Trophic dynamics in the San Juan Channel during fall 2012

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Abstract

The seasonal dynamics of trophic interactions in diatoms, calanoid copepods, and Pacific sand lance in the San Juan Channel were examined over the fall season. There was a very large diatom bloom on October 10th (118,707.53 diatoms L^{-1}) after which density remained low. Calanoid copepod density also peaked on the 10th (5,159.31 individuals m^{-3}) then decreased with slight fluctuations. Nauplii decreased in abundance during the season, especially relative to adult calanoids, probably due to their life history pattern which favors development to copepodite stage V before over-wintering diapause. Lipid reserves in calanoid copepods increased immediately following the diatom bloom, then remained low the rest of the season. The greatest percent of sand lance with calanoids in their stomachs (23.1%) was found before the plankton blooms. It is suggested that this may be because they begin hibernation without regard to a fall bloom, since fall bloom timing is very inconsistent. Overall, a temporal linkage in trophic dynamics was evident between primary and secondary productivity, but not between the plankton and sand lance. Sampling the sand lance feeding in the water column would strengthen further evaluation of sand lance trophic interactions with diatoms and copepods.

Introduction

Seasonal change in temperate marine waters affects organisms at all trophic levels. At the foundation of these seasonal transitions are changes in physical factors such as sunlight, temperature, and wind. Sunlight warms the sea surface and provides radiation for photosynthesis; however, in higher latitudes daily sunlight varies quite widely throughout the year. Temperature also varies by season and is important because it controls rates of chemical processes and, based on their physiological tolerances, influences what organisms live in certain areas (Lalli and Parsons 2000).

The San Juan Archipelago (SJA) is located at approximately 48^{o}N latitude and experiences prominent seasonal changes. During the transition from fall to winter, these include a shorter photoperiod, lower temperatures, and a shift in the direction of prevailing winds with subsequent impacts on the water column. None of these seasonal changes are favorable for primary productivity (Carlotti and Radach 1996). Secondary productivity, which depends on primary producers, must respond to these changes. In the SJA, the majority of secondary producers are copepods in the genus *Calanus* (Zamon 2002). Calanoid copepods are an important trophic link because they feed on phytoplankton and are a primary food source for many invertebrates, fishes, birds, and whales (Bergvik et al. 2012; Hirche, 1996; Li et al. 2000). They are known to feed on a variety of plankton (Kleppel et al. 1991; Ban et al. 1997) and tend to eat whatever plankton is most abundant in the water (Marshall and Orr 1972). Because of their large abundance, they are vital to the success of pelagic fisheries (Hirche 1996).

Forage fish are another important part of this food chain because they feed on zooplankton and are a primary source of food for upper trophic levels such as seabirds. In the San Juan Channel, members of one abundant species of forage fish, the Pacific sand lance, are found in a large sand-wave field. They feed on plankton during the day in the water column when not burrowing in the sediment of the wave field to rest or hide from predators (Greene et al. 2011).

Both sand lance and calanoid copepods exhibit overwintering behaviors in autumn and winter. Calanoid copepods enter a state of diapause during the winter when they reduce their metabolism and cease development before becoming active again in the spring to reproduce (Marshall and Orr 1972; Hirche 1996; Marcus 1980). Sand lance bury in sandy substrate for several months during the winter to conserve energy (Green et al. 2011; Haynes and Robinson 2011). They also emerge in the spring to spawn (Green et al. 2011; Healy 1984).

The objective of my research was to observe trophic interactions in these three populations, each a different trophic level, by examining how they change in relation to each other over the course of the season. To do so I compared during autumn (1) abundances of diatoms, (2) abundance of calanoid copepods, (3) abundances of calanoid copepod adults and nauplii, (4) abundances of adult calanoid copepods with varying lipid storages, and (5) abundance of Pacific sand lance found to have eaten calanoid copepods. I looked for temporal relationships in these trophic groups in terms of seasonal changes.

Methods

Study site

The San Juan Channel, running north-south through the San Juan Archipelago, is an estuarine environment located between the Fraser River delta and the Strait of Juan de Fuca. It is connected to the Pacific Ocean. Pronounced seasonal changes in sunlight, temperature, and wind occur during the transition from summer to winter. The channel supports a productive pelagic ecosystem composed of taxa including phytoplankton (among the most dominant are *Coscinodiscus spp., Ditylum spp.,* and *Chaetoceros spp.*), zooplankton (most dominant are *Calanoida spp.*), forage fish (such as Pacific herring and Pacific sand lance), birds (gulls, alcids and murres), and mammals (porpoises, seals, and sea lions).

Sampling stations

All field data were collected from the R/V Centennial, a University of Washington research vessel. For plankton samples and hydrographic measurements, two stations, North Station (48˚35.00’ N 123˚02.50’ W) and South Station (48˚25.20’ N, 122˚56.60’ W) were chosen for sampling due to differing influences on their water properties. North Station experiences a high level of tidal mixing and freshwater input from the Fraser River which enters the Strait of Georgia to the north (Fig. 1). South Station is characterized by salt water input from the Pacific Ocean via the Strait of Juan de Fuca. Pacific sand lance were sampled from the sand-wave field where they are known to burrow, located between these two stations (Fig. 2). These sites were sampled seven times throughout the autumn: September 28th, October 10th, 17th, 23rd, and 30th, and November 7th and 13th.

Hydrographic measurements

At each station a Seabird SEACAT SBE-19 conductivity-temperature-depth instrument (CTD) was deployed, recording data on salinity (PSU), temperature (^{o}C), depth (m), dissolved oxygen (mg/L), and fluorescence (µg/mL) continuously as it descended to 10 m above the substrate. At South Station this depth was normally about 80 m and at North Station about 115 m. Water samples from depths of 0 m, 10 m, 30 m, 50 m, and 10 m above the substrate were collected in each of two 2 L Niskin bottles on the CTD for chlorophyll and nutrient samples. A Secchi disk was used to measure the depth of the euphotic zone. The weighted, white disk was deployed by hand into the water until it was no longer visible from the surface, and this depth was recorded to the nearest half meter.

Plankton sampling

Phytoplankton were collected in a 26 cm diameter ring tow net with 80 µm mesh fitted with the top half of a plastic bottle on the narrower end in which the plankton collected. The net was deployed by hand and towed vertically from 34.8 m depth to the surface. Zooplankton were collected in a 70 cm diameter ring tow net with 153 µm mesh fitted with a cod end in which the plankton collected. The net was hauled in vertically using the ship's winch from 10 m above the substrate to the surface. Each tow was duplicated at North and South Station. Samples were transferred into jars and fixed with a buffered formalin solution.

Pacific sand lance sampling

Pacific sand lance were collected from sediment in the San Juan Channel sand-wave field. This was done using a Van Veen sediment grab. It was deployed from the R/V Centennial using a winch until it hit the sea floor, and then was retrieved, capturing sediment and any sand lance within it. The Van Veen was opened into tubs on board and sand lance were removed from the sediment. They were then given a lethal dose of MS-222 and preserved in formalin for later analyses.

Photosynthetically active radiation sampling and analysis

Photosynthetically active radiation (PAR) values (µmol photons m^{-2} s^{-2}) taken in 15 minute intervals were obtained from the Friday Harbor Labs Weather Station. PAR values versus time were integrated using trapezoidal integration to obtain units of µmol photons m^{-2}. For each cruise date, integrated PAR values from that day and the four days leading up to it were added, to assess radiation used for the phytoplankton population sampled.

Hydrographic analyses

The euphotic zone was calculated using Beer's law for irradiance

$$E(z) = E(0)e^{-kz}$$

where z=depth of euphotic zone (m), $E(z)$=% irradiance at depth z, $E(0)$=% irradiance at surface (100%), e=Euler's number (2.718...), and k=the attenuation coefficient (m^{-1}). In Puget Sound waters, k is equal to 1.6 divided by the Secchi disk reading in meters (Holmes 1970, derived from Poole and Atkins 1929). The bottom of the euphotic zone is defined by a light level too low for photosynthesis to occur—1% of surface irradiance—where $E(z)/E(0)$=0.01, and the equation can be solved for the depth of the euphotic zone.

Nutrient concentrations were measured in water samples from the Niskin bottles. Water was filtered through a 0.45 µm filter, frozen, and then sent to the University of Washington School of Oceanography Laboratory for determination of nitrate, nitrite, ammonium, silicate, and phosphate concentration.

Plankton sample analysis

Phytoplankton net tow samples were poured through an 80 µm sieve, rinsed with tap water, and split using a plankton splitter to an appropriate counting density. The split was diluted to 400 mL and diatoms were counted from a 0.1 mL aliquot using a Nikon Eclipse 50*i* compound light microscope. Individuals in the five most abundant genera were counted: *Coscinodiscus, Ditylum, Rhizosolenia, Asterionellopsis,* and *Chaetoceros*. Density was calculated for each tow, taking into account the volume the net tow filtered, the net diameter, and the sub-sampling split.

Zooplankton tow samples were poured through a 118 µm sieve and rinsed with tap water. The collected plankton were split using a plankton splitter to an appropriate counting density. Splits were diluted with tap water to 700 mL. From a 5 mL aliquot in a gridded petri dish, calanoid copepod adults and copepod nauplii were counted using a Nikon SMZ645 dissecting microscope. Calanoid adults were classified based on lipid stores, which were orange in color. Class one had no lipid stores, class two had lipids but were less than half full, class three were half full of lipids, class four were more than half full but not completely full, and class five were completely full. Densities were calculated for each tow volume.

Pacific sand lance sample analysis

Five fish from each age class were dissected for gut contents per sampling region, up to 20 for each Van Veen grab. Calanoid copepods were identified using a dissecting microscope and counted when possible.

Results

Diatom densities of *Coscinodiscus* and *Chaetoceros* were compared from 2006 through 2012 with the exception of 2008 when no data on diatom abundances were recorded. These two taxa were selected for this interannual comparison because they were the only two in the PEF database counted every year for North and South station. Average yearly densities were 0.43 diatoms L^{-1} in 2006; 191.55 in 2007; 40.55 in 2009; 238.29 in 2010; 255.73 in 2011, and 3,980.52 this year. There was no consistent seasonal pattern in the timing of a diatom bloom across the six fall seasons (Fig. 3). Some years lacked a bloom, some had an early bloom, and others a late bloom. However, one consistent trend was that diatom density at the end of the season was lower for all years except 2007.

This year, diatom density was on average at least 15 times higher than in the other years examined. There was a large diatom bloom on October 10th of this season (118,707.53 diatoms L^{-1}) that was over an order of magnitude larger than the next highest diatom density for any other year (897.79 diatoms L^{-1} in 2011). This year, diatom densities for the first three cruises were all higher than the highest for any other year. Then, after the first three cruises this year, diatom densities remained lower with values comparable to past years.

The large bloom on October 10th was characterized by increases in five different diatom taxa (Fig. 4). *Asterionellopsis* was dominant at the north station and *Chaetoceros* at the south. The average depth of the euphotic zone decreased during the diatom bloom, from 27.34 m to 20.15 m, which means that something in the water was absorbing and attenuating light. After the tenth, the depth of the euphotic zone increased but continued to vary (Fig. 5). Overall, the general trend is that euphotic zone depth decreased over time.

The concentration of nitrate in the surface layer dropped to its lowest for the season on the day of the bloom (15.46 µM) (Fig. 6). This decrease is consistent with the active uptake of nitrate by diatoms for growth during the period. Excluding this date, the nitrate concentration increased steadily throughout the season, from 20.48 to 23.02 to 24.51 µM, and never fell to limiting levels—typically below 5 µM; (Newton et al. 2002). To assess the light-limitation of diatom growth, the correlation of diatom growth and PAR data was assessed. Since diatom blooms typically respond to light after a period of three to five consecutive sunny days (Newton et al. 2002), PAR was totaled for five consecutive days and then compared. During 2012, high diatom density consistently followed five-day periods of high PAR, providing up to $1.33*10^8$ µmol photons m^{-2} (Fig. 7). After October 10th, diatom density and five-day PAR values dropped, reaching a low of $3.19*10^7$ µmol photons m^{-2} on the last sample day.

Total diatom and calanoid densities covaried early in the season, up until October 30th when calanoid density increased despite very low diatom density (Fig. 8). Over the entire season, the average density was 2,722.07 copepods m^{-1}, and the highest and lowest average calanoid densities for a given sample date during this time were 5,159.31 and 1,497.59 copepods m^{-1}, on October 10th and November 7th, respectively. Later, calanoid density was comparatively low but continued to fluctuate despite consistently low diatom density.

Similarly, the density of adult calanoids increased during the diatom bloom (3,869.53 individuals m^{-3}). In the second part of the season, their density varied with the same pattern of fluctuations as observed of total calanoid density, and there was an increase in the average adult density on the last sample date (1,762.83 individuals m^{-3}) (Fig. 9). Density of nauplii generally decreased as the season went on, with a high on October 10th (1,289.78 individuals m^{-3}) and a low on November 13th (153.89 individuals m^{-3}). The ratio of adults to nauplii increased over time, starting at 1.47 and ending at 11.52 (Fig. 10).

The average proportion of calanoids containing lipids in the first three days of sampling was twice as high as the average for the whole rest of the season (0.33 and 0.17 individuals m^{-3}) (Fig. 11). After it dropped on the 23rd of October to 0.167 individuals m^{-3}, it fluctuated with an increase to 0.20 individuals m^{-3} on October 30th. The density of calanoids in all lipid classes peaked during the diatom bloom (1,442.73 individuals m^{-3}) and so did the density of each class (class one 2,426.80; class two 732.25; class three 446.60; class four 216.00; class five 47.88 individuals m^{-3}) and decreased over the next two weeks (Fig. 12). Class one remained the dominant lipid class throughout the season. Class two had similar temporal variation at the second highest density. Both these classes peaked again slightly on October 30th (class one 1,401.32; class two 346.35 individuals m^{-3}). Classes three, four, and five were consistently the third, fourth, and fifth most dense, and dropped to extremely low densities during the last four sampling dates, when they averaged 18.72, 4.20, and 0 individuals m^{-3}, respectively.

A total of 67 Van Veen grabs were made, catching 155 sand lance. The highest percent of sand lance found with calanoids in their gut was on the first sample date, before the plankton blooms (23.1%) (Fig. 13). Fewer were found throughout the rest of the season, averaging 0.019% found with calanoids per sampling date.

Discussion

Over the six years examined, diatom density showed no consistent seasonal trend, and the timing or presence of the fall diatom bloom varied widely between and within years. This may be due to the fact that local weather is the biggest indicator of primary productivity in the Strait of Juan de Fuca (Li et al. 2000), and other physical factors such as water temperature, salinity and tidal mixing play a role, as well as biological factors such as grazing by higher trophic levels (Hirche 1996). Since 2006 there have been both El Niño and La Niña years as well as positive and negative index values in the Pacific Decadal Oscillation, providing evidence that there may have been significant climatic variations during these years (NOAA 2012; Mantua 2012).

The 2012 fall season was characterized by an overall decreasing trend in diatom abundance with time, but with one exceptionally large bloom early in the season. The pattern was observed at both stations and in five different diatom taxa. Dominant diatom taxa differed by station, indicating that the two stations were ecologically distinct on the day of sampling, most likely due to influences of different water bodies. This season, surface waters at the south station were on average colder and saltier than the north station (Williams 2012). This is likely because the south station is closer to the Strait of Juan de Fuca which inputs oceanic water and the north station is closer to the Fraser River which inputs freshwater. Growing conditions were good at both stations.

The bloom was dense enough at both stations that it blocked sufficient sunlight to cause a shoaling of the depth of the euphotic zone, which otherwise consistently decreased over the course of the season. The decrease was probably a result of, but not limited to, cloudier weather and strong tidal mixing that prevented terrigenous particles from settling out. Because the nitrate concentration decreased substantially during the bloom, we can infer that the diatoms were actively growing. Furthermore, nitrate concentrations did not drop to what is considered limiting in estuarine environments (Newton et al. 2002), a result which is supported by the observation that phytoplankton in the Puget Sound are typically light- and not nutrient-limited (Li et al. 2000). Therefore, we would expect that available sunlight would be a strong driver in diatom abundance, which the results of this study confirm.

The presumably light-limited diatoms were in bloom concentrations on October 10th most likely because it was after a five-day period of high PAR early in the season. Consistent with this correlation, the end of the season was characterized by low PAR and low diatom density. However, the most sunlight occurred on the days leading up to September 28th, yet there was no bloom observed then. The hydrographic data for this season show a strong pycnocline at the south station on October 10th at about 39 m depth (Williams 2012). This prevented surface waters from mixing downward, such as would have occurred during September 28th when the pycnocline was deeper and less pronounced. A strong and relatively shallow pycnocline would keep the diatoms in the euphotic zone where they could access the ample PAR and grow rapidly. Furthermore, on average the temperature of the euphotic zone was highest on the 10th compared with other sampling dates, which favors growth. The result of a bivariate fit of diatom density and five-day PAR including and excluding the bloom date supports the conclusion that multiple external factors played a role in the diatom bloom this year. The relationship is better correlated and more significant when the 10th is excluded (R^2=0.321, P=0.0346 with the 10th; R^2=0.759, P=0.0002 without the 10th).

The exceptionally large diatom bloom this season potentially provided a signal to be traced through other trophic levels. This signal was seen in calanoid copepod density, since it peaked at the same time. In other marine ecosystems, a lag time between primary and secondary productivity is expected (Carlotti and Radach 1996), but in the Strait of Juan de Fuca, zooplankton abundance has been known to increase and decrease with phytoplankton abundance due to advection of a seed population of zooplankton from the Strait of Georgia (Li et al. 2000). The resolution of sampling time should also be taken into consideration when looking for temporal patterns. There were two weeks between when the first and second samples were taken, and a week between the second and third. Actual peaks in density could have occurred on a day that was not sampled.

Other factors not measured in this study would also have influenced the apparent diatom and copepod abundances. First, secondary productivity is not limited to calanoid copepods. For example, *Coscinodiscus spp.* have been found in the stomachs of Pacific sand lance (Zamon 2002; Sisson 2012), suggesting that they are trophic omnivores, which would blur the boundaries of the trophic levels and complicate the analysis of trophic interactions. Furthermore, sedimentation and respiration may play a large role in reducing diatom biomass (Kleppel et al. 1991). For the copepods, predation, especially from forage fish, and the availability of other food organisms drive calanoid density (Ban et al. 1997; Kleppel et al. 1991; Carlotti and Radach 1996). In fact, while diatoms make up a large part of copepod diet during certain seasons, alone they are not a sufficient diet for copepods (Ban et al. 1997). Diatoms were only a small part of the diet of calanoids in one study, where instead they preferred dinoflagellates and microzooplankton (Kleppel et al. 1991).

If the calanoids were actively reproducing during the diatom bloom, one would expect a subsequent increase in nauplii abundance, which was observed on the 30th of October. However, the overall seasonal trend was a decrease in nauplius density. This can be explained by the copepods' life history. Calanoid copepods develop to the latest copepodite (CV) stage before entering diapause for the winter (Marshal and Orr, 1972), so, presumably as the fall season progressed, the nauplii matured. In addition, the presence of diatoms may have contributed to the decline in nauplii density. The ingestion of diatoms in a high enough concentration can decrease fecundity and developmental success in copepods. Diatom densities ranging from 10^5 to 10^7 cells L^{-1} may be enough to cause embryonic mortality in copepods (Ban et al. 1997). This season, diatom density during the bloom reached $1.19*10^5$ cells L^{-1}. It is possible, then, that diatoms reduced the reproductive ability of calanoids.

Lipid storage is important in overwintering calanoid copepods. Calanoids must have lipid reserves in order to survive diapause, so as the season went on it was expected that they would contain more lipids (Hirche 1996; Bergvik et al. 2012). However, in this study there were more copepods sampled with lipids during the first half than the latter half of the season. The difference in the expected and observed patterns may be explained in light of three previous findings: that calanoid copepods can store more lipids when food is plentiful (Marshall and Orr 1972), that lipid content can be a signal for diapause (Bergvik et al 2012), and copepods preparing for diapause seek deeper waters (Hirche 1996; Bergvik et al 2012; Carlotti and Radach 1996; Fiksen 2000). The seasonal dynamic could have progressed as follows. First, the copepods fed on the abundance of diatoms early in the season and stored lipids. Then, their fuller lipid sacs signaled them to drop to deeper waters for diapause. Finally, since the plankton tows did not sample the bottom 10 m of the water column, it is possible that the net missed the concentration of diapausal copepods full of lipids in this depth layer.

It is likely that many copepods were overwintering during our sampling because it has been demonstrated that copepods begin sinking to deep layers as early as June or July (Carlotti and Radach 1996; Bergvik et al. 2012). In addition, in previous studies many of these deep CV copepodites contained more lipids than those in upper layers (Bergvik et al. 2012). Overall, much of calanoid copepod life history is either unknown or dependent on a number of variables collectively such as lipids, photoperiod, food availability, temperature, depth, and predation, so it is conceivable that in the San Juan Channel they have adapted specifically to local conditions (Marcus 1980; Bergvik et al. 2012; Hirche 1996; Fiksen 2000). Future studies could examine driving factors of calanoid diapause in this area. For example, an interesting experiment might include capturing live, non-diapausal copeopds and subjecting them to varying light regimes, temperatures, or foods to determine to what degree diapause is induced by changes in these external factors.

While diatom and calanoid densities may be closely related, this was not the case with sand lance feeding. The most sand lance were found with calanoids in their guts before the plankton blooms, which indicates their feeding was not driven by plankton abundance. This could be for a variety of reasons. Sand lance eat a large variety of organisms such as polychaetes, cyclopoid copeods (Sisson 2012), gastropods, larvaceans, and cladocera (Rood 2010), and may prefer to eat these prey over calanoids. They also may have adopted a consistent feeding behavior that is not influenced by seasonal fluctuations in certain species of plankton. Since the timing and presence of a fall bloom is highly unpredictable in this area, the fish also may not be adapted to exploit excessive food resources late into the season when they may be preparing for hibernation.

This final trophic dynamic, however, could be an artefact of the sampling method. Sand lance feed in the water column, but our method only sampled those burrowed in sediment. Sand lance are thought to rest and hibernate in the sediment, and infaunal fish may not be a good representation of the actively feeding population. This year, it is possible these fish had begun hibernation at the time of the study, at which point they stop feeding for long periods of time (Greene et al. 2010). There is evidence of this hibernation this season because many fish had empty stomachs by the second week of October this year (Heller 2012). Also, much of the stomach content of the sand lance was unable to be identified due to high amounts of digestion, so they may have been feeding on more calanoids than were able to be counted.

In summary, the results of this study indicate that during fall 2012 a linkage in the trophic dynamics between diatoms and calanoid copepods was apparent; however, linkage of these producers with sand lance was not demonstrated, but may be influenced by the sampling design of this study. Further research should employ fish sampling methods that can more accurately assess feeding fish. Overall, it is difficult to detect seasonal trends in trophic dynamics with such coarse resolution of sampling time and variability in ecological factors. Without a finer temporal scale both within fall and covering more seasons, we are limited in the ability to make many strong inferences about trophic dynamics.

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Figures

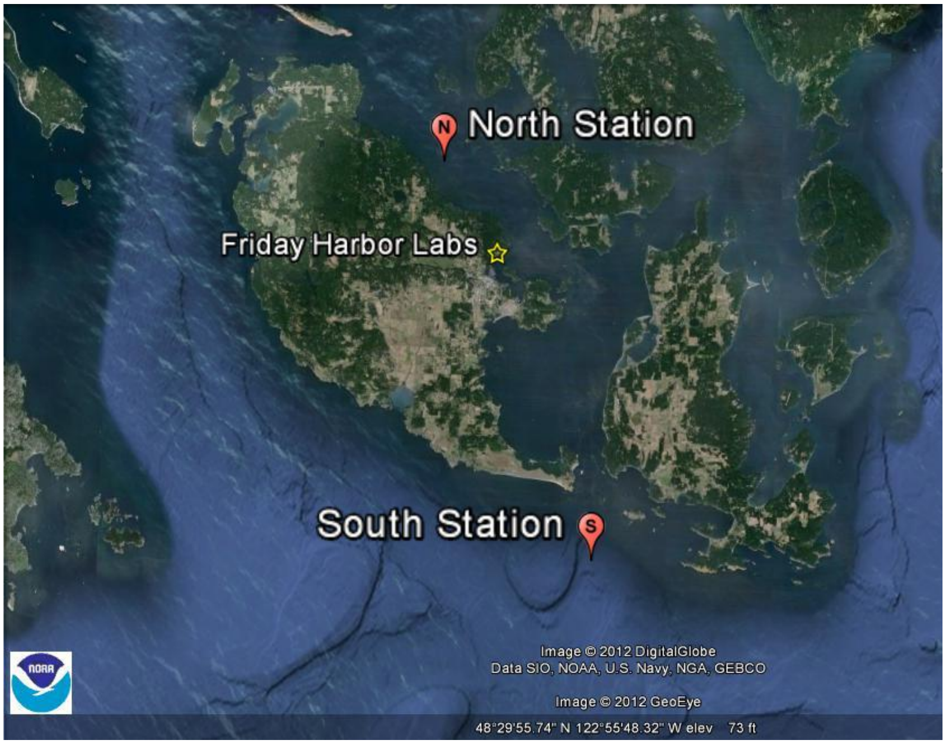

Fig. 1 North and South stations where plankton were sampled and hydrographic measurements were taken.

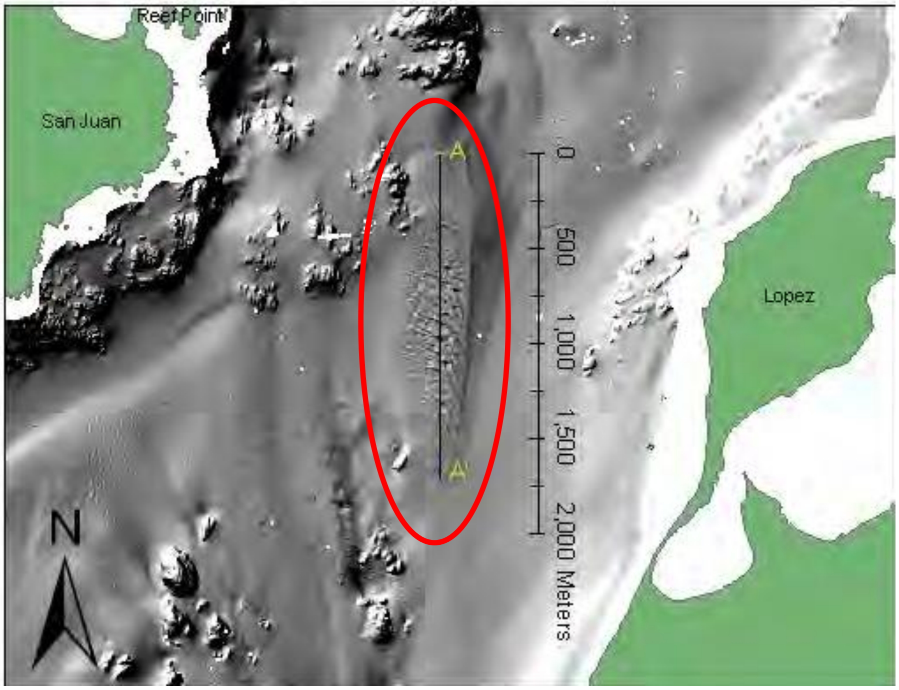

Fig. 2 The San Juan Channel wave-field where sand lance were captured.

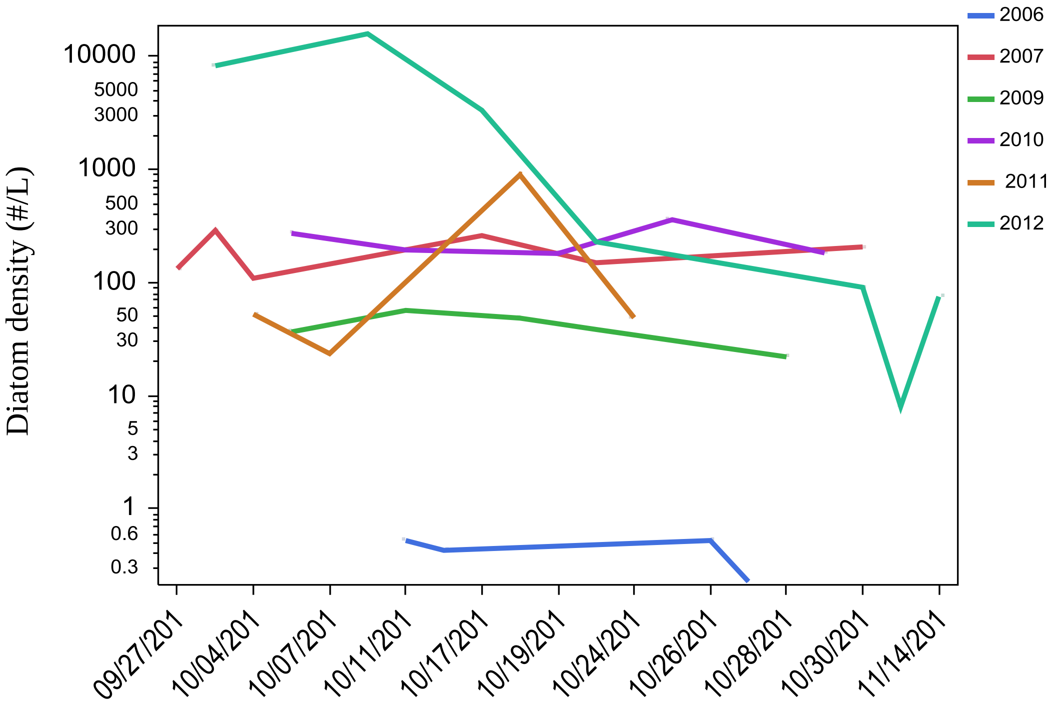

Fig. 3. Average density of *Coscinodiscus* and *Chaetoceros* for six years. Note: for all figures, the final x-axis date label should read 11/13/2012.

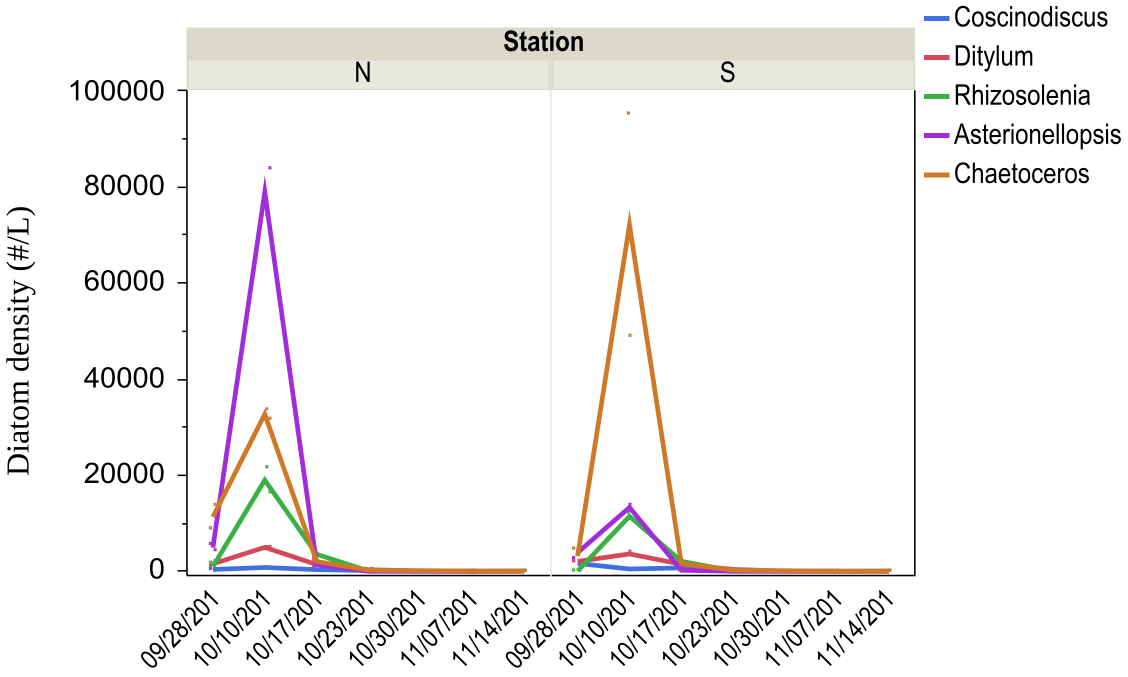

Fig. 4. Average diatom taxa densities by station over the fall season.

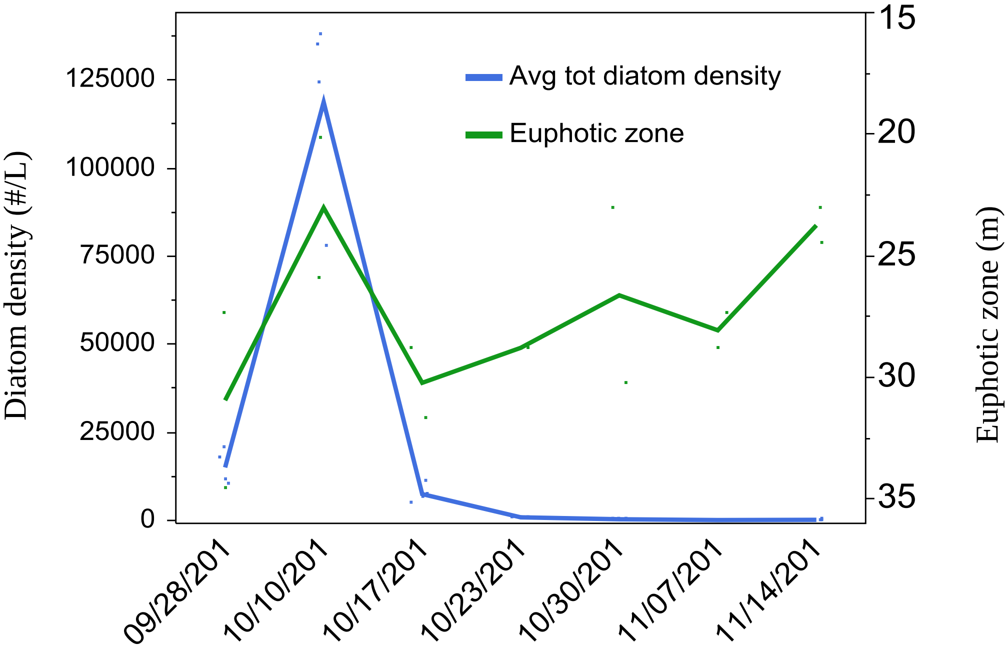

Fig. 5. Average total diatom density and euphotic zone depth over the fall season.

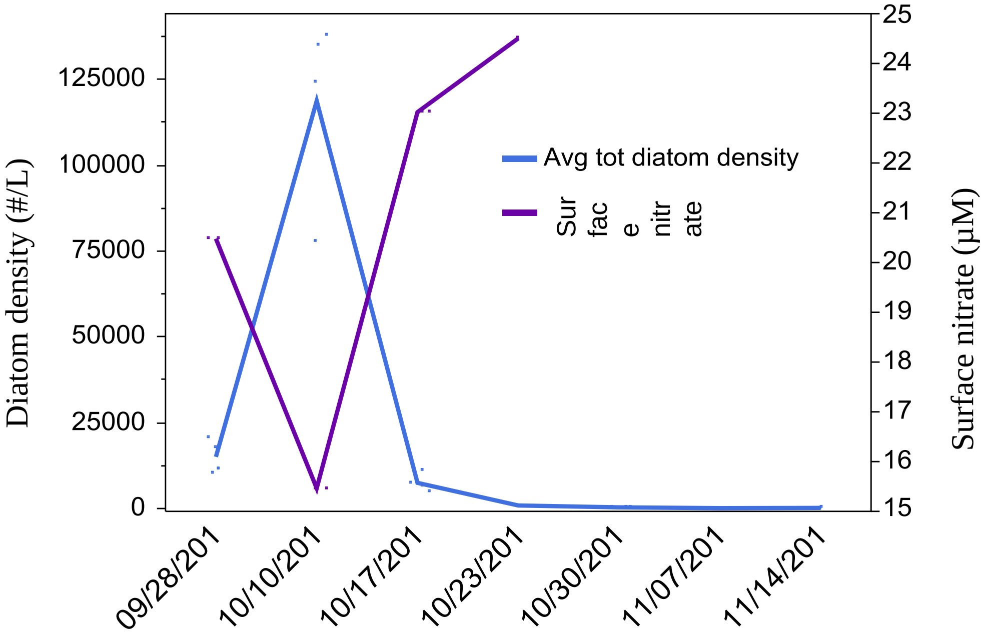

Fig. 6. Average total diatom density and surface nitrate concentration over the fall season.

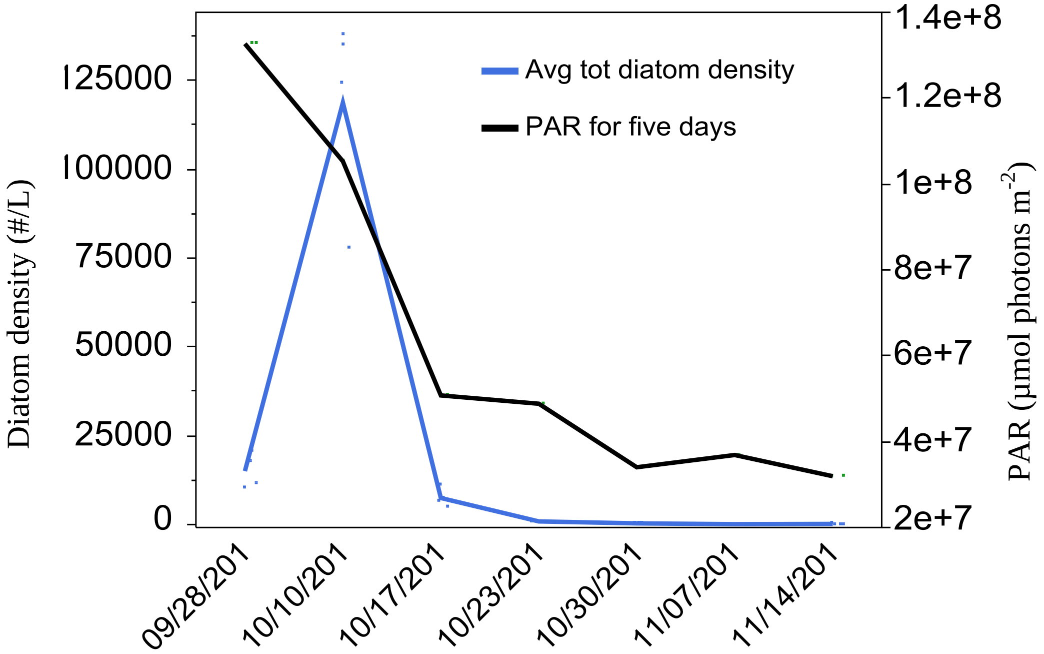

Fig. 7. Average total diatom density and the sum of PAR for five days over the fall season.

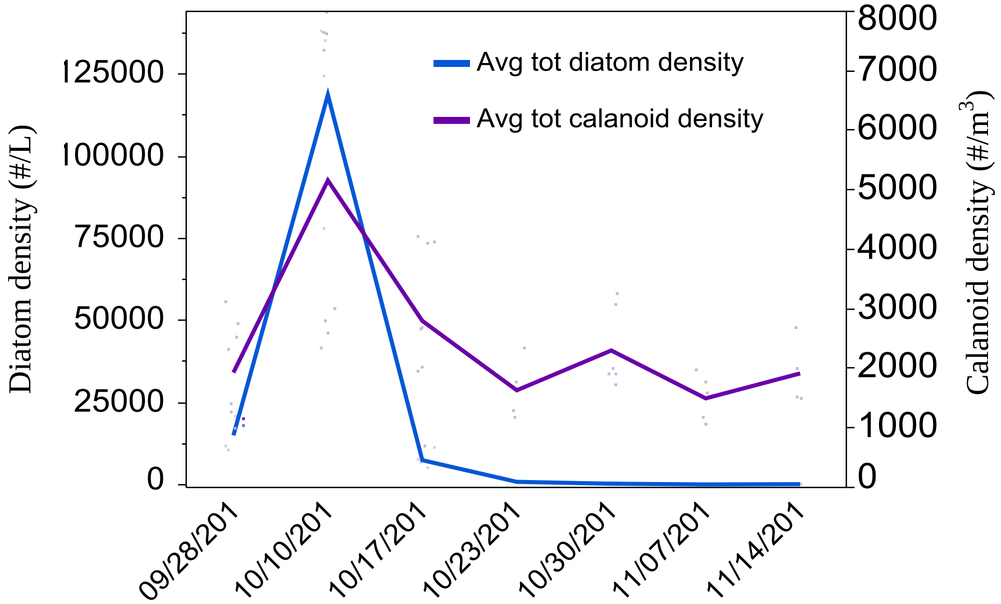

Fig. 8. Average total diatom and calanoid copepod densities over the fall season.

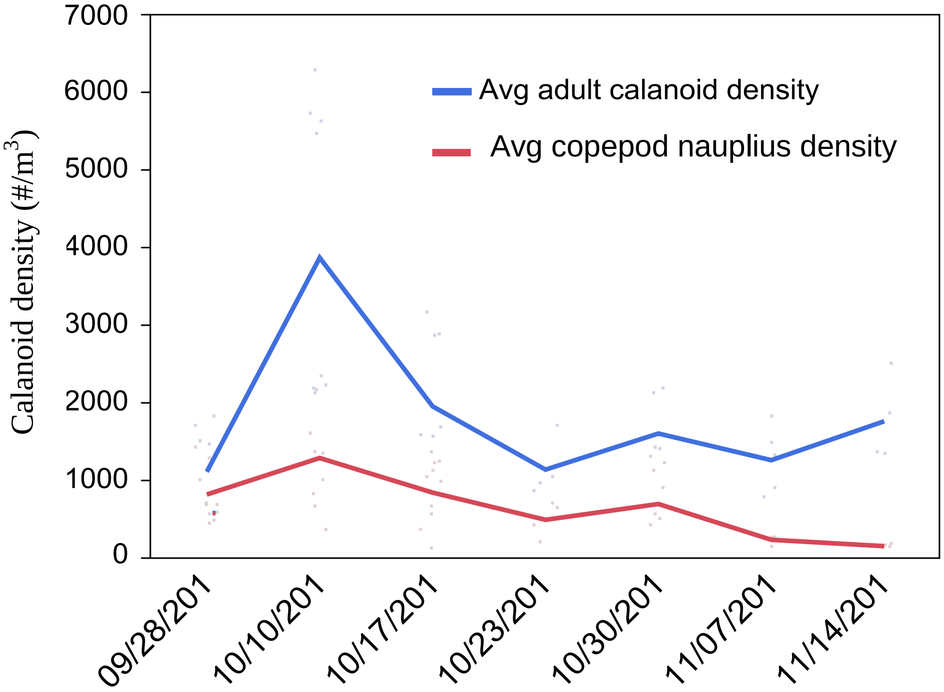

Fig. 9. Average total densities of adult calanoids and copepod nauplii over the fall season.

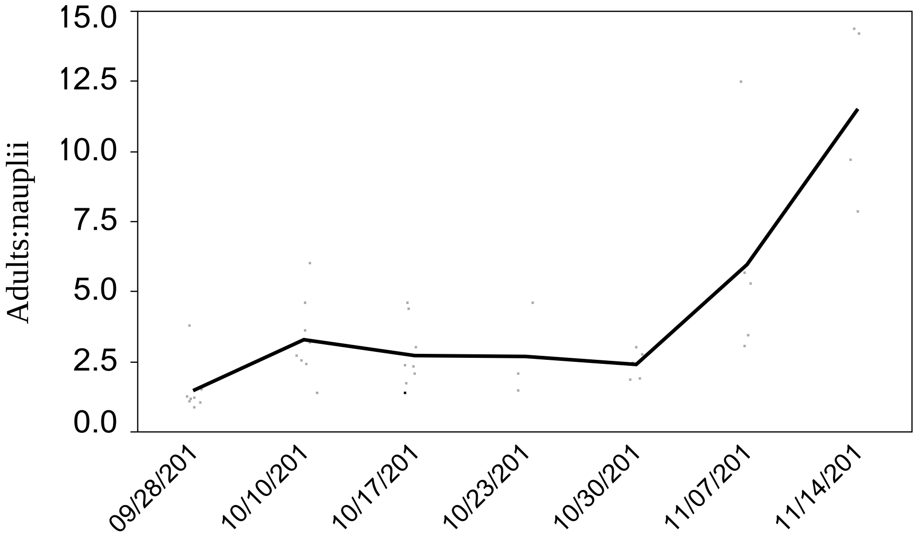

Fig. 10. Average adult:nauplii ratio over the fall season.

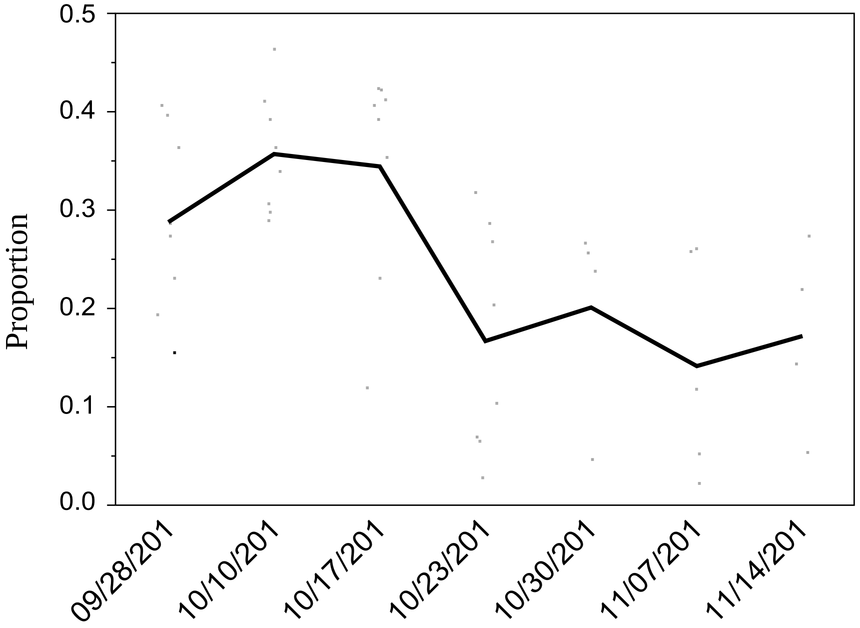

Fig. 11. Average proportion of calanoid copepods containing lipid reserves over the fall season.

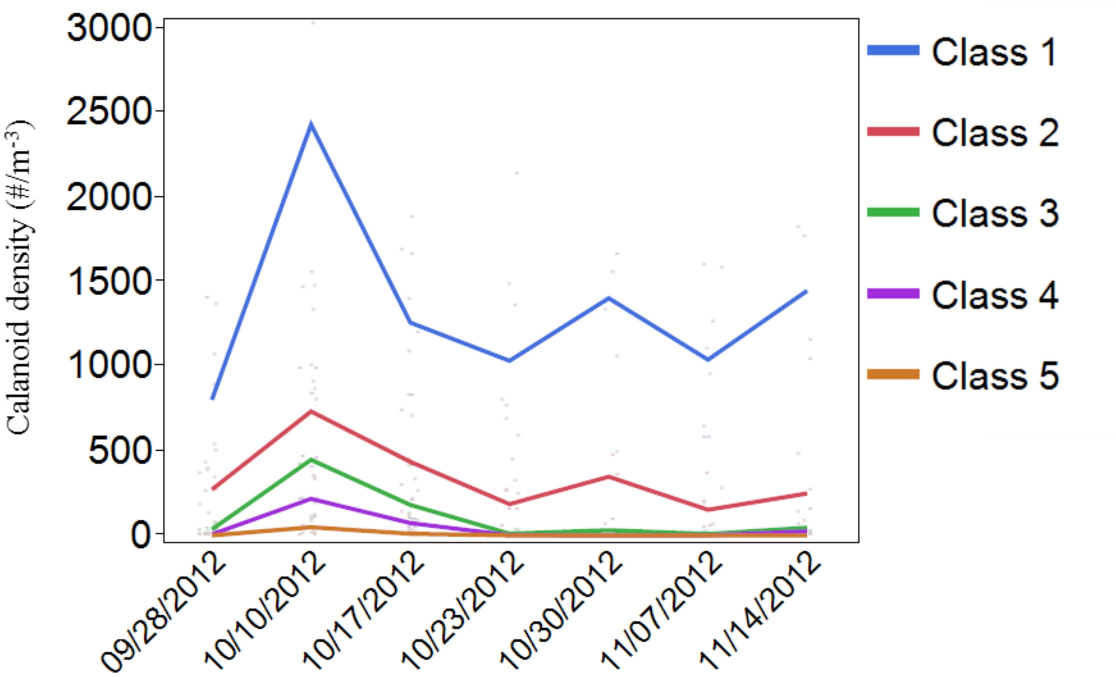

Fig. 12. Average densities of calanoids in each lipid class over the fall season.

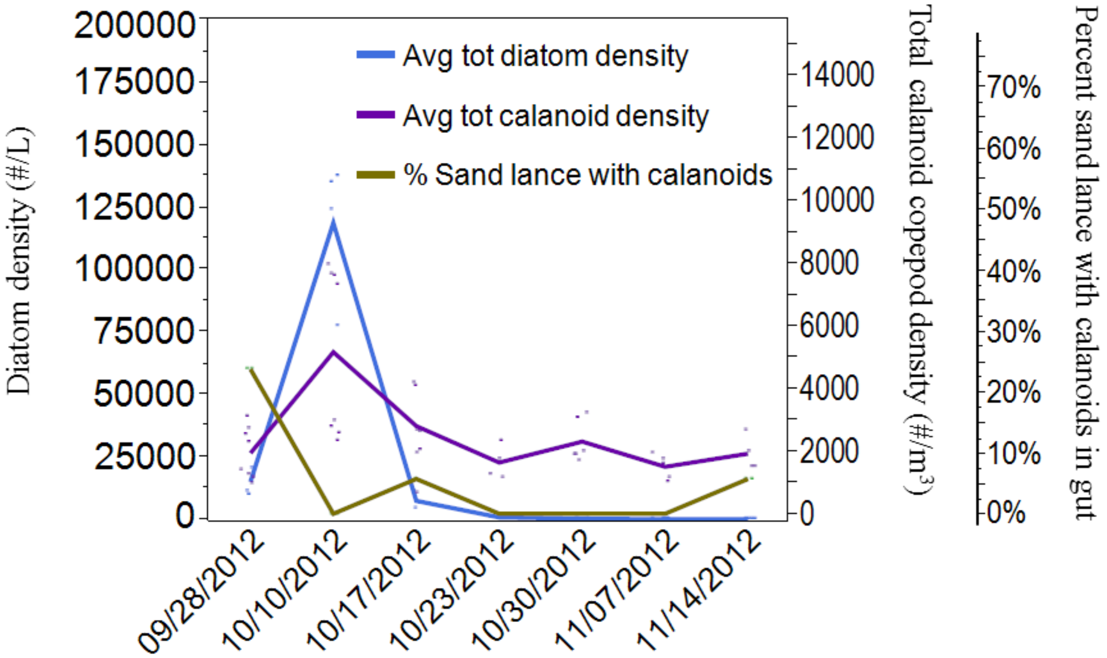

Fig. 13. Average total diatom density, average total calanoid density, and percent of sand lance found with calanoid copepods in their stomachs over the fall season.