

Climate change and the mechanisms behind larval success, recruitment and commercial catch for the Dungeness crab, *Cancer magister*.

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Abstract

We have 23 years of daily light trap sampling of Dungeness crab megalopae, (*Cancer magister*,) in Coos Bay Oregon. The annual megalopae catch varied from ~2,000 to 2.5 million, a factor of ~3,000. Lowest catches occurred during strong El Niño years. Megalopae catch is significantly correlated to the PDO (more caught during negative PDO), the day-of-the year of the spring transition (more caught with an early transition), and the amount of upwelling during the settlement season (more caught with more upwelling). Annual catch of megalopae is significantly correlated to commercial catch of crabs four years later and takes the form of two curves, years with <100,000 megalopae caught (>80% variability explained) and years with >100,000 caught (>70% explained). Using these correlations, we can make accurate predictions ($\pm 12\%$, SD 9%) of the commercial catch four years in advance. However, our predictions underestimate by about a factor of 1.5 in years with spring/summer marine heatwaves. We hypothesize that young crabs grow faster and have higher survival during marine heatwaves. An index of recruitment success (Index = #crabs/megalopae catch) varies strongly with the abundance of settling crabs. It is orders of magnitude higher (Index = ~3,000 crabs/megalopae) at low annual megalopae catch (<3,000) than at high annual catch (>millions megalopae caught) (Index = ~5 crabs/megalopae at). This variation in recruitment success may explain the two correlations between megalopae catch and fishery catch. Annual megalopae catch in Oregon predicts the commercial catch in California, but not Washington.

Introduction

Climate change is altering the oceans. In the Northeast Pacific Ocean, marine heatwaves have become regular events and the effects are being felt throughout the ecoregions (1). These changes have the potential to greatly influence the population dynamics of species in the region including commercially important species. In the California Current ecoregion, many of the economically important species have demersal adults with pelagic larvae; a changing ocean may strongly affect these larvae. The Dungeness crab (*Cancer magister*) is the most economically important single species commercial fishery in Oregon (2) and an ecologically important component of the benthic community. For 23 years, we have been measuring the daily and annual abundance of Dungeness crab megalopae (the final larval phase) using a light trap on the Oregon coast. This unique data set is providing a better understanding of how climate change and hydrodynamic variables affect this important species.

This monitoring study has led to several previous papers (3-8). The last paper focusing on the light trap work presented data from the first 12 years of the study (5), hence, this present publication almost doubles the length of the published light trap results (i.e., 11 additional years of data). The data consists of daily counts of the number megalopae caught in a light trap (Figure 1) fished in Coos Bay, Oregon during the Dungeness crab settlement season (~April through September). These data have been used to address a number of questions; 1) the day-to-day variation in the catch has been used to investigate the mechanism facilitating the onshore transport of the megalopae, 2) to investigate the causes of annual variation in the number of megalopae caught in the trap (i.e., larval success), the year-to-year variation in the total number of megalopae caught has been compared to climatic and hydrographic variables (e.g., Pacific Decadal Oscillation (PDO), El Niño, upwelling, spring transition), 3) the annual catch of megalopae has been used to predict the Oregon commercial ocean crab fishery catch or, from a more ecological

perspective, the size of the four-year-old age class. In addition, we use these data to investigate variation in recruitment to adulthood, i.e., how likely is it that a settling megalopae may survive to adulthood. In the remainder of the introduction, we will briefly describe the relevant life history traits of the species, how the species is fished, what we have learned thus far and indicate how the additional data reported here may affect these insights.

Dungeness crabs reach sexual maturity at approximately 1.5 to 2 years (9). Mating occurs in the spring and early summer. Female crabs release pheromones when they are close to molting. Male crabs 'capture' females near molting and hold them (i.e., pre-mating embrace) until molting at which time mating occurs. A male crab can mate with multiple females and the female stores the sperm until fall when she extrudes and fertilizes eggs (10). Previous work has shown sperm, if stored by the female, may be viable for up to 2.5 years; some individuals skip annual mating and fertilize eggs with stored sperm. Females extrude between 1.5 to 2.5 million eggs and the number extruded is independent of carapace width (11). In the waters off Oregon, egg development takes three to four months and the eggs hatch in winter (January through March). Zoea larvae are released into the coastal waters where they are transported northward by the Davidson Current, the current present over the continental shelf in winter (Figure 1). Over their development, larvae are found progressively further from shore (12) until they are seaward of the shelf and in the southward flowing California Current (Figure 1). Hence, during the pelagic phase, the larvae are first transported to the north and then to the south. There are five zoeal stages after which they metamorphose into a megalopa (13). The megalopae are large (almost 1 cm carapace width), and fast swimming (> 10 's cm/sec swimming speed) (14, 15). The pelagic larval duration is ~ 90 -120 days depending on ocean temperatures (9). In central Oregon, megalopae generally start to arrive in nearshore and estuarine waters in late

March or early April. They settle and molt into juvenile crabs along the open coast and within estuaries. In most years, they continue to arrive at the coast through August/September. During the first months the young crabs go through ~6 molts and grow rapidly from about 5-7 mm to 40 mm carapace width in the late summer and fall (9, 16).

A history of the fishery can be found in Wild and Tasto (17) and Rasmuson (9). The current fishing regulations have been in effect for decades and are simple (9). Crabs are caught with baited traps or pots. Only male crabs with a carapace width larger than about 16 cm carapace width (CW) are kept (9). All female and smaller male crabs are returned to the ocean and survival of returned crabs is high (18). Nearly all legal-sized male crabs are caught each year (19). In Oregon waters, these male crabs are about four years old, hence, they have been able to mate in at least one and perhaps two seasons. Several studies have demonstrated that nearly all female crabs are fertilized each year either because they mated in that year or had stored sperm from an earlier mating in a previous year (8). The fishery is seasonal with start dates varying along the coast. The Oregon commercial ocean fishery start date is 1 December (2) but can be delayed if legal size male crabs have not returned to a sufficient weight (filled out) following the fall seasonal molt or if they have been contaminated by domoic acid (8). The fishing season runs through August 14 (2) and is closed before the fall molt cycle commences. The fishery is a derby with most of the crabs caught within a couple of months of the opening date. The fishing regulations are surprisingly effective; despite the intensity of the fishery, there is no impact on the reproductive output of the population since no females are retained, and fertilization rates are high each year. Because reproductive output is not impacted, over the 100 plus years these fishing regulations have been in effect there is no indication that the population in the California Current has been over fished (20).

In most years, megalopae begin showing up in the light trap in early April. In some years megalopae return is delayed by a month or more. Daily catch generally starts out low, tens to hundreds of megalopae per day, but within several weeks increases to the maximum daily catch for that year (see supplemental material for plots of the daily catch for each of the 23 years sampled). The daily catch is highly pulsed and follows a fortnightly periodicity (2-6). We see low catch for five to 10 days and then for several days or longer during a pulse the daily catch jumps by one to several orders of magnitude. During the entire time series, the day-to-day variation in catch has been significantly cross-correlated with the daily tidal range (21). Peak catches tend to occur between the neap and spring tide or shortly after the spring tide (varies from year to year) (17). Given the day-to-day variation in the catch, the most likely mechanism of cross-shelf transport of the megalopae is via internal waves generated by the tides, the internal tides (17).

We concluded from previously published papers (5, 6) that the year-to-year variation in the number of megalopae caught during the settlement season was primarily driven by the Pacific Decadal Oscillation (PDO), the day-of-the-year (DOY) of the spring transition, and the amount of upwelling during the settlement season. The number of megalopae caught during the settlement season varied by a factor of >1,000 with larger catches tending to occur during years with a negative PDO, early spring transition, and more upwelling (5). The lowest catch (< 2,000 megalopae) occurred during the strong El Niño in 1997 and the largest catch (2,400,000 megalopae) during a negative PDO.

We hypothesized that the PDO and El Niño alter the annual larval success by their effect on the relative north south transport of the larvae (5, 9). During their pelagic development, larvae are first transported north in the Davidson Current, then south in the California Current. The number of megalopae that arrive at the coast at Coos Bay may thus be dependent on the relative amount of north and south transport the larvae experience.

During a strong El Niño, when there is an enhanced Davidson Current, larvae may be carried far to the north potentially to the Gulf of Alaska (22) leading to low larval returns in Oregon. In contrast, during a strong negative PDO, when the California Current is faster, the southward component of the migration is augmented, and more larvae are caught in the light trap in Coos Bay. This hypothesis was supported by the results of a modeling experiment (23).

In earlier papers (5, 6), we hypothesized that megalopae in the ocean seaward of the continental shelf were carried onto the shelf by deep currents generated by wind driven coastal upwelling. This hypothesized onshore transport would occur sooner with an early spring transition and more often with increased upwelling, both of which may lead to higher abundances of megalopae. However, a study by Rasmuson and Shanks (21) suggested an alternate hypothesis, the hydrodynamics during upwelling is conducive to the shoreward transport of the megalopae. In the winter months, due to storms, the thermocline is deeper and the tidally generated internal waves, the likely onshore transport mechanism, formed do not cause transport (24). At the spring transition and during upwelling, the thermocline is shallower which may allow for the generation of transporting internal waves or internal bores (21) that carry megalopae across the shelf to the coast.

In our first published study (8) we tested the hypothesis that the size of the four-year old age class (legal-sized male crabs) was set by the number of returning megalopae, i.e., the annual catch in the light trap. Surprisingly, with just five years of data we found a very strong positive regression between the catch of megalopae and the catch in the fishery in Oregon. Interestingly, we also found a positive relationship between megalopae catch in Coos Bay, Oregon and the commercial ocean catch in California, but not the commercial ocean catch in Washington (8). The relationship between catch of megalopae and Oregon

crab catch held up in the next two published papers (5, 6). The data presented here continues to support this conclusion, however, the relationship between the returning megalopae and age class strength has become more complex and interesting.

In this study, we present an expansion of our time series of larval returns to Coos Bay, Oregon as measured by daily catches to a light trap from a 12 to a 23-year time series. We analyze these data to better understand the hydrographic causes of year-to-year variation in annual larval success and how this variation in success translates into age class strength (recruitment) and fisheries catch.

Materials and Methods

A detailed description of the sampling methods used from 1997 to 2001 can be found in (6, 8). Identical sampling methods have been used since the time series was restarted in 2006 through to the present. Megalopae were caught using a light trap placed at the end of F dock in the Charleston small boat harbor in Coos Bay, Oregon ($43^{\circ} 20' 41''$ N, $124^{\circ} 19' 15''$ W) (Figure 1). In the initial study, we fished replicate traps at several locations within the estuary (8). The pattern of catch was similar at the different locations within the estuary and the abundance in replicate traps at a location were also similar. The largest catches were at the site closest to the mouth of the estuary, F dock. To allow for efficient sampling, critical for a long time series, since 2006 we have fished one trap. In 2000, traps fished simultaneously in the estuary and the ocean demonstrated that the pattern of daily abundance did not differ between the open coast and within the estuary (25). Each year, the trap was fished from roughly the beginning of April through September, the local settlement season for *C. magister*, and megalopae were removed from the trap daily. The total number of megalopae captured in each settlement season was used as an index of the abundance of megalopae returning to the coast, i.e., annual larval success. When a daily

sample of megalopae was < 2000 either the entire sample was counted or it was split using standard methods and then counted) (26). Starting in 2007, the daily and annual abundance of megalopae increased dramatically with daily catches during pulses on the order of 10s of thousands of megalopae (i.e., liters of megalopae in the light trap). We could not efficiently count these huge samples. To estimate the number of megalopae, we carefully drained off the water, weighted the entire sample, and then divided by the weight of 100 megalopae. This method was validated by counting entire samples on multiple occasions.

To test the hypothesis that adult population size was limited by the number of returning megalopae, we correlated the index of settling megalopae (i.e., the summed daily catch of megalopae) to the size of the Oregon, Washington and California commercial catch landed four years later, the time needed for megalopae to recruit into the fishery (20). The California Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, , and the Washington Department of Fish and Wildlife provided annual commercial catch data for each state. During the annual fishing season, essentially all legal sized male crabs are caught (19), hence, the size of the commercial catch is an excellent measure of the four-year old class.

To investigate the causes of the annual variation in the abundance of megalopae caught in the light trap we regressed the catch data with physical variables including the DOY of the spring transition, the PDO index, an El Niño index, and the Coastal Upwelling Transport Index (CUTI). The DOY of the spring transition was calculated using the methods described in Shanks and Roegner (8). Average daily sea level data for Crescent City, California was obtained from <https://uhslc.soest.hawaii.edu/>. The average annual sea level was calculated for each year and subtracted from the daily average sea level. The spring transition was the date after which there were at least seven days with sea level 100 mm

lower than the annual average (27). During strong El Niños, sea level at the coast is elevated. This appears to confound our method of determining the spring transition date. For example, in 1997, a year with a strong El Niño, this method produced a DOY of the spring transition of only 35 days, very early. For the DOY of the spring transition in the two years with strong El Niño conditions (1997 and 2016) we used data from Pierce and Barth ([Shadow.ceoas.oregonstate.edu/damp/windstress/](http://shadow.ceoas.oregonstate.edu/damp/windstress/)). In their calculations they use cumulative wind stress to define the spring transition (see their web page for methods). Data on the PDO index and the CUTI upwelling index for 45° north were obtained from internet sources (PDO - <http://research.jisao.washington.edu/pdo/PDO.latest>, CUTI - https://rdr.io/github/marinebon/ecoidx/man/cciea_OC_CUTI.html). For an El Niño index we used the Oceanic Niño Index (ONI) (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php). The PDO index was summed for the period Dungeness crab larvae are pelagic, roughly January through July. For the CUTI we summed from March through July, the period when megalopae return to the shore and are caught in the light trap. For the ONI index we summed the monthly values for the entire year.

To understand the relationship between the above variables and the number of returning megalopae each year we used generalized additive models (28). The PDO and the El Niño index are significantly correlated ($R^2=0.64$, $n=23$, $P<0.00001$). Because the two indices are correlated, we did not include the El Niño index as a potential variable in our GAM analysis and acknowledge the difficulty in disentangling the relationship between the two variables. Models were fit using the mgcv package in R version 4.3.2 “Eye Holes” (29) and a Tweedie distribution. Explanatory variables included in the model were CUTI, DOY of the spring transition, and PDO. Prior to model fitting we ensured there was no concurvity between the variables. The variables were modeled as smoothed variables and were

restricted to 5 knots to prevent overfitting of the data. All possible models were fit and compared using the corrected Aikake information criterion (AICc) (30). The fit of the best fit model was analyzed using the DHARMA package (31).

Results

On average, the first returns (i.e., catch) of Dungeness crab megalopae occurred on 9 April, (range 28 March, 2015, to 24 April, 2008) and 90% of the annual catch of megalopae occurred by 15 June, the latest date was 26 August (2012) (plots of daily catch and cumulative catch are presented in the supplemental material). Ninety percent of the megalopae were caught, on average, in just 67 days (range 32 (2017) to 146 (2012) days).

The year-to-year variation in the total number of megalopae caught is extremely large (Figure 2A). Annual catches of megalopae, a measure of larval success, have ranged from a low of just over 1,000 animals to highs of almost 2,800,000; larval success, varies by a factor of close to 3,000. During years with low returns, a one-night catch during a pulse is a few tens of animals, but during a year with high returns daily pulses are often liters of megalopae, >10,000s of individuals per day. When viewed as a frequency plot (Figure 2B), the distribution of annual catch of megalopae appears to be bimodal. What causes these extremes in megalopae abundance and why is the distribution bimodal?

The lowest catches of megalopae occurred in years with strong El Niños (1997 and 2016); perhaps larval success varies with El Niños. The relationship between an El Niño index and larval success, catch of megalopae, is a parabolic curve (Figure 3) with 50% of the annual catch explained by the El Niño index. The lowest annual catches of megalopae occurred during the two strong El Niños when less than 3,000 animals were caught (Figure

2). Lower catches also occurred when the index was highly negative while peak catches occurred when the index was between about zero and -5 (Figure 3).

From regression analysis we found that the variability in the number of megalopae caught annually was explained by the PDO, the CUTI upwelling index, and the DOY of the spring transition (regressions explained 44, 12 and 33% of the variability, respectively) (Figure 4). Peak annual catches of megalopae occurred when the summed PDO index was negative, but, when the PDO index was very negative (>-12), catch dropped off (Figure 4). The catch of megalopae was lowest when the PDO index was positive (Figure 4). Higher catches of megalopae tended to occur when the spring transition was earlier (Figure 4). For example, in years when we caught more than a million megalopae, the spring transition occurred before mid-March. The relationship to the CUTI, while statistically significant, was weak (Figure 4). There was a weak tendency for higher catches to occur when there was more upwelling.

The best fit GAM included PDO, CUTI and DOY of the spring transition, though the second-best fit model that included just the PDO and DOY of the spring transition differed by < 2 AICc units. We present the results from the best fit model (Figure 4). The model explained 63.1% of the variability in the data. PDO had a consistent effect on returning megalopae from the lowest values to a value of ~ 5 at which point the influence of PDO declined (Fig. 4A and B). For the upwelling index, as upwelling increased from 2 to 4 there was a positive effect on the number of returning megalopae (Fig. 4C, D). Above a value of 4, upwelling had a declining influence on the number of returning megalopae (Fig. 4C). For the DOY of the spring transition there was a negative relationship with number of returning megalopae (Fig. 4F).

In the California Current, Dungeness crab larvae hatch during the winter and are pelagic for 3 to 4 months (9). Given hatch dates and the pelagic larval duration, we should

not catch any larvae from the California Current population by the end of July. The date when we have caught 90% of the megalopae within a year (20 July) likely reflects this cut off in the presence of larvae from the California Current. To the north of Oregon, in British Columbia and the Puget Sound/Salish Sea, the larval hatch occurs later by one or more months (9), hence, megalopae caught late in the summer may be animals from these more northern populations. During negative PDO's, the California Current is stronger due to the influx of additional water from the North Pacific Drift and this enhanced southward flow may transport larvae spawned to the north to Oregon. We summed the number of megalopae caught annually in the settlement season (20 July, average date when 90% of megalopae were caught plus one SD), summed the monthly PDO index for the same period and ran regressions between the two data sets (Figure 5). Using all the data the regression was not significant, however, one data point (year 2022 data, x in the lower lefthand corner of the graph) is more than two standard deviations below the regression line suggesting that it is an outlier. With this data point removed, the regression is significant with the PDO index explaining 35% of the variability in the catch of megalopae late in the summer. During years with negative PDO and, hence, stronger southward flow in the California Current, we catch more megalopae whose source must be to the north of Oregon.

The settling megalopae will eventually grow into legal-sized crabs that will enter the fishery. In the California Current population, this takes four years. Hence, the number of settling megalopae caught each year may predict the size of the commercial catch four years in the future. Figure 6 shows the \log_{10} megalopae catch in Coos Bay per settlement season plotted with the \log_{10} of the commercial catch of Dungeness crabs in Oregon four years later. The distribution of data points suggests that there are two curves, one associated with data from annual catches of megalopae $<100,000$ and a second associated with years with catches $>100,000$ (Figure 6). In the online supplemental material, we show

how this relationship evolved over time leading to our realization that the relationship is made up of two curves dependent on the number of megalopae caught. Both curves are significant and explain from 70 to 90% of the variability in catch or the size of the 4-year-old age class of crabs.

There have been a number of marine heatwaves on the Oregon continental shelf during the time series (<https://www.integratedecosystemassessment.noaa.gov/regions/california-current/california-current-marine-heatwave-tracker-blobtracker>). A marine heatwave is defined as a 'prolonged discrete anomalously warm water event that can be described by its duration, intensity, rate of evolution, and spatial extent' (32). Thus far we have five paired data points, number of megalopae caught coupled with the subsequent commercial catch, for marine heatwaves in 1997, 2014, 2016, 2019, and 2020. There were likely marine heatwaves on the shelf in 2021-2023 as well, but the megalopae that settled in those years have yet to enter the fishery. In Figure 6, the data from the marine heatwave years are plotted as X's and each of these data points falls well above the established regression relationships generated from the 18 years of data when there were not marine heatwaves. The data from the marine heatwave years were not used in the calculations of these regressions. These data suggest that the probability that settled larvae will survive to adulthood, recruitment, is higher when there was a marine heatwave.

The relationships between the number of megalopae returning to the coast and the subsequent size of the four-year old age class as indicated by the commercial catch is robust, the number of megalopae caught, an indicator of larval success, is a good predictor of commercial catch four years later. To test just how good a predictor, we plotted the predicted commercial catch calculated from the equations in Figure 6 (note that this calculation was made in the settlement year, so four years prior to the fishery) against the

actual observed catch (Figure 7). The size of the annual catch of megalopae explains >82% of the variation in the observed catch; the regression line falls almost on top of the one-to-one relationship. On average, excluding the marine heatwave years, our estimated commercial catch is within $\pm 12\%$ (SD 9%) of the observed catch.

In this analysis we left out the data from the marine heatwave years (filled squares in Figure 7). These data points fall above the one-to-one line and the regression line. The observed catch are about 3,000 metric tons (approximately 3.5 million additional male crabs) higher than that calculated by the regressions. These five data points form a significant regression explaining 99% of the variation, but with just five data points this regression should be treated as tentative. Over time, with continued marine heatwaves, we may see curves composed of marine heatwave data.

The fact that there are two curves relating the number of returning megalopae and recruitment into the four-year old age class (Figure 6) suggests that in years with lower returns of megalopae a higher percentage of settlers survive to recruit than in years with high megalopae returns. To investigate this, we plotted the annual megalopae catch against an index of recruitment success (i.e., the total number of crabs caught in the fishery divided by the number of megalopae caught in the light trap four years prior) (Figure 8). The number of crabs caught was simply the total commercial crab catch in Oregon in kilograms divided by the average weight of a male crab in kilograms (0.84 kg., Oregon Department of Fish and Wildlife). Plotted as \log_{10} data, the relationship is highly significant. The regression line is composed of four clusters of points. 1) When the number of megalopae caught was around several thousand (the years with strong El Niños), the index is several thousand (Figure 8, cluster 1 in the graph), 2) between several thousand and 100,000 megalopae caught the index is in the hundreds (Figure 8, cluster 2 in the graph), 3) At >100,000 to 1 million megalopae caught the index drops to tens (Figure 8, cluster 3 in the graph), and 4)

At >1 million megalopae caught, the index is in the ones (Figure 8, cluster 4 in the graph).

In Figure 6, the left-hand curve is defined by variations in our index of recruitment success from hundreds to thousands (data clusters 1 and 2) while the right-hand curve is defined by index values of from ones to tens (data clusters 3 and 4).

The hydrographic variables that appear to be driving the year-to-year variation in the abundance of returning megalopae, the PDO, ENSO, CUTI and DOY of the spring transition, all vary in a similar pattern and simultaneously across the California Current system. This suggests the possibility that the annual variation in the number of megalopae returning to locations along the west coast could be similar to that seen in Coos Bay. If this were the case, then we might be able to predict the size of the four-year old age class /commercial catch in California and Washington from the megalopae catch in Coos Bay.

Plotting the light trap catch of megalopae in Coos Bay against the commercial catch (four-year old males) in California (Figure 9A) we find a relationship very similar to what we find in Oregon (Figure 6). There are two curves; one describing the relationship when <100,000 megalopae were caught and a second curve describing the relationship when >100,000 megalopae were caught (Figure 9A). Both curves are significant and the megalopae catch in Coos Bay explains about 68% of the variability in California commercial catch. In contrast, we found no significant relationship between Coos Bay megalopae catch and commercial catch from ports on the Washington coast (Figure 9B, open circles). In Oregon through the range of California inhabited by Dungeness crabs (south to Morro Bay), the crab population appears to respond similarly to the hydrography of the California Current (Figure 9C) while the Washington outer coast does not (Figure 9D). A regression between the commercial catch in Oregon and California is significant and explains about 33% of the variability ($R^2=0.329$, $n=15$, $P<0.026$). Similar regressions run between the

Oregon catch and those in Washington, open coast, and Columbia River ports, were not significant.

Discussion

Larval transport

Over the 23-year time series, the number of megalopae caught during the settlement season has varied from a few thousand to almost three million, a variation of almost 3,000 times. Two questions arise. First, what might cause these huge variations in the settlement of megalopae? Surprisingly, while the number of settling megalopae determines the size of the four-year-old age class (i.e., the commercial catch) between the lowest and highest commercial catch, the variation is only a factor of ~ 5 . This observation leads to a second question. Why might the variation in commercial catch be so much smaller than that of the megalopae settlement, a variation of $\sim 3,000$ times compared to a variation of only ~ 5 times? In the following we will present hypotheses that might answer these two questions.

The variation in the number of megalopae settling each year appears to be largely driven by variations in hydrodynamics that affect the north and south transport of zoea and the cross-shelf transport of megalopae. Our model shows that PDO, CUTI upwelling index and DOY of the spring transition explains 63% of the variability in the data; the complex interaction between these three hydrodynamics processes appears to largely determine the number of settling megalopae.

As a reminder, larvae are released in winter over the continental shelf. The actual distribution of larval release sites is unknown, but larval release is likely concentrated toward the shore rather than the shelf break. Larvae released over the shelf during the winter will be carried northward by the Davidson Current. Drifter data suggest that

northward transport during this period could be substantial (33). As larvae develop, they move further offshore until they are off the shelf and in the southward flowing California Current (12). Thus, the larvae are first transported north (Davidson Current) and then south (California Current). We hypothesize, and biophysical modeling work supports this hypothesis (21), that the number of megalopae caught in Coos Bay is in part dependent on the relative amount of north and south transport the larvae experience. The two years with the lowest number of returning megalopae were years characterized by strong El Niño events; northward transport would have been enhanced relative to non-El Niño years. Larvae may have been carried far to the north. In fact, larvae from the California Current have been caught off the coast of Alaska (22). We found a significant regression between the PDO and the annual catch (Figure 4B); lower catches when the PDO was positive, less southward flow in the California Current, and higher when it was negative, more southward flow in the California Current. In other words, when the PDO is negative the larvae are more readily transported back south and more megalopae settle in Oregon coastal waters. The fact that the late season catch of megalopae is also correlated with the PDO (Figure 5), more late-megalopae during negative PDOs, lends support to this hypothesis. In the regression (Figure 4B), notice that during very negative PDOs catch in Oregon tended to be lower. Perhaps the southward transport is so strong that larvae tend to be transported past Oregon and more settle on the California coast.

We developed a biophysical model of dispersal to investigate the hypotheses we generated from the light trap data (24). During positive PDOs, the model indicated that more larvae were lost from the model domain north into the Alaska Current (23). Further, more larvae settled north of their larval release site in positive PDOs, however, the average transport was still southwards. In other words, larval settlement was, in general, more diffuse than during negative PDOs. Interestingly, we also found that during positive PDOs,

perhaps due to the warmer water temperature, larvae molted into megalopae faster but remained in the water column longer (23). While we did not model this explicitly, a longer time as a megalopae could result in increased predation by planktivorous fishes.

The DOY of the spring transition and the CUTI index are correlated with the number of megalopae caught. Both variables relate to different aspects of the upwelling season; the spring transition is the date on which the winter wind pattern (downwelling favorable) shifts to the spring/summer upwelling-favorable wind pattern. CUTI is an index of the amount of upwelling occurring. We hypothesize that the shallower depth of the thermocline during upwelling, sets up conditions favorable to the shoreward transport of megalopae. It is worth noting the relationship between the number of megalopae and the CUTI upwelling index differed between the GAMs (negative linear relationship) and simple linear regressions (positive linear relationship). This combined with the fact that the model without CUTI was < 2 AICc units different from the best fit model suggests weak support for the CUTI index being included in the model. Since we hypothesize this relationship is more reflective of changes in the water column structure rather than the upwelling process, this is, perhaps, not surprising.

The daily catch of megalopae is highly pulsed with catch varying by an order of magnitude or more over a few days. The pulses tended to occur roughly every two weeks and are significantly correlated to the spring neap tidal cycle (21). This can be seen particularly clearly in daily data from 2006 and 2023 (Supplemental Material). Fortnightly pulses correlated with the tides, that is out of phase with the spring neap cycle, and not proportional to the tidal amplitude is an indication that onshore transport is likely due to the internal tides (34-36). Tidal flow off the continental shelf produces packets of large internal waves, collectively known as the internal tides (37). These large internal waves can produce moving surface convergences capable of transporting surface material, neustonic

larvae, and floating flotsam (34, 38, 39), shoreward. In addition, they can produce broken internal waves or internal bores that can transport water and entrained animals shoreward (40).

Recruitment into the fishery

We have analyzed the relationship between the number of megalopae caught and the commercial catch as two regressions (minus the marine heat wave years, Figure 6) (see Figure 2 in the supplemental material for additional discussion). Both curves are significant with the number of megalopae settling explaining from 80% (<100,000 megalopae caught) to 70% (>100,000 megalopae caught) of the variability in the commercial catch. These data lead to three questions. 1) Why are there two curves? 2) The \log_{10} scale of number of megalopae caught (horizontal axis, Figure 6) ranges from 2.5 to 6.5 yet the \log_{10} scale on the commercial catch (vertical axis, Figure 6) ranges from just 3.2 to 4.2. Why is the commercial landing so much less variable than the number of megalopae caught? 3) In Figure 6, there are five data point indicated by Xs. These data are from years when there were marine heatwave conditions over the continental shelf. The points fall well above the two regression lines. What is happening?

Why are there two curves (Figure 6)? The most likely explanation is that recruitment success varies with the number of settling megalopae, with lower recruitment when settlement is higher. To investigate this, we plotted a crude index of recruitment success (number of crabs caught in the fishery/number of megalopae caught in the light trap) vs. the number of megalopae caught (Figure 8). The index of recruitment success dropped sharply as the number of megalopae caught rose, ranging from around 3,000 crabs/megalopae during the low megalopae catches of the El Niño years to just around 5 crabs/megalopae during the years with millions of megalopae caught. In Table 1, we have

made up a set of model data in which we picked megalopae catch over the full range of annual catch (i.e., <3,000, 10,000s, 100,000s, millions), and multiplied this catch by the recruitment index (Figure 8) to get the number of legal sized male crabs (Table 1). At low larval returns, the high recruitment success, despite the low number of megalopae, generates a substantial number of crabs and, as the number of returning megalopae goes up and the recruitment success goes down, there is still a substantial number of crabs produced. But at the transition from 90,000 to 100,000 megalopae caught, there is almost a four-fold drop in recruitment success leading to a sharp drop in the number of crabs produced, e.g., a drop from 22.5 to 6 million crabs (Table 1). The combined effect of sharply decreasing recruitment success with increasing numbers of returning megalopae appears to be the cause of the two regression lines in Figure 6.

Mathematically this explains the two curves in Figure 6 and why the commercial catch, i.e., the four-year-old age class, is so much less variable than the number of megalopae caught, but these observations beg the question, what is the biological mechanism that causes this relationship between megalopae and adults, recruitment. A dramatic decline in a population when a threshold is exceeded is quintessential density dependence (41). Undoubtedly, the relationship will be explained by the differential survival of juvenile crabs, but the curious drop in apparent survival between 90,000 megalopae caught in the light trap and 100,000 suggests the relationship is not simple. Even though the Dungeness crab fishery is one of the most profitable single species fisheries on the west coast and the species is ecologically important, we know surprisingly little about their biology after they settle and molt into young crabs. Much of the research that has been done on this critical phase has occurred in estuaries and the intertidal even though most of the population settles in the subtidal and on the open coast (42-44). As this paper indicates, we have decades of useful data on the relative larvae success, i.e.,

megalopae abundance, but similar data for recruitment is absent. Between the megalopae returning to shore and the commercial catch, there is a black box.

Confronted with this black box, we are reduced to hypothesizing what might be occurring within the box. There are several likely critical observations, the arrival of megalopae to the shore is highly pulsed (Daily settlement data, Supplemental Material), there have been frequent observations of extremely dense aggregations of juvenile crabs (100s to 1,000s/m²) on the seafloor (45), and juvenile crabs are actively cannibalistic (46). We hypothesize that following a pulse of megalopae arriving at the shore, there is a sudden influx of newly molted crabs (i.e., megalopae metamorphosing to crabs) on the bottom. The size of this influx may be proportional to the size of the pulse of megalopae caught in the light trap. During this transition from a pelagic to benthic habitat, the megalopae molt at which point they are likely easy prey to cannibalistic young crabs already on the bottom. In addition, each time a young crab molts and is briefly a soft shell crab, it is again vulnerable to predation by cannibalistic congeners. We hypothesize that during years with low megalopae returns, the density of young of the year crabs is much lower and predatory cannibalistic interactions between the juvenile crabs is lower (47). In contrast, during years with high returns and regular large pulses of settling megalopae, predatory interactions may be continuous throughout the settlement season. During years with low returns, the food supply may be better than in years with high returns and this would also impact the rate of cannibalism. Recent work has even suggested that cannibalism enhances stability of populations with large boom and bust cycles (47). In this scenario, smaller, more recently settled crabs, may be at a disadvantage relative to larger individuals that settled earlier (44, 46, 48). Another possibility is that during years with many settlers, food is scarce and young crabs starve. This is not an alternate hypothesis (49) as starving crabs are likely more susceptible to predation by cannibalistic congeners and cannibalism is likely higher due to

a lack of alternate food. While cannibalism is well known in juvenile crabs in their first year, it is unclear how cannibalistic older adults are.

The relationship between megalopae settlement and commercial catch, i.e., the four-year old age class, is altered during marine heatwaves; during marine heatwaves, more settlers survive to become adults and enter the fishery. In other words, mortality rates of YOY crabs appears to be lower during marine heatwaves. It is possible that with the now regular occurrence of marine heatwave years that such data will eventually generate additional curves, curves displaced upward from the curves generated by data from non-marine heatwave years.

This leads to our third question, why has recruitment during marine heatwaves been more successful than during years with more normal seawater temperatures? In 0+ and 1+ (i.e., young of the year and year-old crabs, respectively), warmer water leads to higher metabolism and faster growth (16). Most marine heatwaves have been identified from satellite measurements of surface temperatures, but to affect the benthos and the juveniles crabs, the heatwave must extend to the bottom and on the Oregon coast this appears to be the case (50). Hence, during a marine heatwave, young of the year crabs likely grow more rapidly through the smaller early molts and reach sizes that are less susceptible to predation, particularly predation by cannibalistic congeners. This would cause an increase in recruitment success, which would, in our calculations, appear as a higher-than - predicted commercial landing.

The snow crab (*Chionoecetes opilio*) population in the Bering Sea has declined to the point that the fishery for the crab has been closed (51). There have been several explanations proposed for this decline: including over-fishing and that the adult crabs migrated to cooler, deeper water due to marine heatwaves. A recent and, perhaps, the most likely explanation is the following scenario (51): following a strong recruitment event there

were marine heatwaves. The metabolic rate of the adult crabs was elevated in the warmer water causing higher feeding rates. The large population of abnormally hungry crabs simply consumed all the available resources and starved to death.

The California Current Dungeness crab population has been affected by repeated marine heatwaves and during these events our data suggests the crab population has experienced enhanced recruitment. Since the metabolic rate of Dungeness crabs increases in warmer water (16), conditions similar to that observed in Snow crabs could be occurring. Could a similar marine heatwave induced die off, as seen in Snow crabs, occur with Dungeness crabs? We do not have enough data to answer this question, but we do have evidence suggesting that recruitment is about 1.5 times higher during marine heatwaves. During the two marine heatwave years with the highest catch of megalopae, the enhanced recruitment was equal to about 8 million additional male crabs (fishery is limited to males) or total (male plus female crabs) about 16 million additional crabs in the Oregon coastal waters. 2023 was a year with very high megalopae catch (~2.5 million megalopae) and a marine heatwave. If recruitment in 2023 is similarly enhanced as in previous marine heatwaves, then the population may receive an estimated 30 million additional crabs. Marine heatwaves are occurring regularly (i.e., 2015, 2016, 2019, 2021, 2022, 2023). Several marine heatwaves in a row may mean that the recruitment to the adult population is repeatedly being enhanced. As with the Snow crabs, these adult crabs will be living in warmer than normal waters with a higher metabolic rate with a consequent increase in their food requirement. Could the California Current Dungeness crabs follow the same fate as the Bering Sea Snow crab? Without data on warm water changes to Dungeness crab food intake, their population density, and the food resource density there is no way to know.

The Coos Bay light trap catches are significantly correlated with commercial catch in California, but not Washington (Figure 9). The relationship between Coos Bay megalopae

catch and California commercial catch looks remarkably like the relationship between Coos Bay megalopae catch and Oregon commercial catch. The number of megalopae caught in Coos Bay is primarily driven by El Niño (lowest catch during strong El Niños), the PDO, the DOY of the spring transition, and the amount of upwelling during the settlement season. From Oregon south along the California coast to the Southern California Bight, these variables fluctuate synchronously. Hence, when the catch of megalopae is high in Coos Bay due to a negative PDO, early spring transition and consistent upwelling or the megalopae catch is low due to a strong El Niño, similar conditions are present in California, and they appear to affect the California Dungeness crab population similarly.

The Washington coast is no further away from Coos Bay, Oregon than the California Coast, the Washington coast is still within the California Current system and the driving hydrographic variables tend to vary in synchrony here as well. So why is there not a significant correlation between the Coos Bay megalopae catch and the Washington commercial catch? We are not sure. Washington has a wider continental shelf than Oregon. The Washington continental shelf is bifurcated by many large deep marine canyons (52, 53). These two variables may affect the cross-shelf movement of larvae. Or the difference may be due to a significant change in the coastal oceanography that occurs at the Washington-Oregon border. The border between Washington and Oregon is defined by the Columbia River, a very large river. In the winter, when Dungeness crab larvae are pelagic, the estuarine plume formed by the Columbia River spilling into the ocean is spun to the north by the Coriolis force and pushed north by winter winds from the south (52, 53). Under these conditions, the Columbia River estuarine plume extends along most of the Washington coast (52-54). At the northern end of the Washington coast is a second large estuarine plume, the waters exiting the Straits of Juan de Fuca. This plume also has a semi-permanent eddy associated with it (52-54) that may mechanistically affect how many

larvae are lost or retained. A bit further north, along the coast of Vancouver Island, the coastal flow is persistently to the north year-round (55). We suspect that these changes in the nearshore hydrodynamics create conditions different enough from those to the south off Oregon and California such that the recruitment dynamics of Dungeness crabs is different, but we have no idea how or if this change in hydrodynamics affects larval dispersal or delivery to the shore.

Roegner et al. (4, 56) sampled Dungeness crab megalopae during two cruises in the coastal waters off Washington and simultaneously fished light traps in two Washington estuaries, Grays Harbor and Willapa Bay. During one cruise the Columbia River estuarine plume was parallel to the coast and up against the shore and in the second, following wind-driven upwelling, the plume had moved offshore, dissipated, and recently upwelled water was adjacent to the coast. The distribution of Dungeness crab megalopae appeared to have been unaffected by the water mass change while other meroplankton were clearly affected. Light traps, sampled daily, were fished for 90 days (1 May-30 July, 1999) in both estuaries. The daily catch was pulsed, but the pulses were not related to the fortnightly tidal cycle, the winds, or whether the Columbia River plume was present or absent at the mouth of the estuaries. A light trap was fished in Coos Bay during this same period. There the catch of megalopae was also pulsed and the pulses were significantly cross-correlated to the fortnightly tidal cycle. Peak catches occurred shortly after the spring tides and the catch was >ten times larger, 14,000 in Coos Bay vs about <600 in Washington. Throughout the 23-year time series from Coos Bay, the daily samples have been cross-correlated to the spring to neap tidal cycle and, even in years with strong El Niño conditions, the catch has been larger to very much larger than what Roegner et al. (4) found in the Washington estuaries. We have no explanation for these differences.

Summary

With 23 years of monitoring, our understanding of the relationship between ocean conditions, larval success and recruitment to the adult population continues to evolve. In summary; 1) The daily abundance of megalopae is pulsed and cross-correlated to the spring neap tidal cycle suggesting that the onshore transport of megalopae is due to the internal tides. 2) The annual abundance of megalopae has varied by a factor of about 3,000, from lows of around several thousand to highs of over 2.5 million megalopae caught. 3) The annual catch varies with the El Niño (lowest catches during strong El Niño conditions), PDO (more megalopae during negative PDO), the DOY of the spring transition (more megalopae with an early transition), and upwelling (more megalopae with more upwelling). 4) The annual abundance of megalopae determines the size of the four-year old age class of males, i.e., the size of the commercial catch. Our prediction of the commercial catch made four years in advance and excluding the data from marine heatwave years are on average within $\pm 12\%$ (SD 9%) of the observed catch. 5) The relationship between megalopae abundance and commercial catch consists of two curves, one for years with $<100,000$ and a second for years with $>100,000$ megalopae caught. Strong dependence of recruitment success on the abundance of settling megalopae may be the cause of these two curves. 6) While the annual catch of megalopae varies by a factor of 3,000, the commercial catch varies by only a factor of about 5. This also appears to be due to recruitment success varying with the abundance of megalopae, high recruitment success in low megalopae settlement years and orders of magnitude lower in high settlement years. 7) In years with marine heat wave conditions on the Oregon shelf, settling megalopae have higher recruitment success. We hypothesize that this is due to more rapid growth of the YOY crabs such that they pass through the most vulnerable small sizes more rapidly and suffer less mortality. 8) The annual catch of megalopae in Coos Bay, Oregon can be used to predict the commercial catch in California, but not Washington. The similarity between Oregon and

California is likely because variables driving the abundance of megalopae caught in Coos Bay (#3 above) are similar throughout the California Current. It is not entirely clear why a similar relationship is not observed between Coos Bay and Washington.

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Author Contribution

Equal contribution

Conflict of Interest

The authors have no conflicts of interest.

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Tables

Table 1. Demonstration of the combined effect of the recruitment (Recruitment Index, crabs/megalopae caught) and the number of megalopae caught on the Commercial Catch. The Recruitment Index values are from Figure 8. Values were selected across the range of data and multiplied by the number of megalopae caught to get an estimate of the commercial catch in number of crabs. Note how the size of the commercial catch rises as the number of megalopae caught increases from 2,500 to 90,000 and then abruptly drops by a factor of nearly 4 with an increase in megalopae caught to 100,000.

Annual Megalopae Catch	Recruitment Index, Crabs/Megalopae Caught	Commercial Catch, Millions of Crabs
2,500	3,000	7.5
40,000	400	16
90,000	250	22.5
100,000	60	6
900,000	8	7.2
2.5 million	6	14.4

Table 2. $\Delta AICc$ s of model selection for generalized additive model. The best fit model selected by $AICc$ includes PDO, Spring Transition and the CUTI. Though the effects of CUTI are minimal as show by the < 2 units difference between the model with and without CUTI. PDO is the Pacific Decadal Oscillation, CUTI is the Coastal Upwelling Transport Index.

Model	$\Delta AICc$
PDO+Spring Transition+CUTI	0
PDO+CUTI	6.85
PDO+Spring Transition	1.24
Spring Transition+CUTI	10.00
CUTI	14.45
PDO	9.35
Spring Transition	7.87

Figure Captions

Figure 1. Map of the West coast with A) spring/summer coastal currents and B) fall/winter coastal currents. The numbers indicate the locations of landmarks mentioned in the paper. C) Location of the light trap fished in Coos Bay, Oregon. D) Line drawing of the light trap.

Figure 2. A) 23-year time series of total annual catch of megalopae to a light trap fished in Coos Bay, Oregon. Annual catch is the summed daily catch from April through September. Strong El Niño events occurred in 1997 and 2016 when catch was lowest, 1,094 and 3,040, respectively. A gap in sampling occurred between 2001 and 2006. The annual megalopae catch appears to be bimodal and a frequency plot (B) supports this idea.

Figure 3. Sum of the monthly Oceanic Niño Index (ONI)

(https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php).

plotted with the \log_{10} of the annual catch of megalopae in Coos Bay. Lowest catches occurred during strong El Niño conditions (index >15), lower catches occurred when the ENSO index was very low (<-15), and peak catches occurred when the ENSO index from between 0 and -5, essentially neutral.

Figure 4. Partial effects (left column) from best fit generalized additive models and linear regressions (right column) for the PDO phase (top row), CUTI Upwelling index (middle row) and day of the year of the spring transition (bottom row).

Figure 5. The Dungeness crabs off Oregon and California release larvae in winter. With a larval duration of 3-4 months, we should not catch megalopae after about 20 July. Larval release occurs later to the north (Washington and northward), so larvae caught late in the summer maybe from these northern populations. Enhanced southward transport due a negative PDO may lead to higher catches of these larvae. The summed PDO from August through September is plotted with the \log_{10} number of megalopae caught after 20 July in Coos Bay. Using all data, the regression is not significant, however, the data point labeled with an X appears to be an outlier as it is more than two standard deviations below the regression line. Without this data point the regression is significant and the PDO index explains about 35% of the variability in late summer catches of megalopae.

Figure 6. \log_{10} of the annual megalopae caught in Coos Bay plotted with the \log_{10} of the commercial catch of Dungeness crabs in Oregon 4 years later. There are two significant curves, one associated with annual catches <100,000 megalopae (black squares) and a second associated with catches of megalopae >100,000 (open circles) (see supplemental material Figure 2). There were five years (1997, 2014, 2016, 2019, 2020) when there were marine heatwaves over the Oregon continental shelf during the spring and summer. These data are plotted with X's and fall well above the regression lines.

Figure 7. \log_{10} calculated commercial crab catches made using the regression equations from Figure 6 and the number of megalopae caught four years prior to the fishing season against the actual \log_{10} measured commercial catch in “normal” years (open circles) and in marine “heatwave” years (filled squares). The regression for the normal years is significant explaining 81% of the variability and the data fall around the 1-to-1 line (dotted line). On average, the predicted commercial catch has been within $\pm 12\%$ (SD 9%) of the observed.

The five marine heatwave years also form a significant regression explaining 99% of the variability, however, there are just five data points so this should be viewed as a tentative conclusion.

Figure 8. The annual catches of megalopae are plotted against an index of recruitment success of megalopae surviving to enter the fishery as 4-year-old males. The index of recruitment success is the number of crabs landed in the Oregon fishery divided by the number of megalopae caught in the light trap in Coos Bay lagged 4 years. The relationship is formed from four clusters of points; 1 - <4,000 megalopae caught (years with strong El Niños), 2 - between 10,000 and 100,000 megalopae caught, 3 - 100,000's of megalopae caught, 4 - > 1,000,000 megalopae caught. With increasing numbers of settling megalopae, the index drops by orders of magnitude.

Figure 9. The \log_{10} of the annual catch of megalopae in Coos Bay, Oregon plotted against the commercial catch of Dungeness crabs in California (A) and Washington (B) lagged 4 years. The results in A are very similar to what we present in Figure 6. The data form two significant curves, one associated with annual catches of megalopae <100,000 (open squares) and the second associated with catches >100,000 (open circles). B) There is no relationship between the number of megalopae caught in Coos Bay and the catch from coastal Washington suggesting that the variables driving the annual variation in the size of the Dungeness crab population off Washington are different from the drivers off Oregon and California. Commercial catches are plotted in C (Oregon and California) and D (Washington outer coast ports); the time series of annual catch in Oregon and California appear similar to each other and different from the time series in Washington.

Figures

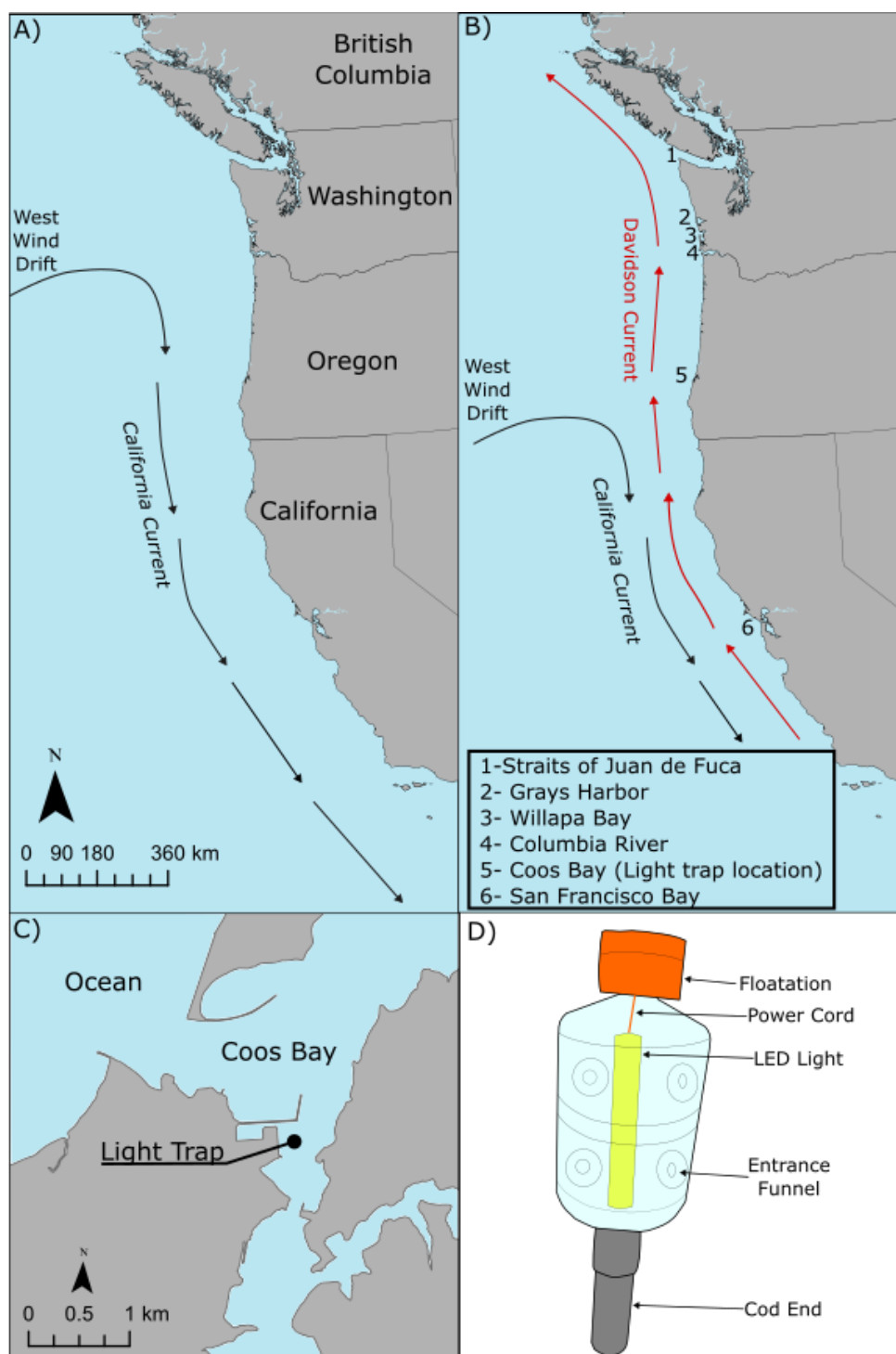


Figure 1

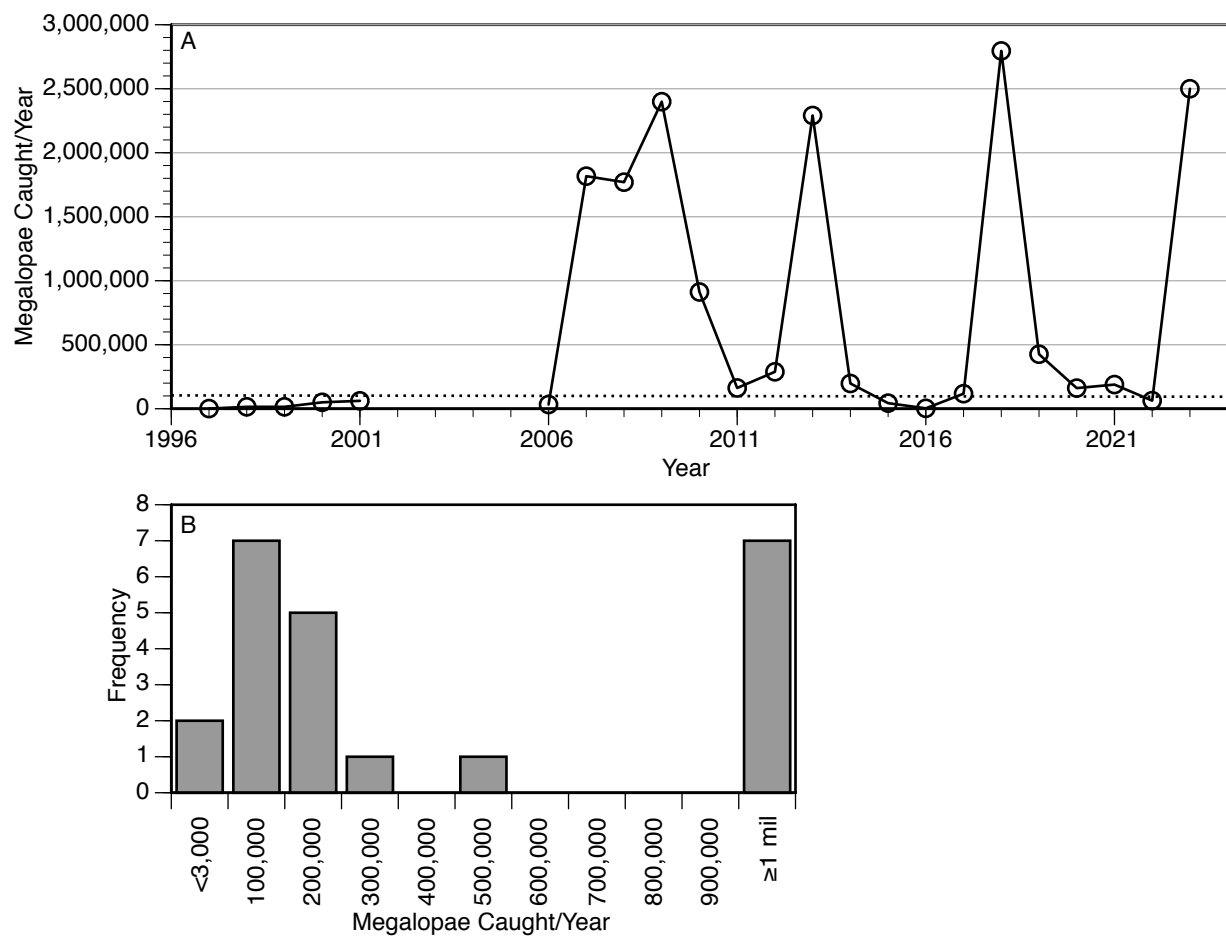


Figure 2

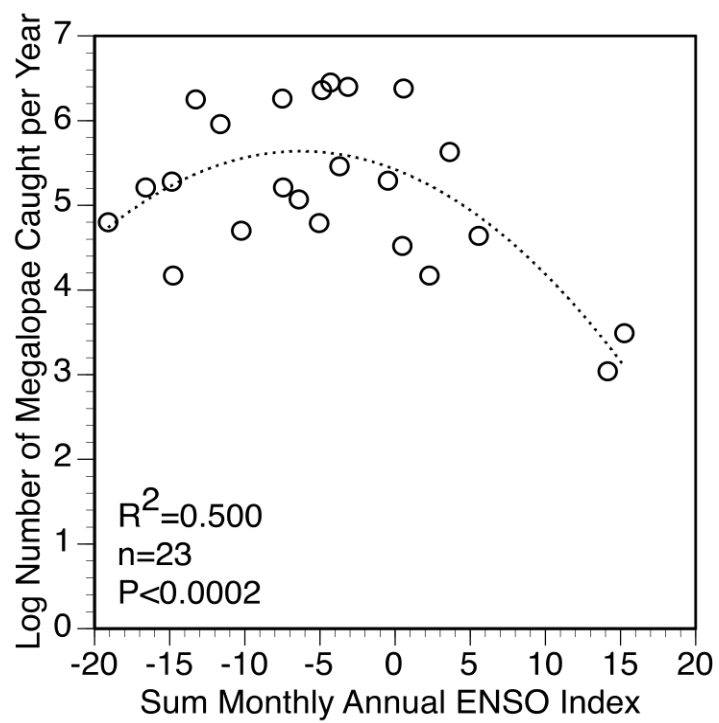


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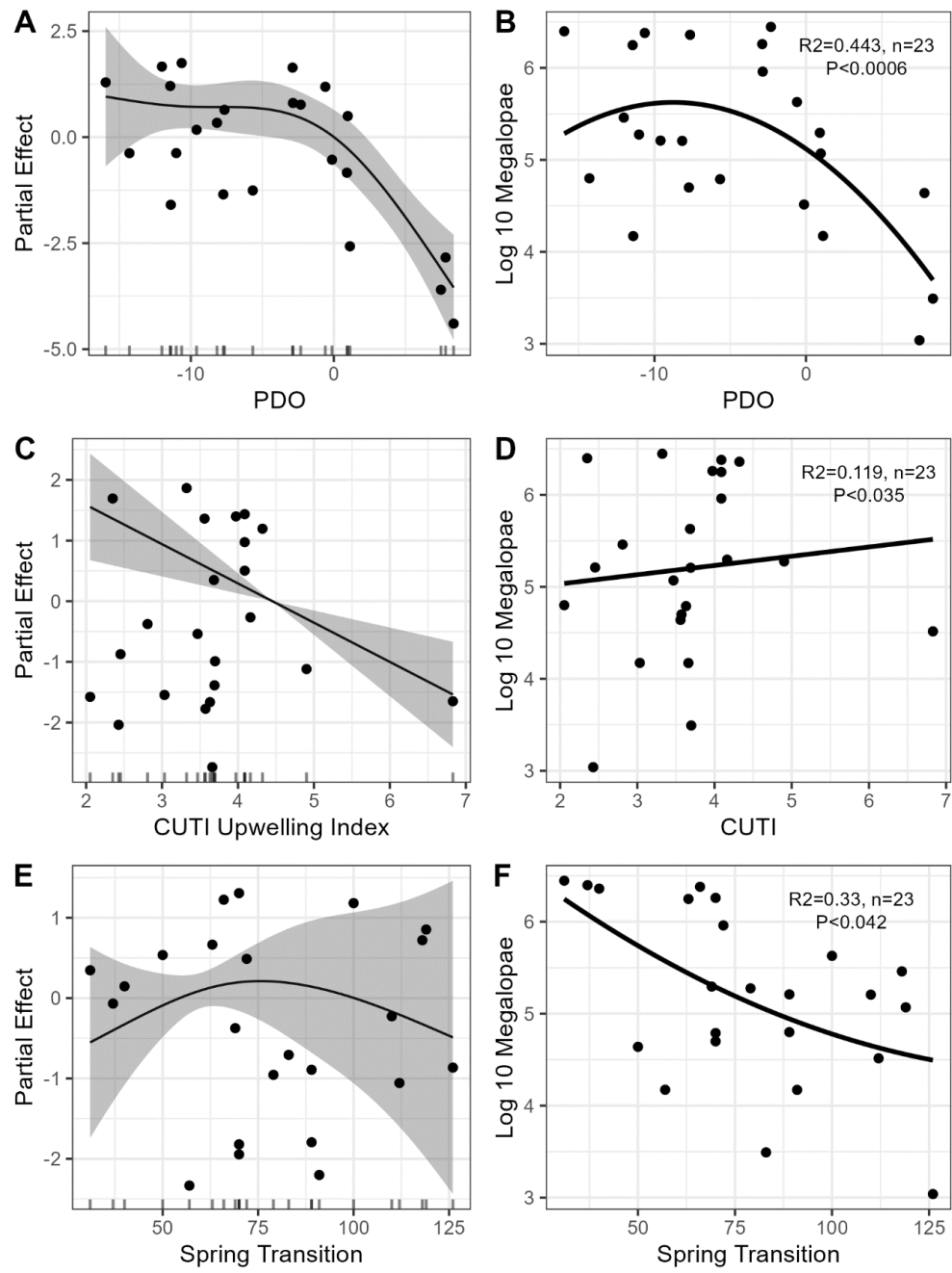


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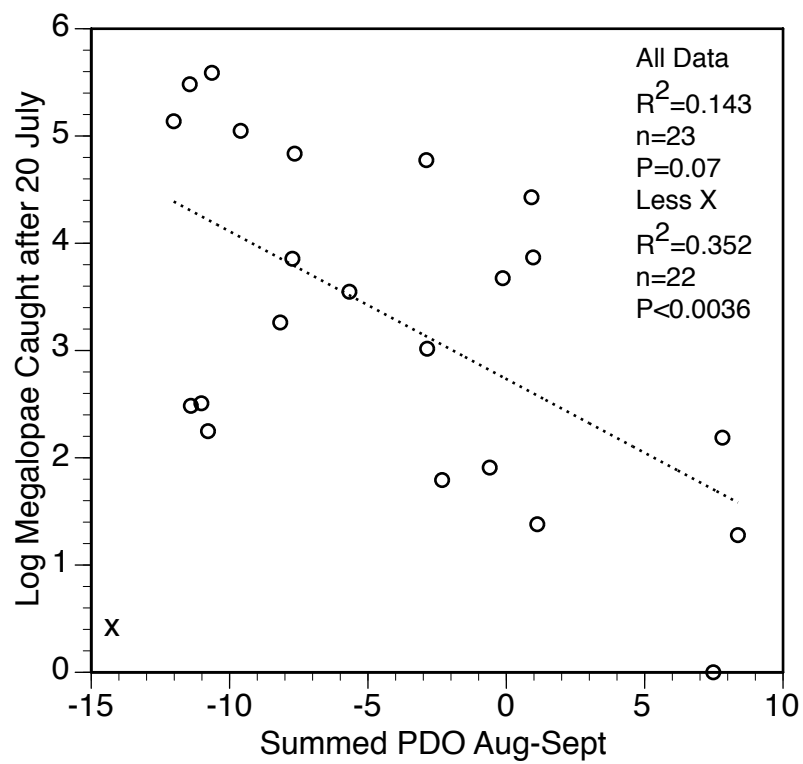


Figure 5

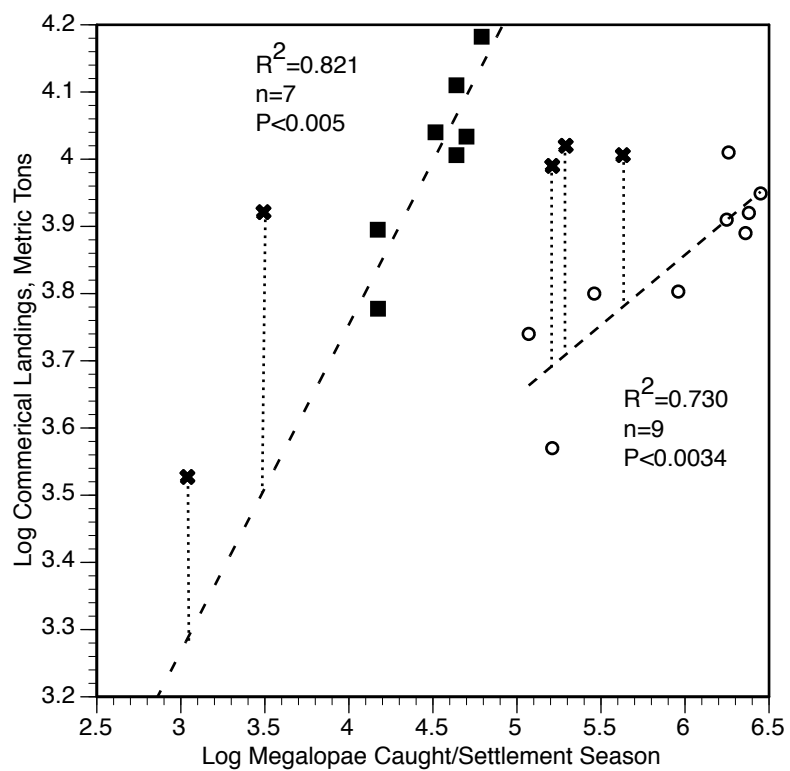


Figure 6

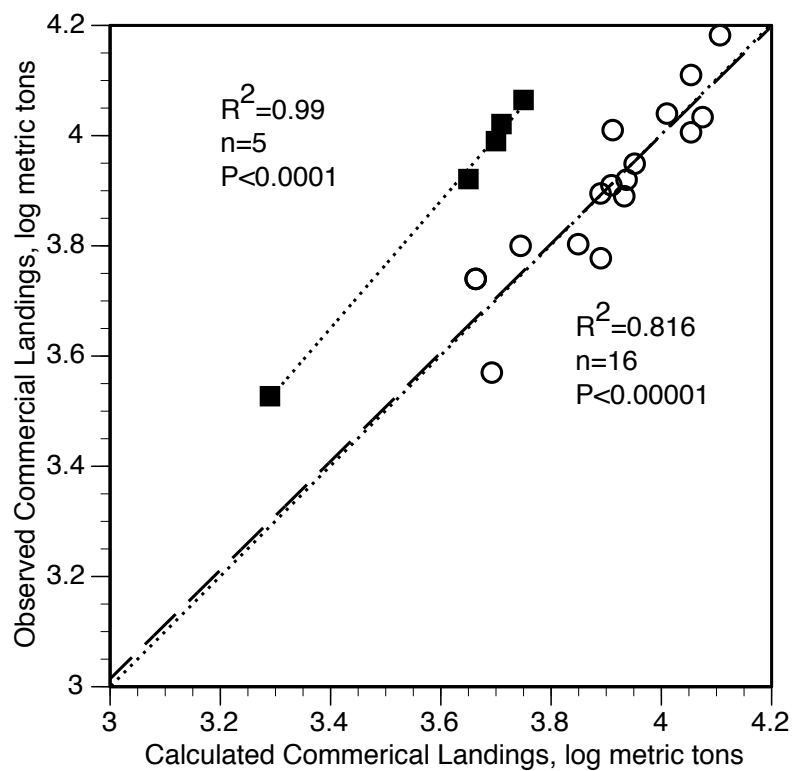


Figure 7

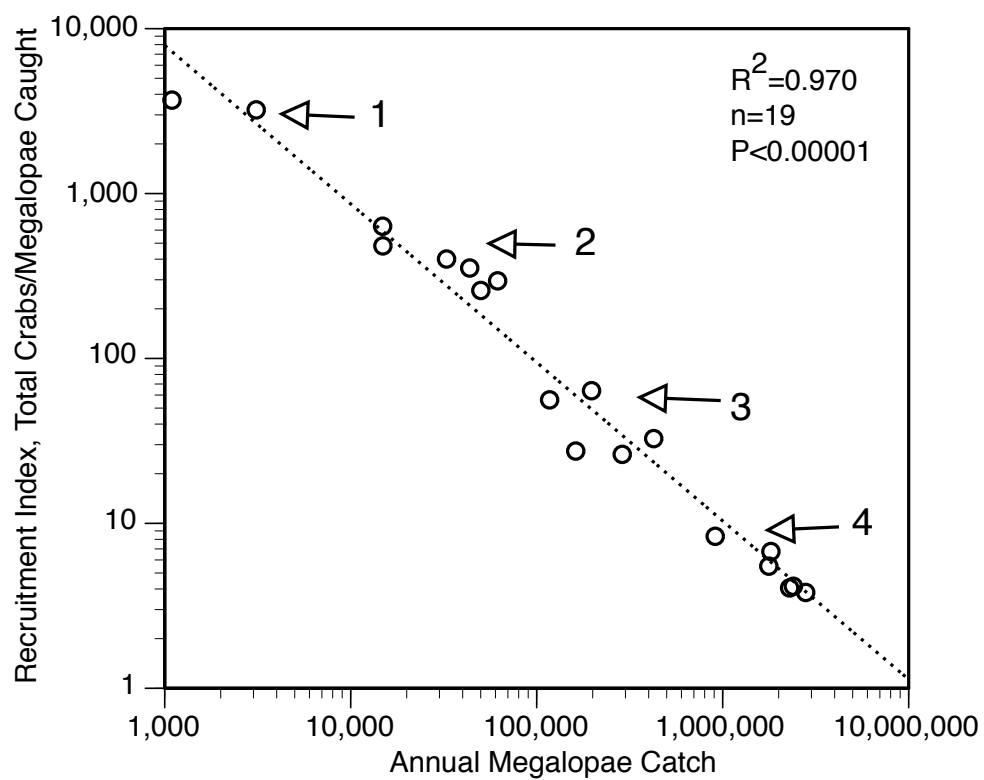


Figure 8

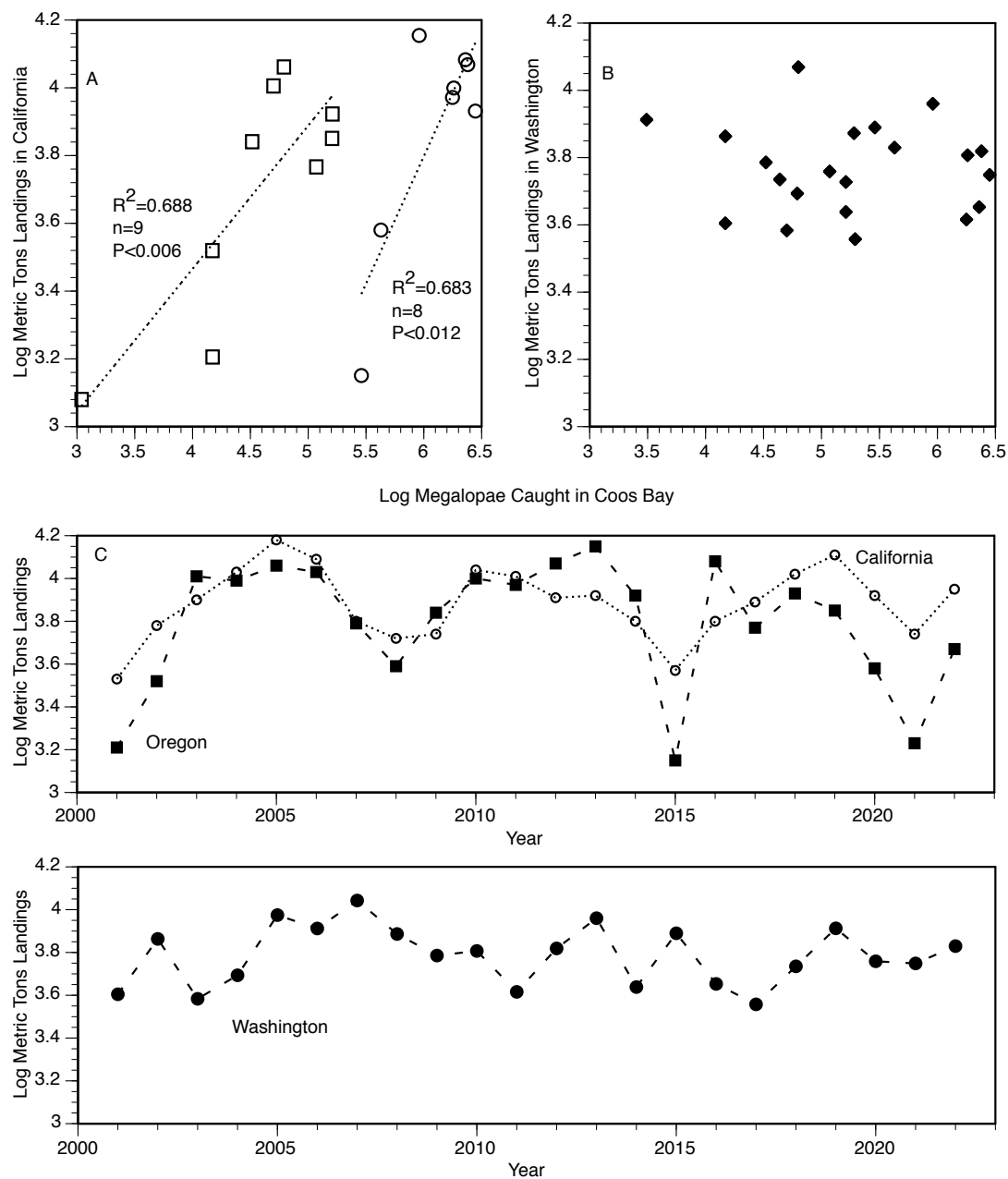
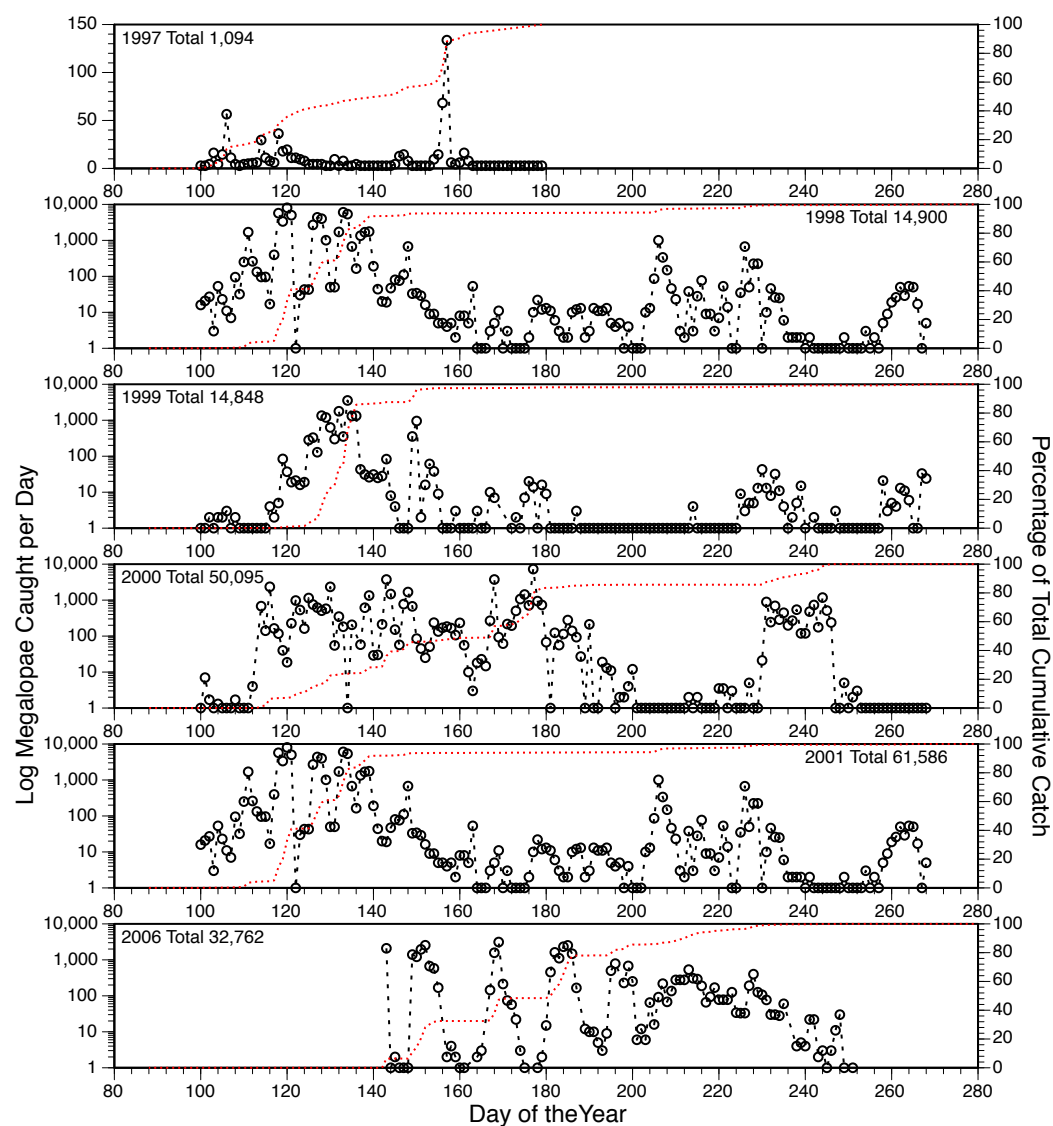
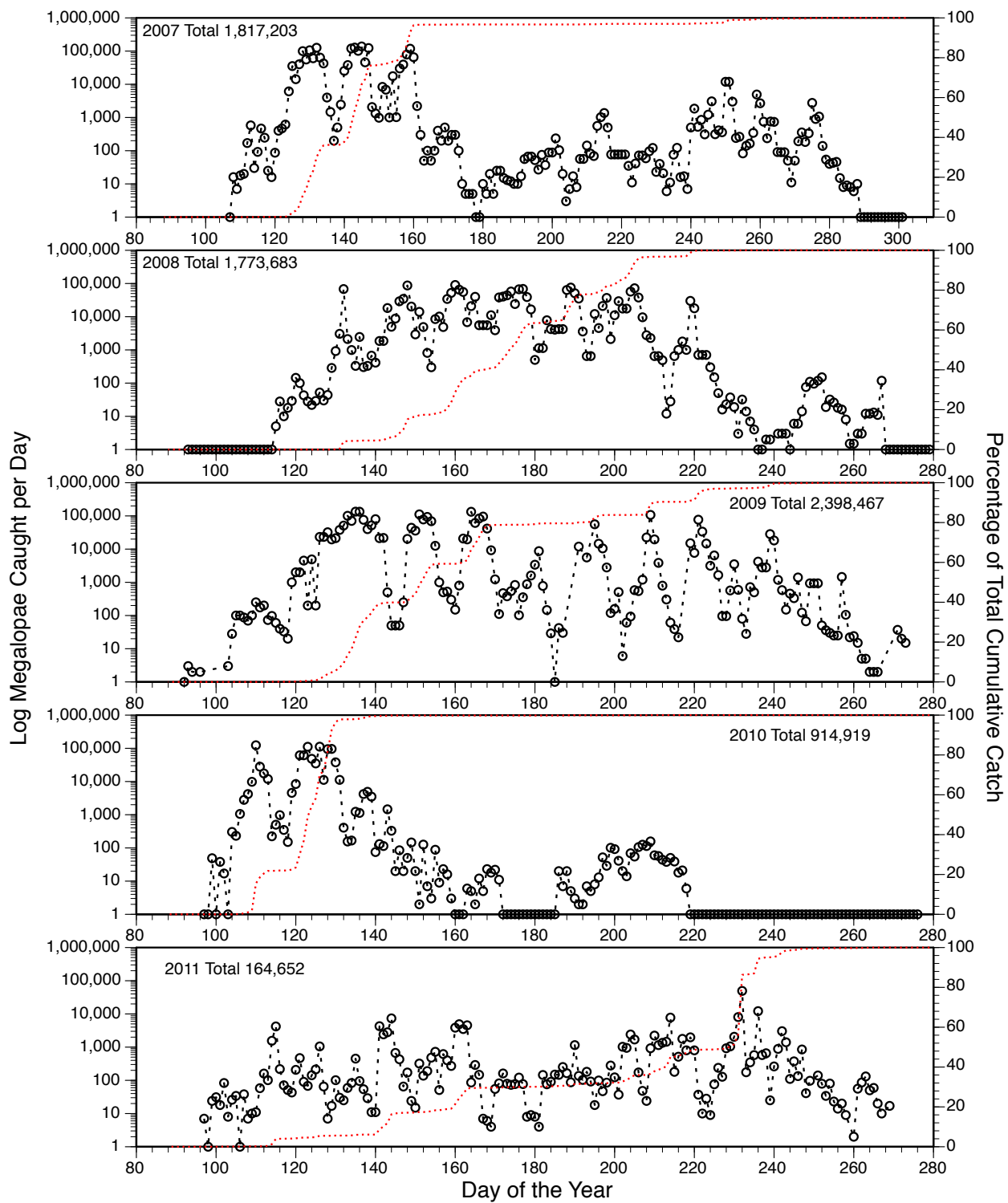


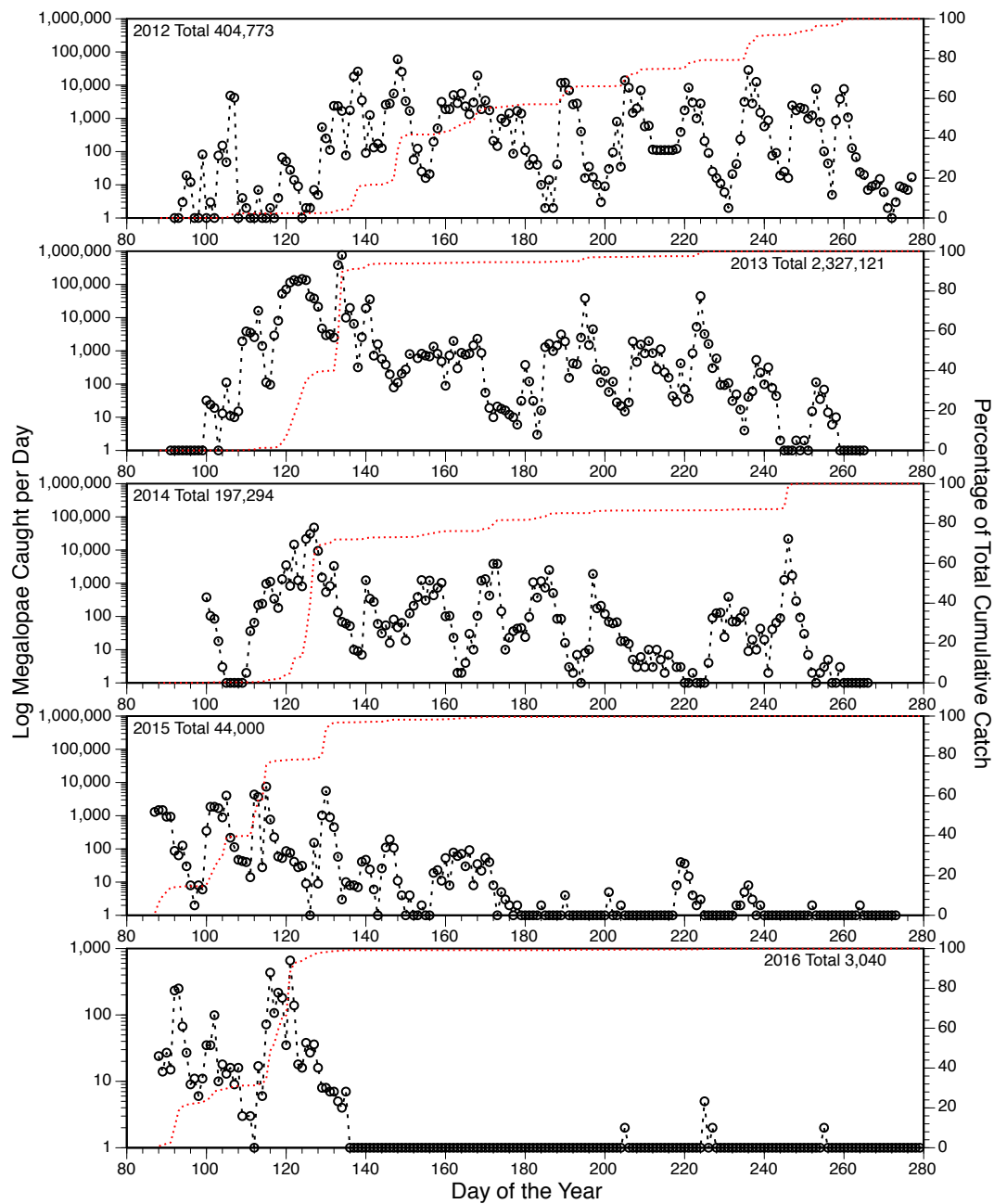
Figure 9

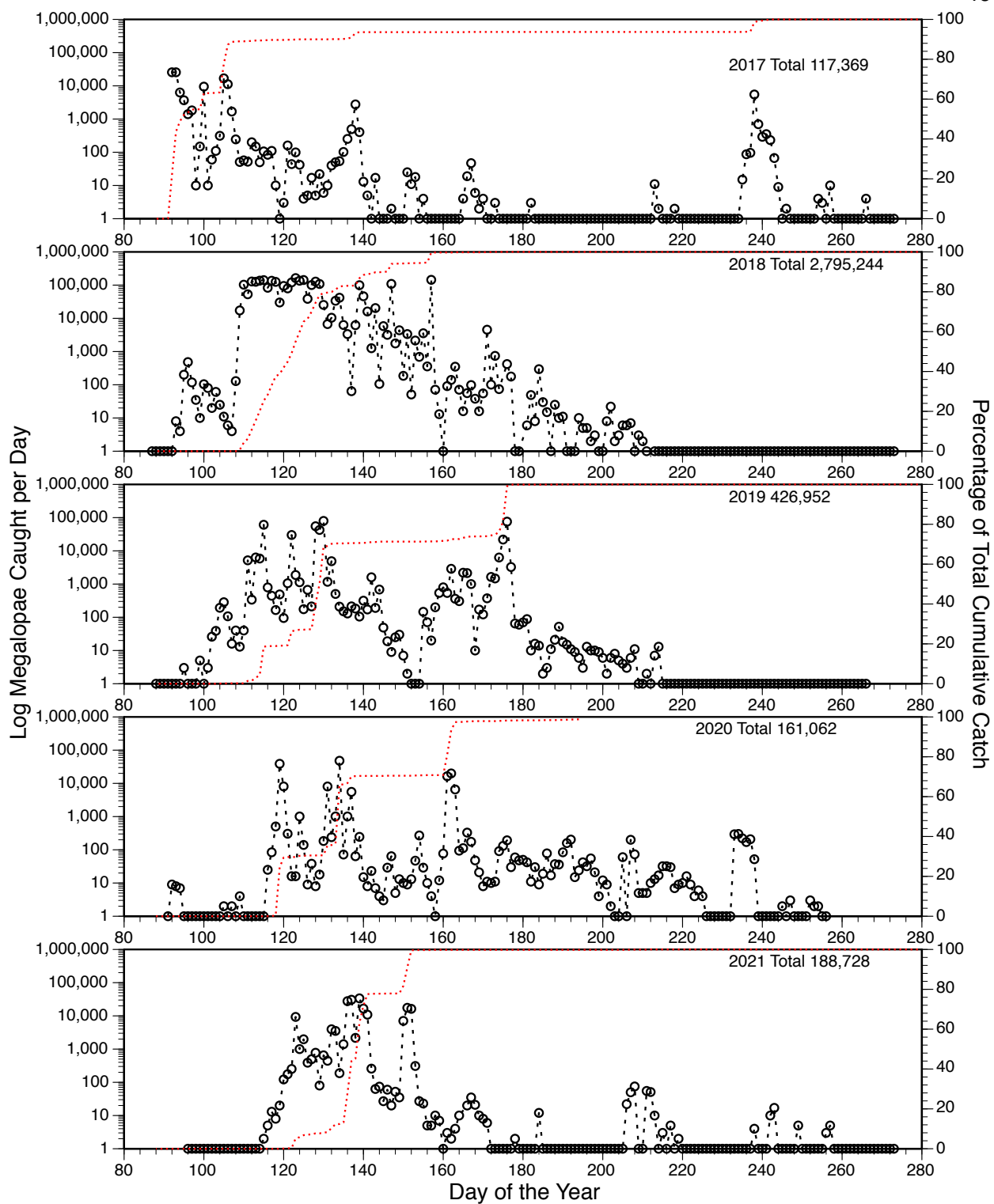
Supplemental Material

Figure 1. Daily catch of megalopae (open circles) plotted with the percentage of the cumulative catch (red dotted line). Note the changes in the scale on the left x-axis. One has been added to the daily catch to allow for plotting on a \log_{10} scale. Day of the year 91=1 April and 273=30 Sept.









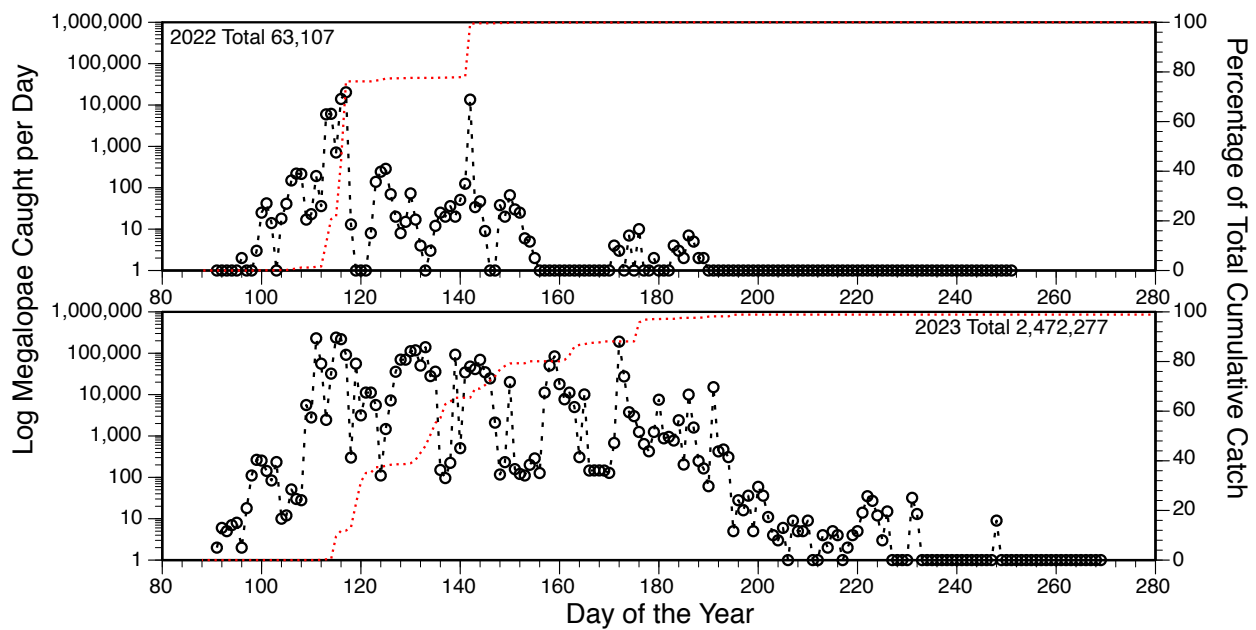


Figure 2. The evolution of the relationship between the \log_{10} of the number of megalopae caught and the \log_{10} of the commercial catch in Oregon lagged four years. A) represents the relationship through 2006, a significant straight regression. B) extends the data one year through 2007, the first year when we caught more than a million megalopae. At this time, we thought the relationship had evolved into a parabolic curve. In C the data has been extended to 2013 and we attempted to fit a parabolic curve to the data, this was not significant. It was at this point that we realized we actually had two curves (D), one for years with catches of megalopae $<100,000$ and a second for years with $>100,000$ megalopae. Both these regressions are and continue to be significant.

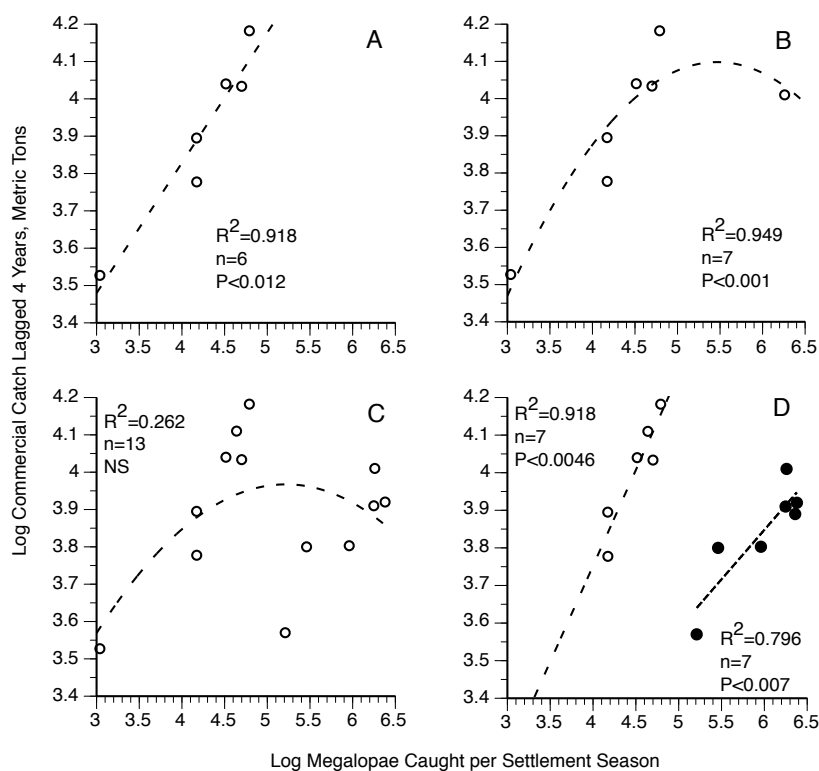


Table 1. Daily catch of megalopae in a light trap fished in Coos Bay, Oregon. Empty cells indicate no data. DOY is Julian day of the year.

Date	DOY	1997	1998	1999	2000	2001	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023
28-Mar	87															1298	0		0					
29-Mar	88															1474	24		0	0				
30-Mar	89															1474	14		1	0				
31-Mar	90															933	27		1	0				
1-Apr	91													0		934	15		0	0	0		0	
2-Apr	92									1			1	0		87	233	25558	0	0	9		0	
3-Apr	93								0	3			1	0		64	250	25558	8	6	8		0	
4-Apr	94								0	2			3	0		126	67	6302	4	0	7		0	
5-Apr	95								0	0			19	0		30	27	3676	201	3	1		1	1
6-Apr	96								0	2		0	12	0		8	9	1400	482	0	1	0	2	5
7-Apr	97								0	0	0	7	1	0		2	11	1821	118	0	0	0	0	4
8-Apr	98								0	0		1	1	0		8	6	10	35	0	1	0	1	6
9-Apr	99								0	0	49	24	82	0		6	11	149	10	5	0	0	3	7
10-Apr	100	3	3	0	0	16			0	0		31	1	32	378	348	35	9453	104	1	0	0	25	1
11-Apr	101	3	6	1	7	21			0	0	38	18	3	24	104	1853	35	10	80	3	0	0	42	17
12-Apr	102	4	4	2	2	27			0	0	17	83	1	19	85	1854	99	60	20	26	1	0	14	110
13-Apr	103	16	1	1	0	3			0	3		8	76	1	18	1679	10	110	61	39	0	0	1	264
14-Apr	104	4	2	2	1	53			0	28	303	26	152	13	3	888	18	313	25	193	1	0	18	253
15-Apr	105	15	0	2	1	23			0	100	232	34	48	112	1	4038	13	16806	11	284	2	0	41	142
16-Apr	106	56	2	3	0	11			0	100	1057	1	4850	11	1	217	16	11204	6	107	1	0	150	83
17-Apr	107	11	0	0	0	7		1	0	87	2800	38	4200	10	0	113	9	1681	4	16	2	0	220	233
18-Apr	108	4	0	2	2	95		16	0	70	4200	7	1	15	1	47	16	244	129	40	1	0	216	9
19-Apr	109	3	1	0	1	32		7	0	100	9800	10	4	1932	1	43	3	51	17290	13	4	0	17	11
20-Apr	110	4	0	0	0	251		18	0	250	12355	11	2	3850	2	40	0	57	10295	40	1	0	23	50

											0							0						
21-Apr	111	5	0	0	0	1690		20	0	175	28000	58	1	3525	36	14	3	52	53006	5184	1	0	192	29
22-Apr	112	6	5	0	4	261		170	0	200	17500	160	1	2575	65	4338	1	200	12851 4	339	1	0	36	27
23-Apr	113	6	1	0	0	133		579	0	73	11900	101	7	16100	223	3674	17	149	12609 4	6318	0	0	5950	5600
24-Apr	114	30	17	0	679	96		30	1	97	224	1550	1	1400	242	28	6	50	13639 3	5868	1	0	6125	2800
25-Apr	115	11	0	0	141	96		92	5	60	500	4200	1	112	963	7465	72	106	14138 3	60966	0	2	711	229600
26-Apr	116	8	1	4	2345	17		465	28	40	971	218	2	96	1120	766	434	84	83214	792	25	5	14000	56000
27-Apr	117	6	0	2	163	396		246	10	33	348	71	1	2900	340	225	107	110	13525 7	445	84	13	20300	2450
28-Apr	118	36	10	5	117	5704		25	18	20	151	51	4	8050	180	59	216	10	12522 9	165	504	8	13	32130
29-Apr	119	18	4	84	40	3355		16	29	1000	4550	43	67	52500	1330	53	181	1	30011	488	38808	20	0	238700
30-Apr	120	20	21	37	19	8045		87	144	2000	8400	207	51	70700	3500	86	35	3	94403	95	8064	122	0	218400
1-May	121	11	10	19	226	5001		400	100	2000	61600	468	28	11410 0	835	76	660	160	79682	1058.4	304	175	0	91700
2-May	122	11	5	21	973	1		468	43	4500	61600	90	14	13510 0	14700	41	139	44	12095 6	30006	16	252	8	300
3-May	123	9	2	16	532	30		613	28	200	11130 0	68	9	12495 0	1225	28	18	99	16277 3	1872	16	9300	139	56000
4-May	124	8	0	19	162	43		6121	22	4900	48300	142	1	14560 0	808	31	16	42	13567 7	1134	1008	1000	244	3150
5-May	125	4	46	282	1143	43		35368	29	200	35000	213	2	13475 0	21700	9	38	4	14242 0	175	140	1975	287	11200
6-May	126	4	477	328	752	2687		14209	52	23300	11200 0	1050	2	42700	30800	1	27	5	38631	671.4	9	389	70	11200
7-May	127	4	588	129	618	4358		40119	30	23300	11200	65	7	37800	47600	153	36	17	10062 8	212	38	496	20	5600
8-May	128	4	323	1340	508	4001		99684	44	32200	94500	7	5	21250	9450	9	16	5	12757 6	55062	8	775	8	110
9-May	129	3		1193	574	1010		55807	286	19600	95900	17	544	4700	1487	1020	8	22	10831 0	42606	18	80	15	1470
10-May	130	3		630	2335	50		10605 3	922	21350	37800	101	250	2950	542	5551	8	6	25342	79578	184	650	73	7210
11-May	131	9		299	55	50		60737	3051	37800	11200	30	112	3150	827	895	7	10	6718	1170	8064	445	17	35700
12-May	132	3	57	1776	348	1718		12598 2	68000	51000	407	25	2380	2525	3325	452	7	40	10423	4878	240	3950	4	70000
13-May	133	8	2	353	182	6039		63789	2123	100800	156	59	2350	38458 7	133	58	5	50	33790	504	1008	3525	1	70000
14-May	134	3	95	3550	0	5362		42509	991	70700	167	83	1680	76665 0	69	3	4	54	41718	209	47880	188	3	112000

15-May	135	3	106	1307	206	674		3990	330	134400	1228	450	77	9975	61	10	10	102	6299	151	72	1400	12	117600
16-May	136	4	815	1327	0	164		1470	2454	133700	1133	95	1750	19600	52	8	0	252	3359	130	1008	27775	25	50400
17-May	137	3	317	43	58	1347		200	303	76300	4200	54	18200	6496	10	8	0	495	64	213	5544	30575	20	140000
18-May	138	3	1675	31	615	1681		500	330	39900	4900	29	25760	319	9	7	1	2757	6224	183	64	2175	36	28000
19-May	139	3	3392	26	1340	1753		2450	671	51800	3500	11	3500	2575	7	41	1	404	99418	105	245	33700		35840
20-May	140	3	921	31	29	191		25281	413	79800	75	11	91	19137	1228	47	0	13	46214	316	15	16600	51	150
21-May	141	3	723	25	30	44		37877	1855	21350	131	4275	1260	35700	344	24	0	5	16055	172	8	10875	125	95
22-May	142	3	358	28	212	20		11961 4	1864	21700	114	2425	133	715	277	6	0	0	1260	1602	23	258	13510	223
23-May	143	3	751	83	3735	19	2093	12757 9	18232	500	1456	2800	173	1577	60	1	0	17	20378	191	7	63	34	92400
24-May	144	3	479	8	1474	47	1	10166 7	4981	50	329	7350	127	571	31	26	0	0	106	684	4	74	47	505
25-May	145	4	115	4	151	80	2	13794 7	8790	50	20	669	2590	383	54	110	0	0	5829	49	3	27	9	34300
26-May	146	13		0	57	76	1	45860	29140	50	85	430	2800	196	16	194	0	0	3186	19	29	60	0	47600
27-May	147	15	823	0	773	111	1	12359 6	34511	250	20	65	5600	79	81	108	0	2	10882 8	9	64	20	0	41440
28-May	148	8	35	0	1675	676	1	2063	87256	20300	50	172	60200	110	47	11	0	0	1754	25	5	52	38	69440
29-May	149	3	10	354	670	33	1401	1326	20186	43925	146	24	25200	206	64	4	0	0	4372	30	13	35	20	34720
30-May	150	3	11	951	85	34	1215	982	2930	36050	20	15	3290	274	19	1	0	0	186	7	10	7050	66	24640
31-May	151	3	58	2	45	29	1959	8351	14000	111300	2	320	1680	797	124	4	0	25	3359	2	9	17500	30	2100
1-Jun	152	3	25	16	25	16	2544	6877	4883	78225	126	138	57	0	211	0	0	11	51	0	13	16275	25	116
2-Jun	153	3	1	61	51	9	668	1000	813	93275	7	190	123	598	385	1	0	18	2149	0	47	310	6	232
3-Jun	154	9	202	38	236	9	581	17544	300	69125	3	482	25	820	1247	2	0	0	692	0	270	27	5	20160
4-Jun	155	15	185	9	134	5	169	1024	8465	12600	88	724	16	720	306	0	0	4	3557	146	29	23	2	157
5-Jun	156	68	310	0	170	5	0	30000	10093	1000	9	51	21	677	1204	1	0	1	357	71	10	5	0	120
6-Jun	157	134	312	0	184	4	2	39298	4883	500	23	618	198	1342	434	19	0	0	14424 8	20	4	5	0	110
7-Jun	158	6	928	0	167	5	4	78596	34186	525	16	400	500	816	734	23	0	0	71		1	10	0	200
8-Jun	159	4	179	3	106	2	2	11789 5	52093	300	3	271	3150	479	1033	11	0	0	13	540	12	7	0	286
9-Jun	160	6	167	0	233	8	1	65474	90186	150	0	3850	1890	89	101	53	0	0	0	797.4	77	0	0	126
10-Jun	161	16	53	0	56	8	1	2211	65116	800	1	4900	1890	725	104	8	0	0	91	540	16380	3	0	11200

11-Jun	162	8	9	0	10	5	0	300	55674	20790	1	3500	5040	1973	23	78	0	0	140	2880	19908	2	0	50400
12-Jun	163	3	12	0	3	53	0	50	6837	19600	6	4550	2875	296	2	61	0	0	350	361	6552	4	0	84000
13-Jun	164	3	5	3	18	1	2	100	20837	133175	5	86	5600	872	2	71	0	1	71	306	94	10	0	17920
14-Jun	165	3	11	0	23	1	3	50	39720	61425	2	290	2310	762	4	30	0	4	16	2196	112	0	0	7700
15-Jun	166	3	23	0	15	1	0	100	5534	83713	12	147	1330	828	30	92	0	19	56	2142	329	20	0	11200
16-Jun	167	3	19	10	267	3	145	400	5534	95495	5	7	3010	1457	10	8	0	47	98	1000	174	35	0	5000
17-Jun	168	3	0	7	3738	5	1573	200	5534	41587	23	6	19600	2319	105	35	0	6	38	10	48	21	0	306
18-Jun	169	3	0	0	93	11	3126	500	11069	9228	18	4	1890	864	1192	22	0	2	16	171	21	10	0	10080
19-Jun	170	3	6	0	62	1	213	200	3906	1226	22	55	3430	55	1332	54	0	4	55	122	8	8	0	145
20-Jun	171	3	6	0	216	3	74	300	38093	111	11	81	1750	19	426	40	0	0	4545	372.6	11	6	4	146
21-Jun	172	3	17		195	1	57	300	40372	471	1	161	211	10	3850	8	0	0	101	1638	10	0	3	146
22-Jun	173	3	19	2	502	1	22	100	43953	379	0	79	147	21	3850	1	0	3	741	1476	11	0	0	145
23-Jun	174	3	21		1069	1	3	10	57302	541	0	73	975	18	143	5	0	0	74	6300	91	0	7	127
24-Jun	175	3		7	1429	1	1	5	24093	830	0	77	775	16	10	3	0	0	0	21888	131	0	1	676
25-Jun	176	3	20	20	715	2	0	5	66906	102	0	121	1425	12	23	2	0	0	420	75654	193	0	10	190400
26-Jun	177	3	33	14	7281	10	0	5	68697	355	0	77	87	10	36	0	0	0	177	3258	30	0	1	27500
27-Jun	178	3	1		938	22	1	1	39093	875	0	8	1675	6	43	2	0	0	0	65	59	2	0	3750
28-Jun	179	3		16	733	12	2	1	16604	1601	0	9	1400	31	45	0	0	0	1	60	48	0	2	3010
29-Jun	180		4	9	68	13	15	10	500	3385	0	8	110	377	24	0	0	0	0	70	50	1	0	1250
30-Jun	181		7	1	0	11	456	5	1135	8700	0	4	40	119	97	0	0	1	6	88	42	0	1	637
1-Jul	182		3	1	123	6	1613	20	1135	778	0	145	60	31	1076	0	0	3	49	10	11	0	0	425
2-Jul	183		2	0	56	3	1111	5	7813	146	1	76	40	3	370	1	0	0	8	16	30	0	4	1250
3-Jul	184		3	0	114	2	2319	25	4232	29	1	90	10	16	1152	2	0	0	295	14	9	12	3	7525
4-Jul	185		2	0	279	2	2522	25	4069	1	1	149	2	1288	738	0	0	0	30	2	19	0	2	875
5-Jul	186		1	0	140	10	1478	15	4232	42	20	146	14	1624	2508	0	0	0	15	3	78	1	7	950
6-Jul	187		3	3	93	12	166	13	4232	30	7	252	2	984	506	0	0	0	0	11	17	0	5	775
7-Jul	188		1	0	27	13	0	12	63814	0	20	164	41	1455	85	0	0	0	25	21	37	0	2	2400
8-Jul	189		1	1	0	2	12	10	75372	0	5	87	11640	3114	85	0	0	0	10	52	36	0	2	203
9-Jul	190		1	0	212	3	10	10	50953	0	3	1150	11900	1910	16	4	1	0	11	18	84	0	1	10000

10-Jul	191		1	1	0	13	10	17	35162	11900	2	136	7000	153	3	0	0	0	1	15	159	0	0	1600
11-Jul	192		1	0	0	11	5	56	3581	0	2	103	2650	417	2	0	0	0	0	11	203	0	0	248
12-Jul	193		0	1	19	11	3	66.5	651	5600	7	181	2800	396	7	0	0	0	0	9	15	0	0	163
13-Jul	194		0	0	13	13	9	66.5	651	0	5	92	399	2512	1	0	0	0	10	6	24	0	0	60
14-Jul	195		1	0	11	5	499	52	12046	55915	8	18	16	38358	8	0	0	0	5	3	42	0	0	15125
15-Jul	196		1	0	1	4	785	27	4558	14525	13	99	35	1492	10	0	0	0	5	13	32	0	0	423
16-Jul	197		5	0	2	5	0	75	21000	10500	52	47	17	4458	1898	0	0	0	2	10	55	0	0	470
17-Jul	198		1	0	2	1	228	37	36790	2800	29	85	10	277	176	0	0	0	3	10	21	0	0	307
18-Jul	199		2	0	4	4	678	88	2116	119	101	279	3	112	210	0	0	0	1	9	4	0	0	4
19-Jul	200		0	0	12	1	252	88	11069	158	92	123	9	243	119	0	0	0	1	6	12	0	0	27
20-Jul	201		0	0	1	1	6	235	29302	509	41	37	30	58	69	5	0	0	8	2	9	0	0	15
21-Jul	202		1	0	0	1	12	104	17581	6	20	1025	95	117	62	0	0	0	22	6	2	0	0	35
22-Jul	203		1	0	0	10	6	20	17581	61	14	950	800	28	67	0	0	0	2	8	0	0	0	4
23-Jul	204		1	0	0	13	65	3	56976	93	69	2400	35	22	18	2	0	0	3	5	1	0	0	58
24-Jul	205		0	0	0	86	16	7	71953	580	55	1700	14000	15	18	1	2	0	6	4	60	0	0	35
25-Jul	206		2	0	0	1006	92	17	37767	544	106	173	8400	28	15	0	1	0	6	3	1	22	0	10
26-Jul	207		0	0	0	336	218	8	9604	1201	125	48	1475	1922	5	0	0	0	7	6	200	50	0	3
27-Jul	208		0	0	0	149	68	56.5	2765	22400	114	24	2000	464	3	0	0	0	1	11	73	75	0	5
28-Jul	209		0	0	0	46	136	56.5	2279	107275	157	925	7000	1547	6	0	0	1	3	1	5	0	0	0
29-Jul	210		0	0	0	23	277	143	651	19600	60	2225	575	837	3	0	1	0	2	1	5	0	0	8
30-Jul	211		0	0	0	3	278	82	651	3850	57	1150	600	1967	10	0	0	0	1	2	5	55	0	4
31-Jul	212		0	0	1	2	278	69	488	792	44	1350	115	855	3	0	0	0	0	1	10	51	0	0
1-Aug	213		0	0	2	38	535	558	12	304	38	1450	111	276	10	0	0	11	0	7	13	10	0	0
2-Aug	214		0	4	0	3	308	1023	28	61	50	7750	111	1116	5	0	0	2	0	13	17	1	0	0
3-Aug	215		0	0	2	28	292	1364	651	39	39	180	111	225	2	0	1	0	0	1	32	3	1	0
4-Aug	216		0	0	0	77	189	500	1000	22	18	514	111	155	7	0	0	0	0	1	32	0	0	0
5-Aug	217		1	1	0	9	66	77	1790	0	21	1775	111	43	0	0	0	2	0	1	30	5	0	0
6-Aug	218		1	0	0	9	94	77	1000	0	6	800	121	29	3	8	0	2	0	1	7	1	0	0
7-Aug	219		2	0	1	3	169	77	29953	15050	0	1975	389	419	3	40	0	0	0	0	9	2	0	0

8-Aug	220		0	0	4	7	78	77	17907	7700	0	800	1750	70	0	36	1	0	0	1	10	0	0	0
9-Aug	221		1	0	4	53	78	77	705	77000	0	37	8400	37	0	15	0	0	1	1	16	0	0	0
10-Aug	222		0	1	0	14	78	35	705	33600	0	10	3000	846	2	4	2	0	0	0	9	0	0	0
11-Aug	223		0	1	3	1	126	11	705	14700	0	28	1000	5278	0	2	1	0	0	0	4	0	0	0
12-Aug	224		1	1	0	1	34	41	300	3150	0	9	2800	44345	0	3	5	0	0	0	6	0	0	0
13-Aug	225		0	9	1	35	33	72	150	6440	0	76	208	3192	0	1	2	0	0	0	4	0	0	0
14-Aug	226		0	3	1	671	33	72	50	1648	0	238	91	1612	4	0	0	0	0	0	1	0	0	0
15-Aug	227		0	5	5	50	191	59	16	96	0	128	25	302	90	1	0	0	0	0	1	0	0	0
16-Aug	228		0	5		224	400	96	23	96	0	925	16	588	125	1	1	0	0	0	0	0	0	0
17-Aug	229		1	13		224	126	121	37	568	0	1050	11	94	130	1	0	0	0	0	1	0	0	0
18-Aug	230		0	43	21	1	107	23	19	3500	0	2050	6	93	24	1	0	0	0	0	0	0	0	0
19-Aug	231		0	13	889	10	77	40	3	593	0	8050	2	107	390	0	0	0	0	0	0	0	0	0
20-Aug	232		0	8	244	46	30	21	32	80	0	49350	21	31	70	0	0	0	0	0	0	0	0	0
21-Aug	233		1	32	691	26	30	6	14	28	0	175	42	49	70	2	0	0	0	0	293	0	0	0
22-Aug	234		0	11	286	25	28	11	7	717	0	348	235	17	91	2	0	0	0	0	300	0	0	0
23-Aug	235		0	4	445	6	60	76	4	499	0	575	3150	4	139	5	0	15	0	0	221	0	0	0
24-Aug	236			1	198	2	0	122	0	4200	0	12129.6	28700	41	9	8	0	87	0	0	171	0	0	0
25-Aug	237		0	2	269	2	0	16	0	2800	0	576	2800	60	20	3	0	96	0	0	208	1	0	0
26-Aug	238		0	5	542	2	4	17	2	2800	1	654	12600	533	10	1	0	5483	0	0	52	4	0	0
27-Aug	239		0	15	119	2	5	7	2	28350	0	25	1500	222	43	2	0	699	0	0	1	0	0	0
28-Aug	240		0	1	119	1	4	500	0	18200	1	262	575	98	20	0	0	292	0	0	0	0	0	0
29-Aug	241		1	0	479	2	22	1850	3	1184	1	885	875	317	2	0	1	351	0	0	0	0	0	0
30-Aug	242		1	2	731	1	22	525	3	582	1	3025	76	76	41	0	0	232	0	0	0	10	0	0
31-Aug	243		4	1	176	1	2	850	3	150	0	1400	91	44	65	0	4	67	0	0	0	17	0	0
1-Sep	244		0	1	1176	1	3	310	1	456	0	110	19	2	89	0	10	9	0	0	0	0	0	0
2-Sep	245		0	0	512	1	1	1217	6	333	0	373	25	0	1261	0	3	0	0	0	2	0	0	0
3-Sep	246		1	0	238	1	3	3064	6	1400	0	134	16	0	21700	1	0	2	0	0	1	1	0	0
4-Sep	247		0	3		1	11	313	14	122	0	850	2450	0	1699	1	0	0	0	0	3	0	0	0
5-Sep	248		0	0		1	30	410	76	67	0	41	1750	2	291	1	0	0	0	1	0	1	0	0

6-Sep	249			0	5	2	1	359	110	933	0	97	2100	0	93	1	0	0	0	1	0	5	0	0
7-Sep	250		0	0	0	1	0	11900	96	933	0		1925	2	30	1	0	0	0	0	1	0	0	0
8-Sep	251		0	0	2	1	1	11900	118	933	0	140	975	0	7	0	0	0	0	1	1	0	0	0
9-Sep	252		0	0	3	1		3000	150	50	0	79	1225	15	2	2	0	1	0	1	3	0		0
10-Sep	253		0	0	0	1		241	19	36	0	34	7775	113	0	0	0	0	0	1	2	0		0
11-Sep	254		0	0	0	3		263	32	30	0	80	775	35	2	0	0	4	0	0	2	0		0
12-Sep	255		0	0	0	1		83	26	25	0	23	101	68	3	0	2	3	0	0	1	0		0
13-Sep	256		0	0	0	2		141	18	25	1	14	44	14	5	0	0	0	0	0	0	3		0
14-Sep	257		0	0	0	1		164	16	1450	0	20	5	6	1	1	0	10	0	0		5		0
15-Sep	258		0	21	0	5		344	8	105	0	9	859	10	1	0	0	1	0	0		0		0
16-Sep	259		0	3	0	9		4925	1.5	22	0	0	3850	0	3	0	1	1	0	0		0		0
17-Sep	260		4	5	0	19		2681	1.5	24	0	2	7700	0	0	0	0	0	0	0		0		0
18-Sep	261		0	4	0	26		747	3	15	0	56	1075	0	0	0	10	0	0	0		0		0
19-Sep	262		0	13	0	50		237	3	5		86	127	1	0	0	0	0	0	0		0		0
20-Sep	263		0	11	0	29		757	12	5	0	131	68	1	0	0	1	0	0	0		0		0
21-Sep	264		0	6	0	53		738	12	2	0	50	24	0	0	2	3	1	0	0		0		0
22-Sep	265		0	0	0	50		91	13	2	0	59	20	0	0	0	0	0	0	0		0		
23-Sep	266		0	0	0	17		90	11	2	0	20	7		0	0	2	4	0	0		0		
24-Sep	267		0	33	0	1		90	118	0	0	10	9			0	0	0	0			0		
25-Sep	268		0	24	0	5		50	0	0	0		10			0	0	1	0			0		
26-Sep	269							11	0	0	0	17	15			0	1	0	0			0		
27-Sep	270							50	0	0	0		6			0	0	0	0			0		
28-Sep	271							192	0	37	0		2			0	0	0	0			0		
29-Sep	272							355	0	20	0		1			0	0	0	0			0		
30-Sep	273							183	0	15	0		3			0	2	0	0			0		
1-Oct	274							334	0		0		9				0							

2-Oct	275							2750	0		0		8				0							
3-Oct	276							901	0		0		7				0							
4-Oct	277							1066	1				17				0							
5-Oct	278							139	0								0							
6-Oct	279							54	0								0							
7-Oct	280							40	0								0							
8-Oct	281							43	0								0							
9-Oct	282							46	0								0							
10-Oct	283							15	0								0							
11-Oct	284							8	0								0							
12-Oct	285							9	0								0							
13-Oct	286							8	0								0							
14-Oct	287							6	0								0							
15-Oct	288							10	0								0							
16-Oct	289							1	0								0							
17-Oct	290							1	0								0							
18-Oct	291							1	0								0							
19-Oct	292							1	0								0							
20-Oct	293							1	0								0							
21-Oct	294							1	0								0							
22-Oct	295							1	0								0							
23-Oct	296							1	0								0							
24-Oct	297							1	0								0							

Table 2 . Summary of best fit generalized additive model (GAM) from the mgcv package in

R. Model was fit using a Tweedie distribution and the model selection was conducted using a backwards AICc approach. edf- effective degrees of freedom, Ref.df- Reference degrees of freedom

Family: Tweedie(p=1.99)

Link function: log

Formula:

Megalopae ~ s(PDO, k = 5) + s(ST, k = 5) + s(CUTI, k = 5)

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	12.5230	0.2302	54.41	<2e-16

Approximate significance of smooth terms:

	edf	Ref.df	F-value	p-value
s(PDO)	2.540	3.017	10.946	0.000302
s(ST)	1.000	1.000	12.028	0.002939
s(CUTI)	1.571	1.886	0.611	0.491579

R²(adj) = 0.628

-REML = 316.3

Deviance explained = 63.1%

Scale est. = 1.3809

n = 23

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