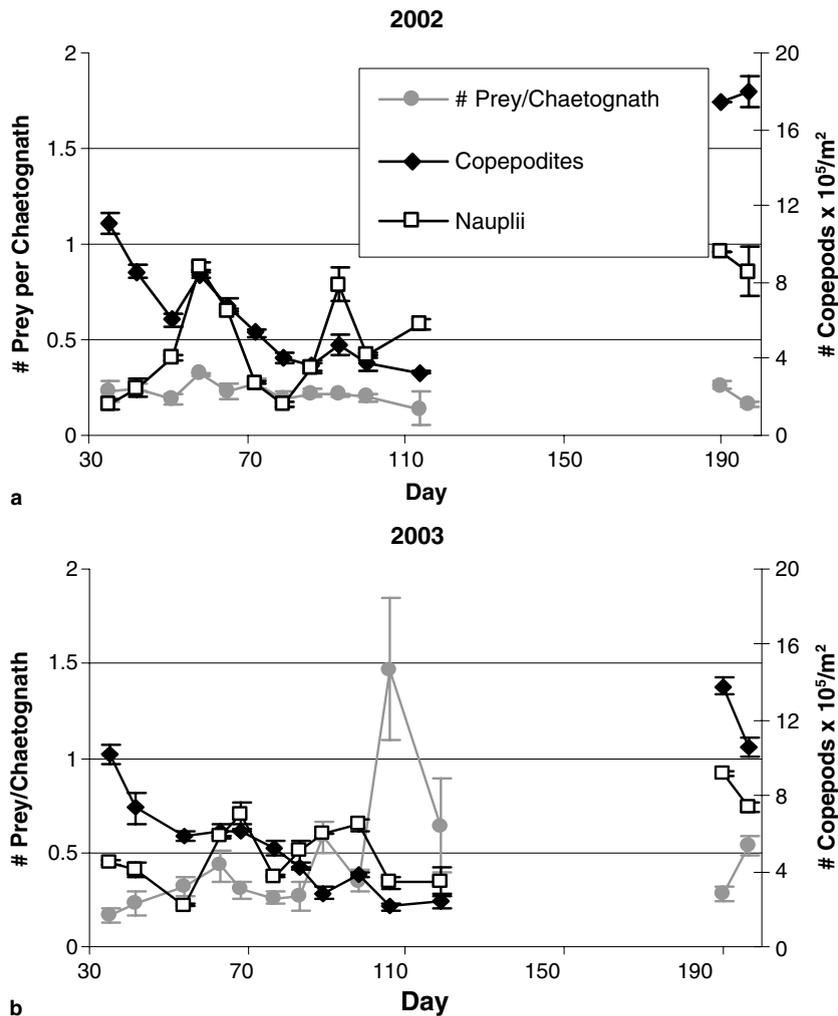


Fig. 4. Prey abundance and feeding success (# prey/chaetognath) for larval and adult *S. elegans* in 2002 (a) and 2003 (b), Dabob Bay, Washington.

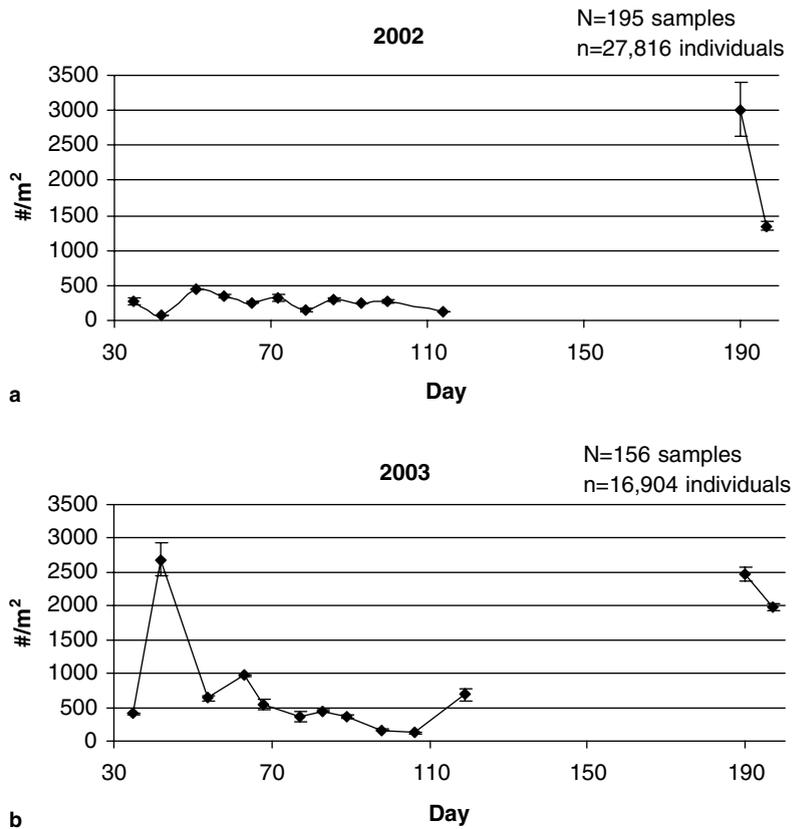


Fig. 5. *Sagitta elegans* abundance in 2002 (a) and 2003 (b), *n* equals the total number of chaetognaths sorted in a total of *N* samples, Dabob Bay, Washington.

sampling as they matured to later reproductive stages. Pulses of reproductive output were revealed by an examination of stage composition. A pulse in abundance of stage I chaetognaths was evident on March 28 in 2002 and a more prolonged increase in production of larval chaetognaths also started on March 31 of 2003 (Fig. 6).

By examining the modal progression of length–frequency distributions, one may often estimate the growth rates of planktonic organisms (e.g., Bollens, Frost, & Lin, 1992b, and references therein). However, comparison of size–frequency histograms for successive sample dates in this study did not show a clear modal progression of *S. elegans* cohorts due to their continuous reproduction. Therefore, it was not possible to determine growth or survival of chaetognaths because they did not occur in distinct cohorts. Stage I chaetognath lengths ranged between 2 and 10 mm. Stage II or developing chaetognaths ranged between approximately 10 and 18 mm, while stage III or reproductive chaetognaths were between 18 and 30 mm long. Although growth cannot be accurately determined in the field, many researchers have used stage composition over a year’s duration to determine generation times and approximate growth. Growth in length varies over the chaetognath life cycle as energy is used differentially for somatic growth or gonadic development. During spring, newly recruited *S. elegans* have been shown to grow rapidly and develop into stage II individuals, while growth slows during later reproductive stages (Alvarez-Cadena, 1993a). This is evident in our stage composition data from both 2002 and 2003, as the abundance of stage I individuals declined and stage II individuals increased during February and March (Fig. 6).

4.3. Chaetognath diet and feeding success

The diet of adult (stages II–IV) chaetognaths consisted mostly of copepodites, particularly in 2003 (Fig. 7). Fewer prey items were identifiable as copepods in 2002, although much gut content was classified as

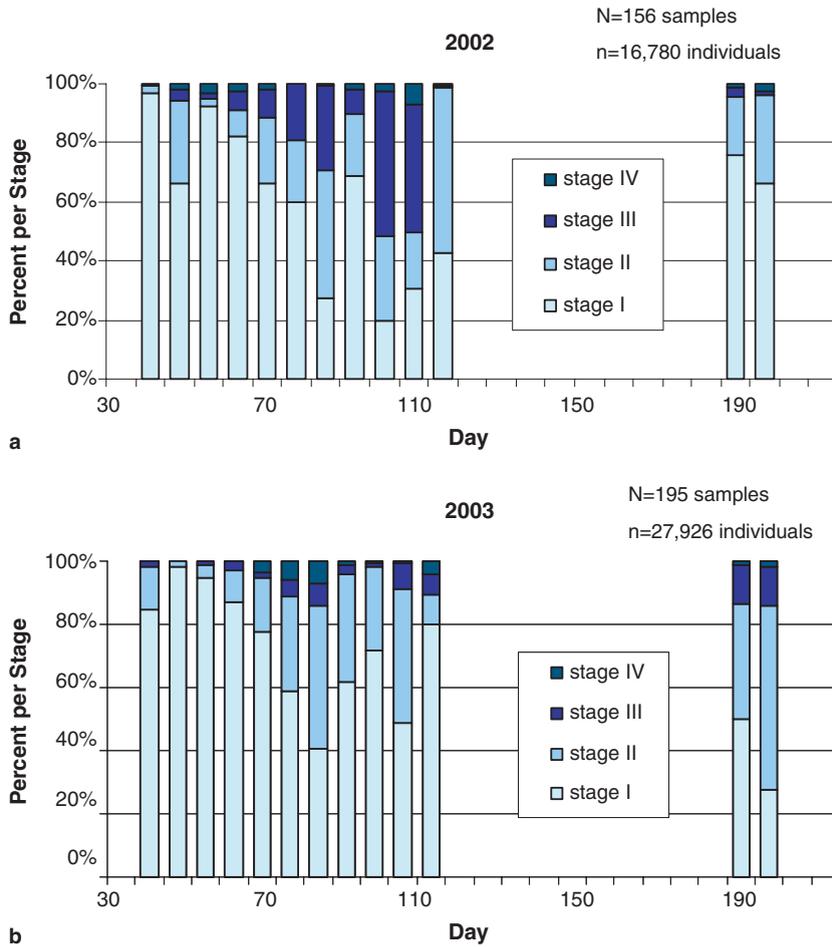


Fig. 6. *Sagitta elegans* stage composition in 2002 (a) and 2003 (b), Dabob Bay.

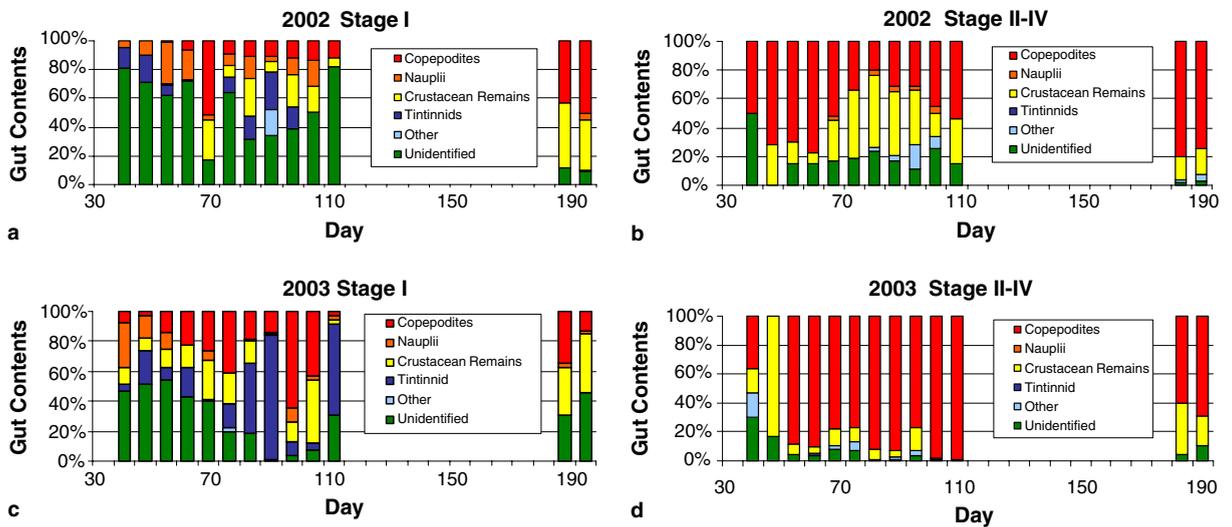


Fig. 7. Prey composition of “larval” (a, c) and “adult” (b, d) *S. elegans* in 2002 (a, b) and 2003 (c, d), Dabob Bay, Washington.

“crustacean remains”. Some prey material was unidentifiable and a small amount was classified as “other” (e.g., cannibalism, amphipod, barnacle nauplius, euphausiid nauplius). Larval or stage I chaetognaths also consumed some copepodites although to a lesser extent than the adults (Fig. 7). Copepod nauplii were present in the larval chaetognath diet, as were tintinnid protozoans, although much of the larval chaetognath gut content was unidentifiable.

Significant and positive correlations were found between the abundances of larval chaetognaths and of copepodites, but not between the larval chaetognaths and copepod nauplii (Table 1). This was the case when each sampling year was examined separately, as well as when the 2 years were combined (Table 1). A significant and positive correlation was found between the abundance of combined stages of chaetognaths and the abundance of copepodites in 2003, as well as both years combined. However, the abundance of reproductive (stage III) chaetognaths was not significantly correlated with any measure of prey abundance. An analysis of covariance revealed that no measure of feeding success was significantly related to the abundance of copepodites, nauplii, or all copepods combined for either larval or adult chaetognaths (Table 2 and Fig. 4).

4.4. Larval pacific hake abundance

Larval hake abundance patterns were similar in 2002 and 2003 in Dabob Bay, peaking at 1144 larvae m^{-2} on February 28, 2002 and 1241 larvae m^{-2} on March 10, 2003 (Fig. 8). Abundance then decreased over both spring seasons and remained low on both summer dates.

4.5. Larval pacific hake condition

Regressions of individual body measurements did show some significantly different slopes between food conditions (Fig. 9 and Table 3). Results comparing regressions of individual body measurements with different food levels varied (Table 3). When the years were combined, anal body depth vs. standard length and pectoral

Table 1
Correlation coefficients between predator and prey abundance in real time and lagged by 1, 2, and 3 weeks, 2002 and 2003 data combined, Dabob Bay, Washington

	Nauplii	Copepodites	Chaetognaths		
			All stages	Stage I	Stage III
<i>0-Week shift</i>					
Chlorophyll	0.024	-0.588**	-0.053	-0.066	-0.124
Nauplii			0.418*	0.319	0.351
Copepodites			0.490*	0.573**	0.073
Copepods			0.468*	0.501**	0.110
<i>1-Week shift</i>					
Chlorophyll	0.088	-0.537**	-0.046	-0.053	-0.059
Nauplii			0.12	0.065	0.102
Copepodites			0.412	0.447*	-0.046
Copepods			0.261	0.282	-0.033
<i>2-Week shift</i>					
Chlorophyll	0.073	-0.560*	-0.075	0.014	-0.162
Nauplii			-0.269	-0.325	0.010
Copepodites			0.459	0.442	-0.064
Copepods			0.201	0.136	-0.070
<i>3-Week shift</i>					
Chlorophyll	-0.076	-0.441	0.126	0.112	-0.228
Nauplii			0.129	0.094	0.016
Copepodites			0.306	0.365	-0.015
Copepods			0.303	0.350	-0.029

Significant correlation coefficients are emboldened. One asterisk signifies a significance value less than 0.05. Two asterisks signify a significance value of less than 0.01.

Table 2
p-Values from ANCOVA on *S. elegans* feeding success and prey availability

	Adult chaetognaths			Stage I chaetognaths		
	% with Prey	Prey per Fed	Prey per All	% with Prey	Prey per Fed	Prey per All
Copepodites	0.063	0.548	0.117	0.665	0.594	0.620
Nauplii	0.325	0.543	0.702	0.460	0.187	0.753
AH Copepods	0.149	0.180	0.579	0.671	0.456	0.276
Year	≤0.001	≤0.001	≤0.001	0.613	0.040	0.230
Day	≤0.001	≤0.001	≤0.001	0.069	0.145	0.055
Year × Day	≤0.001	≤0.001	≤0.001	0.088	0.134	0.042

Significant values are emboldened. % with Prey is the percent of adult or stage I chaetognaths containing prey, Prey per Fed is the average number of prey items contained in adult or stage I chaetognaths already determined to have prey, Prey per All is the average number of prey items contained in all adult or stage I chaetognaths, Dabob Bay, Washington.

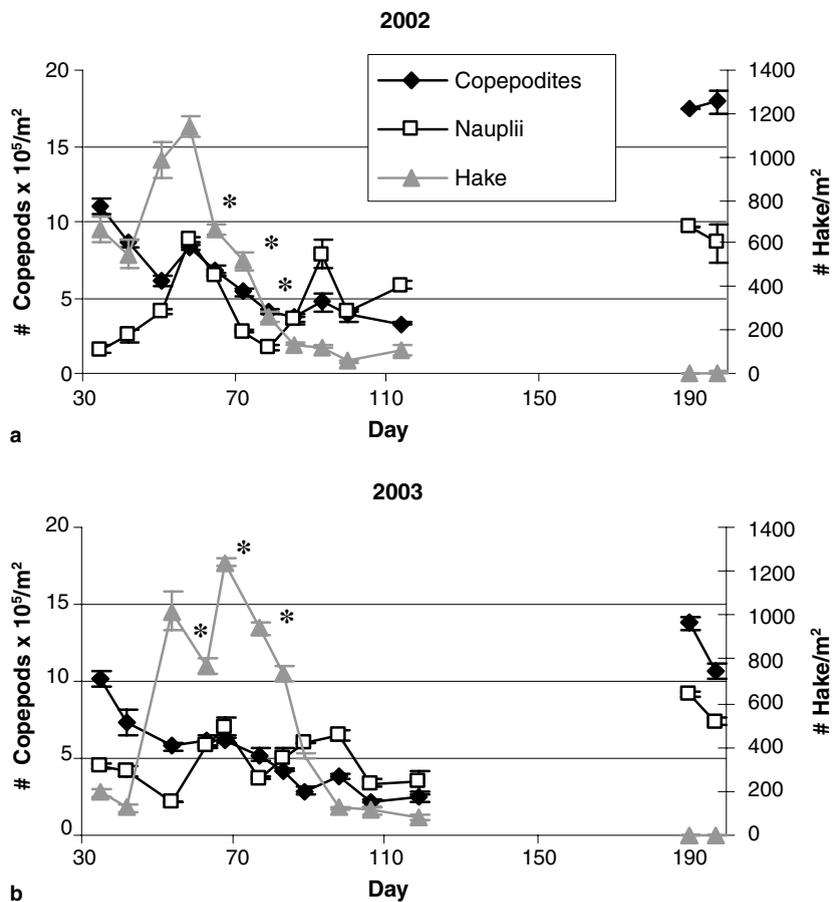


Fig. 8. Larval Pacific hake abundance, copepodite and naupliar prey abundance in 2002 (a) and 2003 (b), Dabob Bay. Asterisks indicate sampling dates from which larvae were measured.

body depth vs. standard length regressions suggested that larval fish experiencing high food availability had higher slopes than fish experiencing low food availability. These higher slopes indicate that the larval fish are able to grow more rapidly under better food conditions. However, comparisons using ED rather than SL showed opposite results for the combined years. Moreover, in 2003 the results of all four metrics (ABD vs. SL, PBD vs. SL, ABD vs. ED, PBD vs. ED) showed that fish experiencing high food availability have significantly lower slopes than fish experiencing low food conditions.

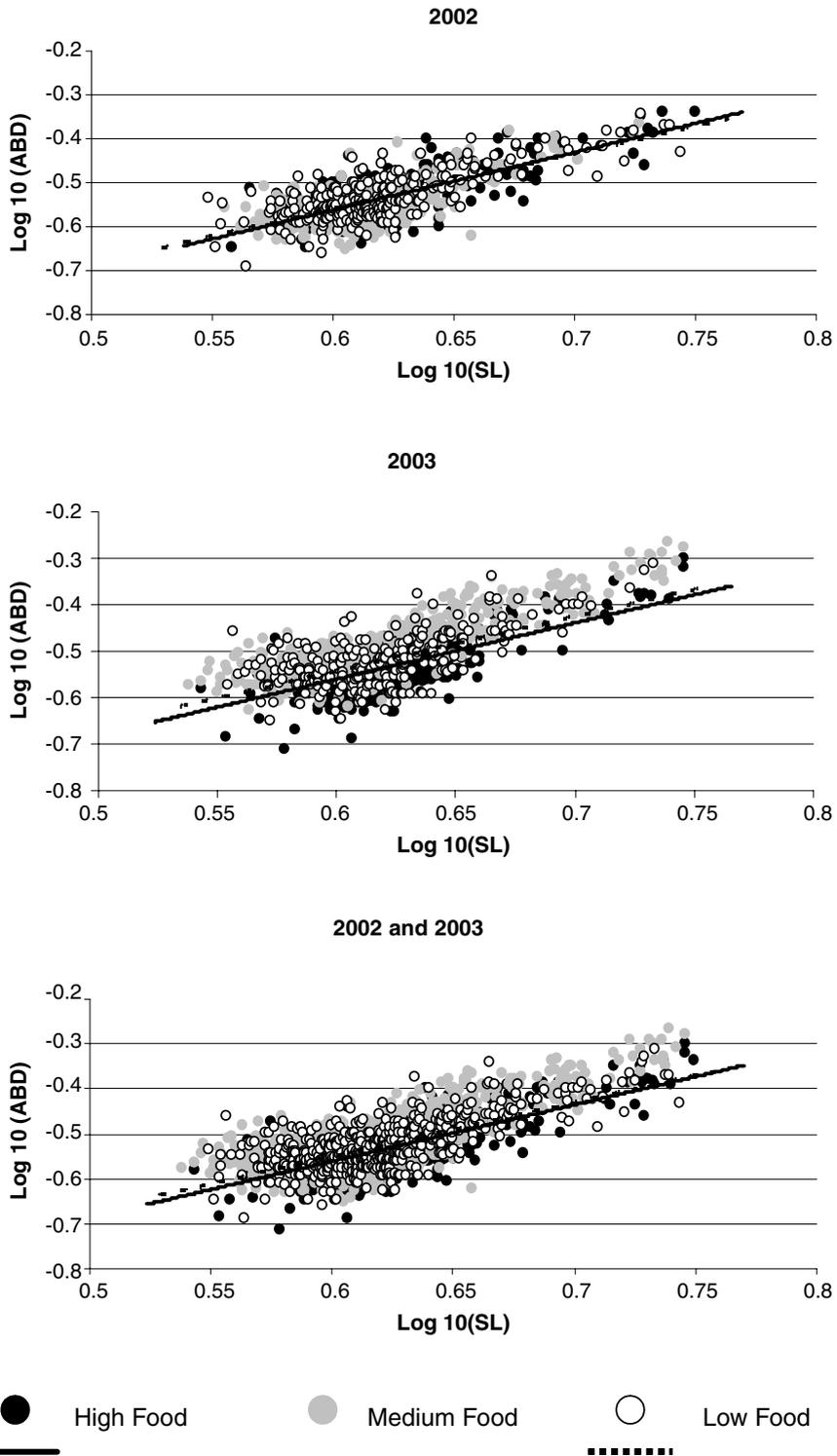


Fig. 9. Regressions of $\log[\text{anal body depth (ABD)}]$ on $\log[\text{standard length (SL)}]$ for larval Pacific hake from low (open circles), medium (grey circles), and high food (black circles) availability periods for the years 2002 (a) and 2003 (b) as well as the years combined (c), Dabob Bay.

Table 3

Results of analysis of covariance of data comparing individual body measurements of larval Pacific hake from high and low food availability periods

Year	High vs. low food body measurements	Significance level intercept/slope	Regression equation
2002	ABD vs. SL	$\ll 0.001/0.662$	High $y = \mathbf{1.305}x - 1.345$ Low $y = \mathbf{1.258}x - 1.314$
	PBD vs. SL	$\ll 0.001/0.726$	High $y = \mathbf{1.379}x - 1.517$ Low $y = \mathbf{1.337}x - 1.492$
	ABD vs. ED	0.086/0.010	High $y = \mathbf{0.869}x - 0.0458$ Low $y = \mathbf{0.920}x - 0.0268$
	PBD vs. ED	$\ll 0.001/0.014$	High $y = \mathbf{0.872}x - 0.169$ Low $y = \mathbf{0.951}x - 0.139$
2003	ABD vs. SL	$\ll 0.001/\ll 0.001$	High $y = \mathbf{1.156}x - 1.253$ Low $y = \mathbf{1.167}x - 1.243$
	PBD vs. SL	$\ll 0.001/\ll 0.001$	High $y = \mathbf{1.091}x - 1.375$ Low $y = \mathbf{1.100}x - 1.358$
	ABD vs. ED	$\ll 0.001/\ll 0.001$	High $y = \mathbf{0.665}x - 0.171$ Low $y = \mathbf{0.868}x - 0.0489$
	PBD vs. ED	$\ll 0.001/\ll 0.001$	High $y = \mathbf{0.594}x - 0.372$ Low $y = \mathbf{0.779}x - 0.254$
2002 and 2003	ABD vs. SL	$\ll 0.001/\ll 0.001$	High $y = \mathbf{1.233}x - 1.300$ Low $y = \mathbf{1.209}x - 1.277$
	PBD vs. SL	$\ll 0.001/\ll 0.001$	High $y = \mathbf{1.286}x - 1.485$ Low $y = \mathbf{1.226}x - 1.430$
	ABD vs. ED	$\ll 0.001/0.143$	High $y = \mathbf{0.775}x - 0.106$ Low $y = \mathbf{0.901}x - 0.0342$
	PBD vs. ED	$\ll 0.001/\ll 0.001$	High $y = \mathbf{0.719}x - 0.289$ Low $y = \mathbf{0.845}x - 0.208$

Significance levels for tests for homogeneity of slopes of the two regression lines and for tests of differences in intercept are shown. Slopes are emboldened. Dabob Bay, Washington.

The regression of anal body depth (ABD) on standard length (SL) was chosen as the most meaningful morphometric comparison, due to the higher R^2 values resulting from these regression analyses across all sample dates. Larval hake condition, for years 2002 and 2003 combined, as indicated by the slope of this regression, was significantly higher after high food availability (Table 3). However, slopes were not significantly different in 2002 between fish experiencing high and low food conditions. In 2003, the slope was significantly higher after a period of low food availability than after high food availability. The slope of larvae experiencing intermediate food conditions was significantly lower than both the high and low food conditions in 2002, 2003 and when the years were combined (data not shown).

The regression analysis of food-sensitive and food-insensitive PC scores indicated no significant differences in slopes or intercepts among any of the sample dates or food levels, which we interpret as a lack of difference in body morphology among dates and food levels (Table 4). The regression lines comparing the condition of fish that experienced high and low food were indistinguishable for 2002, for 2003, and for the years combined (Fig. 10). Each of the two food-sensitive and food-insensitive measurements produced high R^2 values when regressed against the principal component intended to reflect them. This indicated that the principal component was sufficient to explain variation expressed by each individual body measurement. Regressions of food-sensitive and food-insensitive principal components on each other also had higher R^2 than the regressions of anal body depth on standard length.

Table 4

Results of analysis of covariance of data comparing food-sensitive and food-insensitive principal components of larval Pacific hake from high, medium, and low food availability periods

Year	Food level	Significance intercept/slope	Regression equations
2002	High vs. Low	>0.999/>0.999	$y = \mathbf{0.780}x - 4.300 \times 10^{-6}$ $y = \mathbf{0.801}x + 4.925 \times 10^{-6}$
	High vs. Med	>0.999/>0.999	$y = \mathbf{0.780}x - 4.300 \times 10^{-6}$ $y = \mathbf{0.684}x - 1.970 \times 10^{-6}$
	Med vs. Low	>0.999/>0.999	$y = \mathbf{0.684}x - 1.970 \times 10^{-6}$ $y = \mathbf{0.801}x + 4.925 \times 10^{-6}$
2003	High vs. Low	>0.999/>0.999	$y = \mathbf{0.702}x + 2.362 \times 10^{-5}$ $y = \mathbf{0.722}x + 1.709 \times 10^{-6}$
	High vs. Med	>0.999/>0.999	$y = \mathbf{0.702}x + 2.362 \times 10^{-5}$ $y = \mathbf{0.871}x + 7.269 \times 10^{-6}$
	Med vs. Low	>0.999/>0.999	$y = \mathbf{0.871}x + 7.269 \times 10^{-6}$ $y = \mathbf{0.722}x + 1.709 \times 10^{-6}$
2002 and 2003	High vs. Low	>0.999/>0.999	$y = \mathbf{0.727}x + 1.556 \times 10^{-5}$ $y = \mathbf{0.762}x + 3.232 \times 10^{-6}$
	High vs. Med	>0.999/>0.999	$y = \mathbf{0.727}x + 1.556 \times 10^{-5}$ $y = \mathbf{0.782}x + 2.262 \times 10^{-6}$
	Med vs. Low	>0.999/>0.999	$y = \mathbf{0.782}x + 2.262 \times 10^{-6}$ $y = \mathbf{0.762}x + 3.232 \times 10^{-6}$

Significance levels for tests for homogeneity of slopes of the two regression lines and for tests of differences in intercept are shown. Slopes are emboldened. Dabob Bay, Washington.

5. Discussion

5.1. Response of *S. elegans* to prey availability

To determine the effect of the availability of copepod prey on chaetognath population dynamics, we examined the relationships among prey abundance and chaetognath feeding, recruitment, and stage composition over two spring phytoplankton and copepod blooms. One would expect chaetognath feeding success to covary with prey abundance, if they experienced food limitation. Although *S. elegans* has been observed to feed upon several planktonic groups including Amphipoda, Euphausiacea, Ostracoda, Chaetognatha, fish larvae, and microzooplankton (Terazaki, 1998), copepods were the major source of prey for adult chaetognaths in Dabob Bay in 2002 and 2003 (Fig. 7).

Food limitation in chaetognaths is suggested by the frequently noted phenomenon of chaetognath ontogenetic shifts coinciding with copepod population pulses (King, 1979; McLaren, 1966; Sameoto, 1973; Zo, 1973). For instance, Zo (1973) noted that in Bedford Basin, periods of low copepod abundance in January and February coincided with no population growth of *S. elegans*, but periods with large numbers of copepods in April, September and October were followed by growth and maturity of *S. elegans*. Sameoto (1973) noted increases in *S. elegans* egg production immediately after increases in copepod biomass in Bedford Basin. Pearre (1981) compared the respiratory demands of *S. elegans* with caloric intake in Bedford Basin during December; he found that stage I chaetognaths experienced a caloric deficit and then drastically declined in abundance. King (1979) suggested that the unsuccessful spawning of individuals in Autumn in Dabob Bay may have been due to low levels of copepod prey for the young and that maturation of *S. elegans* coincided with the first large spring cohort of small herbivorous copepods.

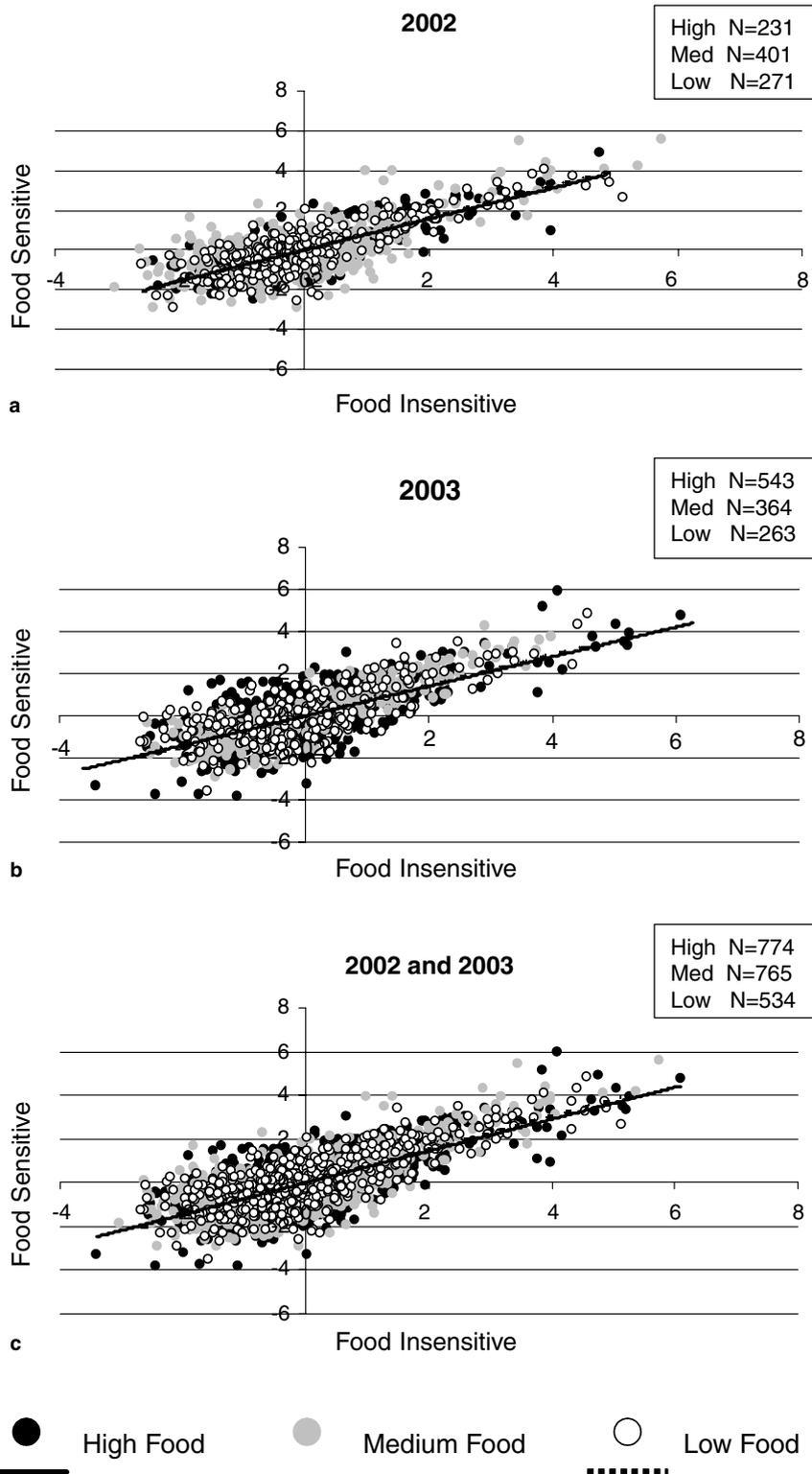


Fig. 10. Regressions of food-sensitive on food-insensitive principal components for larval Pacific hake from low (open circles), medium (grey circles), and high food (black circles) availability periods for the years 2002 (a) and 2003 (b) as well as the years combined (c), Dabob Bay.

However, there is also considerable evidence that food limitation is in fact rare in *S. elegans*. Sameoto (1973) found growth rates of *S. elegans* were equal between Bedford Basin and the more copepod-deficient St. Margaret's Bay. Pearre (1973) found that copepods were not found in *S. elegans* guts in similar proportions to their abundance in the water column in Bedford Basin, and that chaetognath vertical migrations did not appear to be following a preferred prey species. In the subarctic Pacific Ocean, no relationship was found between feeding and prey abundance for either juvenile or adult *S. elegans* (Sullivan, 1980). Our finding of a lack of a significant relationship between *S. elegans* feeding success and copepod abundance in 2002 and 2003 suggests that food limitation was not a significant factor during spring of these years in Dabob Bay, although sampling at scales smaller than the whole water column might have produced different results.

Moreover, we found that the development of *S. elegans* to stage III (or reproducing) was not correlated with the abundance of copepodites, nauplii or all copepods combined. This was true even when the abundance of stage III chaetognaths was compared with prey abundance 1, 2 and 3 weeks earlier (Table 1). This would indicate that chaetognath reproductive output was not food-limited or that all stage II chaetognaths had already been triggered to come out of the overwintering stage and begin gonad development before spring. The latter seems likely due to the great abundance of larval *S. elegans* already present in February (Fig. 6). This suggests that reproductive development and recruitment were already well underway in January and possibly even by December of both years. Most other populations of *S. elegans* have been found to produce one generation per year, with the main recruitment of new individuals produced by overwintered chaetognaths in spring (Alvarez-Cadena, 1993a; Øresland, 1985; Tande, 1983), although many of these populations also produce a significant second cohort in fall (King, 1979; Sameoto, 1973; Zo, 1973). The timing of spawning we observed in 2002 and 2003 was strikingly early in comparison to King's (1979) one-year study in Dabob Bay. He found that stage III individuals dominated the population in March and April and that a substantial increase in the number of stage I individuals was not noted until May.

Our observed stage composition patterns of *S. elegans*, and differences from those seen by King (1979), might have been caused by varying advection rates with depth that might affect larval and adult chaetognaths differentially. During late winter–early spring, it is possible that fresh-water runoff or wind events could push surface waters out of the bay and this would have a larger effect on more shallowly distributed larval chaetognaths than on the more deeply distributed adults. Osgood and Frost (1996) found that the seasonal abundance of three species of copepods in Dabob Bay could not be predicted based on knowledge of their life histories alone, and that advective exchange could be detected for most of the year except summer. Another consideration in estimating abundance and stage composition of *S. elegans* is the depth of our sampling. The depth of our station was 175 m, but the net tows extended only to 160 m to avoid net damage. Stage III and IV *S. elegans* are known to live close to the bottom in neritic areas, especially during breeding, and therefore the abundance of these stages may have been underestimated (Alvariño, 1965; Jakobsen, 1971).

The significant, positive correlation between abundances of larval *S. elegans* and copepodites seems to suggest that fluctuations in abundance of larval *S. elegans* and copepodites are related to similar processes. This is unlikely to be a causal relationship, however, because there was no significant relationship between feeding success of either larval or adult chaetognaths and copepod abundance. The limited instances of correlation between larval abundance and time-lagged copepodite abundance (i.e., significant only when data were shifted by one week and both years were combined) suggests that new recruits are probably not generated by an enhanced feeding response of adult chaetognaths on copepods. Moreover, it seems unlikely that *S. elegans* adult reproductive development is triggered or enhanced by increased availability of prey sources other than copepods, given the demonstrated dominance of copepods in the adult diet (Fig. 7; see also Alvarez-Cadena, 1993b; Ohman, 1986; Saito & Kiørboe, 2001). However, we cannot rule out the possibility of chaetognaths requiring some other prey constituent.

It may be possible though, that larval *S. elegans* survival is enhanced by the abundance of other prey sources not quantified in this study, such as protozoans. The diet of stage I *S. elegans* is more varied than that of adults and includes tintinnids and dinoflagellates, as well as copepod nauplii (Alvarez-Cadena, 1993b; Terazaki, 1998). Although much of the prey contained by larval *S. elegans* in our study was unidentifiable, they

consumed both copepod nauplii and tintinnid protozoans to a greater degree than did adult *S. elegans* (Fig. 7). Microzooplankton may appear to be underrepresented in chaetognath diets because such prey would be rapidly digested and would not leave identifiable hard parts. However, Reeve and Walter (1972) suggested that larval chaetognaths would not prey on loricate ciliates because they do not exhibit the characteristic jump and roll movement seen in loricate ciliates, and therefore would not be detected by the chaetognaths. Nevertheless, the role of microzooplankton in chaetognath feeding dynamics requires further clarification as significant feeding on protozoans other than tintinnids could significantly mitigate larval chaetognath dependence upon copepods.

5.2. Larval hake abundance and morphometric condition in relation to copepod prey

Prior to this project, two other studies have reported abundance patterns of larval Pacific hake in Dabob Bay. Bailey and Yen (1983) found similar, though somewhat higher, densities (approximately 1360 larvae m^{-2} in March of 1973) than we did. Bollens et al. (1992a) reported abundances of larval fishes during 1985–1987, with peak abundances of Pacific hake larvae of 135 m^{-2} in April 1986 and 326 m^{-2} in March 1987. The substantially higher densities found by us and Bailey and Yen (1983) compared to Bollens et al. (1992a) may be due in part to interannual differences, but more likely are a result of different net mesh sizes employed during the studies: Bollens et al. (1992a) sampled with a 571 μm mesh net, compared to a 209 μm mesh in our study and that of Bailey and Yen (1983), which likely resulted in the extrusion of the smallest larvae through the larger mesh.

Larval Pacific hake have been found to prey primarily upon copepod eggs, nauplii and copepodites (Sumida & Moser, 1980). However, our principal components analysis and analysis of individual morphometric measurements of larval Pacific hake in Dabob Bay both indicated that larval condition did not appear to depend upon copepod prey availability during the springs of 2002 and 2003. This may result from several factors, including limited variation in prey abundance in our data set. That is, the period of “high” densities of copepodite and naupliar prey were 2.12 times greater than the period of “low” densities in 2002 and only 1.65 times greater than the period of “low” densities in 2003 (Fig. 8). This may not have been a sufficient difference in prey densities to produce detectable change in larval condition, given the level of sensitivity of the morphometric technique. For instance, Suthers, Fraser, and Frank (1992) did not observe significant difference in morphometric condition of wild juvenile cod despite an order of magnitude difference in prey abundance. However, Cass-Calay (1997) was able to discern a significant difference in larval Pacific hake growth rates between stations that differed in average concentrations of prey-sized particles by less than a factor of two. Moreover, Koslow, Brault, Dugas, Fournier, and Hughes (1985) found that larval cod, *Gadus morhua*, showed changes in condition with prey concentration and that ABD vs. SL was the most sensitive morphometric parameter when compared to other body measurements.

These studies suggest that the differences in prey availability we observed in Dabob Bay may be great enough to generate differences in morphometric condition of larval Pacific hake, and that further tests over a broader range of prey conditions are warranted. For instance, it is possible that some of the copepods included in our “total copepod” estimate of over-all food availability were too large for the hake larvae to eat (although these larger forms constituted only a small proportion of the total copepod assemblage, which included many small species, early copepodite stages, and nauplii).

Indices of starvation, such as biochemical and histological tests, respond rapidly to environmental conditions and are most sensitive but also require high resolution sampling in order to correlate fish condition with immediate environmental conditions. Morphometric indices, while less sensitive, also allow lower resolution sampling because size-related organismal effects of food-limitation are likely to persist and be measurable despite greater time lags between cause and effect. The morphometric condition of hake larvae is likely to be the result of feeding conditions integrated over several days prior to capture. We sampled weekly, thus, we opted to use morphometric indices of condition. The size of hake larvae used in our analyses ranged from approximately 3.5 to 5.5 mm. Based on growth at age data from laboratory-reared Pacific hake larvae, this size range corresponds to larvae with approximately 5–15 daily otolith increments (Bailey, 1982). Daily increments begin to be added 1–2 days prior to total yolk sac absorption, which was suggested by Bailey (1982) to correspond to the onset of first feeding. Therefore, we estimate that larval

hake in our study had been feeding for approximately 1 day to 2 weeks prior to capture. Hake larvae at a length of 3.5 mm have been found to feed on prey ranging from 50 to 350 μm in width (Sumida & Moser, 1980). The range in width of prey extends to between 50 and 450 μm when the larvae reach a length of 5.5 mm (Sumida & Moser, 1980).

The lack of a significant relationship between larval hake condition and copepod prey, seen in both the analysis of individual body measurements and in principal components analyses, may be in part attributable to several aspects of the species' biology. Hake larvae have relatively large mouths compared to other larvae and feed on a wide size range of prey (Sumida & Moser, 1980). Hake larvae in Dabob Bay were found in greatest abundance in the 160–100 m depth stratum and thus typically inhabit cooler waters below the thermocline. This was suggested by Bailey (1982) to be an adaptation to take advantage of lower metabolic costs, which he supported by estimates of daily ration that were low and number of days to starvation that were high, in comparison with Pacific mackerel and northern anchovy. This capacity to feed on a wide range of prey items and to obtain metabolic benefits by residing in deeper, cooler water may make larval Pacific hake less sensitive to food limitation and starvation than some other species.

Several other sources of inter-annual and inter-seasonal variability such as turbulence, light, temperature and maternal condition may all affect hake condition, although it was beyond the scope of this study to test for such effects. Moreover, it is possible that net avoidance obscured the true condition of the population, i.e., healthy hake larvae may have been more capable of avoiding the net and were underrepresented in our analysis, thus, reducing our ability to detect real variation in condition within the population. Differences in capture and fixation processes may also obscure results of morphometric analyses, although post-preservation studies of shrinkage in Pacific hake have not been performed. Hay (1981) monitored the shrinkage of larval Pacific herring following preservation with formalin for 60 days and found that most of the shrinkage occurred within the first 20 min after fixation. Shrinkage for two trials of 60 day duration was 5.7% in each. Shrinkage after 23 days in a separate trial was 5.3%. Given that changes to larval morphology appear to mainly occur very soon after preservation, and that all larvae used in this study were preserved for several months prior to measurement, it is unlikely the preservation time had a considerable effect on the larval hake morphology.

5.3. Summary and conclusions

The controversy over the requirements of *S. elegans* for prey centers on the apparent linkage between chaetognath ontogeny and copepod population pulses, contrasted with a lack of evidence for a relationship between feeding success and prey density. Our study reinforces previous findings that feeding success in *S. elegans* is not related to copepod prey availability. Adult *S. elegans* preyed heavily upon copepodites, however, feeding success of neither larval nor adult *S. elegans* showed a relationship to copepod availability. The common observation of a relationship between *S. elegans* recruitment and copepod pulses was also demonstrated in our study by the significant correlation between the appearance of larval *S. elegans* and copepodite abundance in both 2002 and 2003. However, copepods and chaetognaths may simply be responding to similar environmental (biotic and abiotic) factors, rather than there being a direct causal linkage between abundances of predator (chaetognaths) and prey (copepods).

For larval Pacific hake, regression analysis of food-sensitive and food-insensitive body measurements produced no indication of consistent changes in larval condition with differing prey concentrations. Likewise, principal components analysis showed no significant relationship between larval condition and copepod prey availability. Further field and/or laboratory studies that include a broader range of prey conditions may help clarify the role of food-limitation in larval Pacific hake.

Based on these analyses, it appears unlikely that springtime variation in copepod abundance caused by deleterious diatom blooms would greatly affect these two planktonic predators in Dabob Bay. Diatom toxicity and/or nutritional deficiency has had drastic effects on copepods in the laboratory (Uye, 1996), although it is not known under what conditions diatom effects may be significant in the field (but see Halsband-Lenk, Pierson & Leising, this issue and Pierson, Halsband-Lenk & Leising, this issue). To the extent that there are deleterious effects of diatoms on copepods (see other papers in this issue), our results suggest that the repercussions for higher trophic levels will be dampened.

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