**Primary Production Anomalies Differently Impact the Density of Viviparous and Oviparous Fishes**

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**Abstract**

Primary productivity is a factor that can dramatically shift annually, and the effects of this cycle on marine species is not yet fully understood. This analysis of the comparative impact of years with anomalously high primary productivity (measured in chlorophyll-*a*) on egg-laying, or oviparous, and live birth, or viviparous, fish is intended to more meaningfully explore the effects of primary productivity on marine species. I found that the change in size of oviparous and viviparous fish was not significantly impacted by years with high primary productivity; both experienced increases in average size during high-productivity years of 2.1 cm on average. However, there was significant change in the population density of these fish during high-productivity years—viviparous fish increased in density by an average of 13.8%, whereas oviparous fish experienced a 33.5% decline in population density. These results demonstrate that certain fish populations may be differentially influenced by years of high primary productivity, and the need to understand the intricacies of this phenomenon is increasingly important as we excavate the catastrophic consequences of climate change on our marine ecosystems and its anomalous impacts on primary productivity.

**Introduction**

Primary production is critical to sustain the food web and to maintain and grow fish populations. However, in scenarios of nutrient over-enrichment, excessive primary production can lead to eutrophication of fish habitat, leading to hypoxia and death (National Research Council 2000). Understanding the marginal effects of eutrophication and what species are most resilient to its impacts is an important step in discerning the characteristics of fisheries and habitats (Diaz *et al.* 2008). Grasping the full range of consequences that increased primary production may have has been made more urgent by the presence of climate change, which is likely to contribute to heightened primary production rates in many parts of the world over the coming decades (Lei *et al.* 2009, Azhdari *et al.* 2020, Pinkerton *et al.* 2021). This paper will analyze the comparative effects of high primary production on embryonic development; specifically, I will be analyzing the density of viviparous (live birth) and oviparous (egg-laying) species in the calendar year following a high-primary production bloom in my beach seine database. This study will address the question of whether the birth type of a given species suggests the degree to which it will be affected by blooms of high productivity in its habitat. Notably, this study is investigating the assumption that external embryonic development, wherein oxygen is pulled directly from the egg’s surroundings, would be differently impacted by eutrophication than viviparous development, where the embryo is delivered oxygen by its mother (Serigstad 1987).

The impact of primary productivity on oceanic environments and fish populations is still being studied. However, it is known that eutrophication can begin to have deleterious effects well before reaching hypoxic or anoxic states, indicating that there could be a sliding scale of negative impacts on fish development as the amount of productivity increases (National Research Council 2000). Further, we know that the most common cause of nutrient over-enrichment in oceanic habitats is agricultural runoff, which could be predictive of the geographic and anthropological patterns of eutrophication (Malone *et al.* 2020). The ongoing impacts of climate change on primary production remain murky, but Blanchard *et al.* (2012) and Lei *et al.* (2009) demonstrated that not only is lower primary productivity correlated strongly with lower relative fish growth rate, but that the impacts of climate change on primary production vary significantly by region and temperature.

It is also valuable to understand the known relationship between fish survival rate and birth type. Oviparous fish require significantly less energy per egg by the mother, which means that oviparous fish may spawn many thousands of eggs in one spawning cycle (DeMartini *et al.* 2006). While viviparous fish mothers require much more energy during gestation and labor than oviparous mothers, the direct intake of nutrients (known as matrotrophy) and protection allows for a much greater chance of survival for each offspring (Helmstetter *et al.* 2016).

Considering this research, I would expect to see lower density increases in oviparous fish than viviparous fish during high primary productivity years. I anticipate the difference in these fish densities to increase commensurately with primary production levels, especially at the upper end where the habitat may be hypoxic or even anoxic. The result will be that there is a significant difference in the composition of fish population by birth type in all locations when comparing high and low productivity periods. I do not expect to see any difference in relative size between oviparous and viviparous fish during high productivity years, as the effects of eutrophication should normalize after birth or hatching.

**Methods**

To collect our fisheries-independent data, I sampled eight open coast and estuarine locations in southern California between 2002 and 2021 (excludes 2020) using a 30m beach seine (Bag Length = 1.89m, Bag Square = .8cm, Wing Square = .5cm) (Figures 1, 2, and 3). Replicates were performed at different times of year and at different frequencies each year (n = 398) (Table 1). Samples were taken by wading out perpendicular to shore until either the seine’s 1.8m height had been matched by depth or until the 30m rope length had been reached, at which point the seine was stretched parallel to shore until its full width had been unfurled and the seine was pulled to shore by the attached ropes. Individuals caught were categorized by species, count, and size class before being released. Surface area measured was recorded for each replicate.

I downloaded NOAA NMFS metadata from the US Global Change Research Program’s Ocean Chlorophyll Concentration project to find the year-by-year anomalies in primary productivity in the California Current region (Globalchange.gov, 2021). Anomalies were measured in percent change over or under the mean chlorophyll content for all years (0.54mg/m3), and each year in which replicates were sampled was assigned a Chlorophyll-a concentration level, either “high” (σ > 1, σ = 8%) or “normal” (σ < 1) (Figure 4). Since I was not studying the effects of low chlorophyll-a concentrations and the years that contained my data had no chlorophyll concentrations greater than 1 standard deviation below the mean, none of my years studied would be categorized as a “low” chlorophyll-a concentration.

Finally, I aggregated a list of fish species to be designated as viviparous from the *FishBase* online database, which contains known designations for all fishes (Froese and Pauly 2000). I assigned every species recorded in my beach seine collections a designation of either *Viviparous* or *Oviparous*, while excluding any ovoviviparous (internal egg development species that give live birth) species.

All data analysis was performed in Microsoft Excel 2021. Fish size analyses were performed by comparing the average size of oviparous and viviparous species during “high” and “normal” recorded years. Density analysis was performed by first summing the aggregate surface area measured during “High" years (59,697m2) and “normal” years (106,815m2), then calculating the density (individuals per 100m2) of oviparous and viviparous fish caught during each year type. Density was used instead of abundance to control for variance in the number of replicates performed during different years. The decision to aggregate the comparison to the total number of fish by birth type, as opposed to analyzing the trends by species, was an effort to control for significant statistical outliers that occurred as byproducts of low catch rates of certain species.

**Results**

Density of oviparous fish declined from 14.6 individuals/100m2 during years with normal chlorophyll-a concentration to 9.7 individuals/100m2 during years with high chlorophyll-a concentration—a 33.5% decrease (Figure 6). Conversely, the density of viviparous fish increased from 0.088 individuals/100m2 during normal years to 0.1 individuals/100m2 during high years, accounting for a 13.8% increase (Figure 7). The size of fish recorded had a weak positive correlation with high chlorophyll-a concentration, but there was no measurable difference in the strength of this correlation between oviparous and viviparous fish (Figure 5).

**Discussion**

My analysis showed that there was a decrease in the population density of oviparous fish but an increase in population density of viviparous fish during years with unusually high chlorophyll-a concentration (Figures 6 and 7). This implies that there may be a different relationship between chlorophyll concentration and egg survivorship than there is between chlorophyll concentration and *in utero* embryo survivorship. My results also determined that there is little difference in the relative size of these groups (when compared to their “normal” year size) during “high” years; both sets of species tend to be slightly larger during years with high chlorophyll-a concentration (Figure 5).

The results of my analysis conflict slightly with my hypothesis. While I expected for both birth type groups to increase in density during “high” chlorophyll-a years—and for the difference between groups to lie in how strongly they increased—I actually found that oviparous fish, the group expected to increase by a lesser degree, experience a sharp decrease in recorded population density during “high” years. The difference between my expectations and results may lie in the degree of severity by which high chlorophyll-a concentrations affect egg development. My hypothesis indicated that survivorship of oviparous fish would increase despite potentially hypoxic conditions due to the increased food quantity that comes with periods of high primary productivity. Instead, my findings would support the argument that periods of high primary productivity have a strong negative impact on oviparous fish egg survivorship. Further research could indicate whether this change is due to hypoxia or different factors entirely.

There are multiple ways in which this research could be improved or expanded. The simplest would be to have a larger dataset that contains years where primary productivity was abnormally low; such a dataset would allow for us to control for some of the randomness and low sample sizes that are inherent to beach seine data collection. A limitation on this front is that I used size and density to approximate fish populations during these periods, but both measurements have significant flaws in terms of controlling for external factors. Ideally, this analysis would be performed on data that include biomass, as such a measure would allow us to avoid issues of highly biased samples where one species overwhelmingly dominates the density data. Further studies will also have to be performed to eliminate potential confounding factors for my analysis, including the possibility that high primary productivity is correlated with a different factor that caused these results, or that these fish stocks simply spawned in deeper waters as a result of warmer temperatures and higher productivity extending their food reach further from seining sites.

The study also had strict limitations based on the data used. There was a stark difference in the number of oviparous fish (n = 213,606) and viviparous fish (n = 1,532) captured. While both are well above a statistically significant sample size, there is enough chance and variation involved in beach seining that I do not feel confident in with the viviparous sample size. This concern was especially impactful in size class analysis, as most species were captured infrequently enough that size comparisons between high and low productivity years were not statistically significant.

This study is also reliant on several assumptions. Among those, Iassumed that changes in chlorophyll-a concentration directly correlates with primary productivity and that primary productivity changes in the California Current region match primary productivity changes at my beach seining sites. A reason this latter point might not hold true is that nutrient runoff from humans is a large driver of primary productivity nearshore, and my results may be more impacted by fluctuations derived from this phenomenon than by macro-scale changes in productivity (National Research Council, 2000).

Global temperatures have a strong positive correlation with primary productivity, and past research has predicted that primary productivity will shift significantly as the climate warms (Cheung *et al.,* Chassot *et al.*). Understanding how different fish species will be affected by significant changes in not only temperature but also primary productivity will help researchers to predict changes in fish populations as these factors shift. The impacts of this type of research extend beyond climate change, though, as it is also important on an annual basis to understand how changes in primary productivity may shift fish population densities and sizes. In order to maximize conservation efforts, researchers and scientists must know which species are most at-risk of being impacted by large-scale shifts in our oceans.

**Tables**

**Table 1.** Beach seine sampling location, coordinates, beach type, and the number of replicates performed at each site between 2002 and 2021.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Location** | **Latitude** | **Longitude** | **# of Replicates** | **Beach Type** |
| Inner Cabrillo | 33.70919 | -118.27917 | 117 | Estuary |
| Marina del Rey | 33.97969 | -118.45742 | 82 | Estuary |
| Belmont Shore | 33.75214 | -118.13511 | 70 | Open Coast |
| Naples Island | 33.75884 | -118.12022 | 64 | Estuary |
| Outer Cabrillo | 33.70894 | -118.28369 | 44 | Open Coast |
| Alamitos Bay | 33.75283 | -118.13015 | 9 | Estuary |
| Paradise Cove | 34.01955 | -118.78727 | 6 | Open Coast |
| Torrance Beach | 33.83470 | -118.39070 | 5 | Open Coast |

**Figures**

Map

Description automatically generated

**Figure 1.** Site map of the three northernmost sampling locations—Paradise Cove, Marina del Rey, and Torrance Beach. All sampling done with 100ft beach seines.

Map

Description automatically generated

**Figure 2.** Inner and Outer Cabrillo sampling sites. Both sites were nearshore sampling locations that were collected using 100ft beach seines.

Map

Description automatically generated

**Figure 3.** Belmont Shore, Alamitos Bay, and Naples Island nearshore sampling sites. All replicates were completed using a 100ft beach seine.

Chart, line chart, waterfall chart

Description automatically generated

**Figure 4.** Annual percentagy anomaly in chlorophyll-a production in the California Current region, 1998-2000. Created by Todd O’Brien using adapted SeaWiFS and MODIS-Aqua data series (NOAA 2021).

**Figure 5.** Size of oviparous and viviparous fish during normal (σ < 1) versus high (σ > 1) chlorophyll-a production years. Each marker represents a species. Average size increase of viviparous fish during high concentration years = 2.1cm; average size increase of oviparous fish during high concentration years = 2.0cm. X = Y line plotted; markers above this line indicate that individuals caught were larger during high-productivity years.

**Figure 6.** Density per 100m2 of oviparous fish (n = 213,606) in normal and high chlorophyll-a concentrations for all replicates in all years. Figure shows that there is a 33.5% decrease in oviparous fish density recorded, on average, during years with abnormally high primary production.

**Figure 7.** Density per 100m2 of viviparous fish (n = 1,532) in normal and high chlorophyll-a concentrations for all replicates in all years. Figure shows a 13.8% increase in the density of viviparous fish, on average, in years where chlorophyll-a concentration is abnormally high.

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