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Bloom or Bust: Retrospective Analysis of the Giant Jellyfish, *Nemopilema nomurai* (Scyphozoa: Rhizostomeae), Ecology in the East Asian Marginal Seas

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BLOOM OR BUST: RETROSPECTIVE ANALYSIS OF THE GIANT JELLYFISH, *NEMOPILEMA NOMURAI* (SCYPHOZOA: RHIZOSTOMEAE), ECOLOGY IN THE EAST ASIAN MARGINAL SEAS

by

Naomi Yoder

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ABSTRACT

BLOOM OR BUST: RETROSPECTIVE ANALYSIS OF THE GIANT JELLYFISH, *NEMOPILEMA NOMURAI* (SCYPHOZOA: RHIZOSTOMEAE), ECOLOGY IN THE EAST ASIAN MARGINAL SEAS

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December 2016

The Giant Jellyfish, *Nemopilema nomurai*, is a large-bodied bloom-forming jellyfish that occurs in the semi-enclosed basins of the East Asian Marginal Seas. *N. nomurai* has bloomed more frequently in the past 20 years than in any period previously recorded. In Japan, recent *N. nomurai* blooms were responsible for millions of dollars in lost revenue and equipment damage to commercial fisheries alone. This study statistically analyzed 21 environmental factors in connection with *N. nomurai* occurrence (using occurrence as a proxy for blooms). Eight factors resulted in a statistically significant or marginally significant ($p \leq 0.10$), linear or non-linear relationship with jellyfish occurrence. Significant linear factors were jellyfish aquaculture, kelp aquaculture, benthic structures, Pacific saury fisheries and shellfish fisheries. Significant non-linear factors were chub mackerel, jellyfish, Okhotsk mackerel fisheries. Jellyfish aquaculture and jellyfish fisheries target *Rhopilema esculentum*, a very similar species to *N. nomurai*, and the results of the analysis show that the two species are intertwined ecologically. One of the factors with a significant relationship, jellyfish aquaculture, matched the expected trend (positive linear correlation). Three non-linear significant relationships resulted in a partial confirmation of the expected trend. The results and lack of expected response is likely at least partially due to limitations of the *N. nomurai* data.

The jellyfish dataset was left skewed, and when summarized by year (average occurrences/year), was reduced to nine data points. Analysis of more jellyfish occurrence data, along with continued exploration of the statistical relationships with aquaculture, fishing, and coastal development, is recommended.

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LIST OF ABBREVIATIONS

CNBS	China National Bureau of Statistics
CPUE	Catch-per-unit-effort
DO	Dissolved oxygen
EAMS	East Asian Marginal Seas
EASMI	East Asian Summer Monsoon Index
ECS	East China Sea
FAO	Food and Agriculture Organization of the United Nations
GAM	Generalized Additive Model
GLM	Generalized Linear Model
IBTrACS	International Best Track Archive for Climate Stewardship
LME	Large Marine Ecoregion
MAFF	Ministry of Agriculture, Forestry and Fisheries (Japan)
SAU	Sea Around Us project
SOJ	Sea of Japan
YS	Yellow Sea

CHAPTER I – INTRODUCTION

Many pelagic cnidarian species have the capacity to bloom, which results in large, dense groups of medusae. Jellyfish blooms can have a broad impact on the ecosystem and on human industries such as fishing, aquaculture, tourism, and energy production (Brotz et al., 2012; Lucas et al., 2014; Purcell, 2012). Despite the impacts associated with blooms, the causes and mechanisms of jellyfish blooms are poorly known (Brotz et al., 2012; Condon et al., 2012; Duarte et al., 2013; Richardson et al., 2009). The frequency of blooms of many jellyfish species has increased in recent decades, especially in East Asia (Condon et al., 2012; Duarte et al., 2013; Lucas et al., 2014; Uye, 2014). There is no consensus on the cause of bloom increases, although recent publications state that there is most likely a suite of variables that influence blooms (Purcell et al., 2007; Uye, 2014). Increase in bloom frequency and intensity in the past 25 years appears to be the case in Asia, especially for the Giant Jellyfish (Brotz et al., 2012; Dong et al., 2010; Lucas et al., 2014; Uye, 2014). The Giant Jellyfish, or *Nemopilema nomurai* Kishinouye, 1922 (Scyphozoa: Rhizostomeae), has bloomed in the majority of years since 2000 in the Sea of Japan. Before 2000, the species bloomed far less frequently, about once every 40 years in the same basin (Kawahara et al., 2013; Kitajima et al., 2015; S. Sun et al., 2015; Uye, 2008, 2014). Throughout its range in the East Asian Marginal Seas (EAMS), *N. nomurai* blooms since 2000 have increased and consequently impacted industry. In Japan alone, recent *N. nomurai* blooms were responsible for millions of dollars in lost revenue and equipment damage to commercial fisheries. Revenue has also been lost when fish catch was damaged or reduced as a result of a bloom. For example, in 2003 a *N. nomurai* bloom in the East China Sea reduced the catch per unit effort (CPUE) of yellow croaker (*Pseudosciaena polyactis*) by 20% (Dong et al., 2010). The impacts of *N. nomurai* blooms to ecosystems and industry have led to an urgent need to understand the causes of and mechanisms of those blooms.

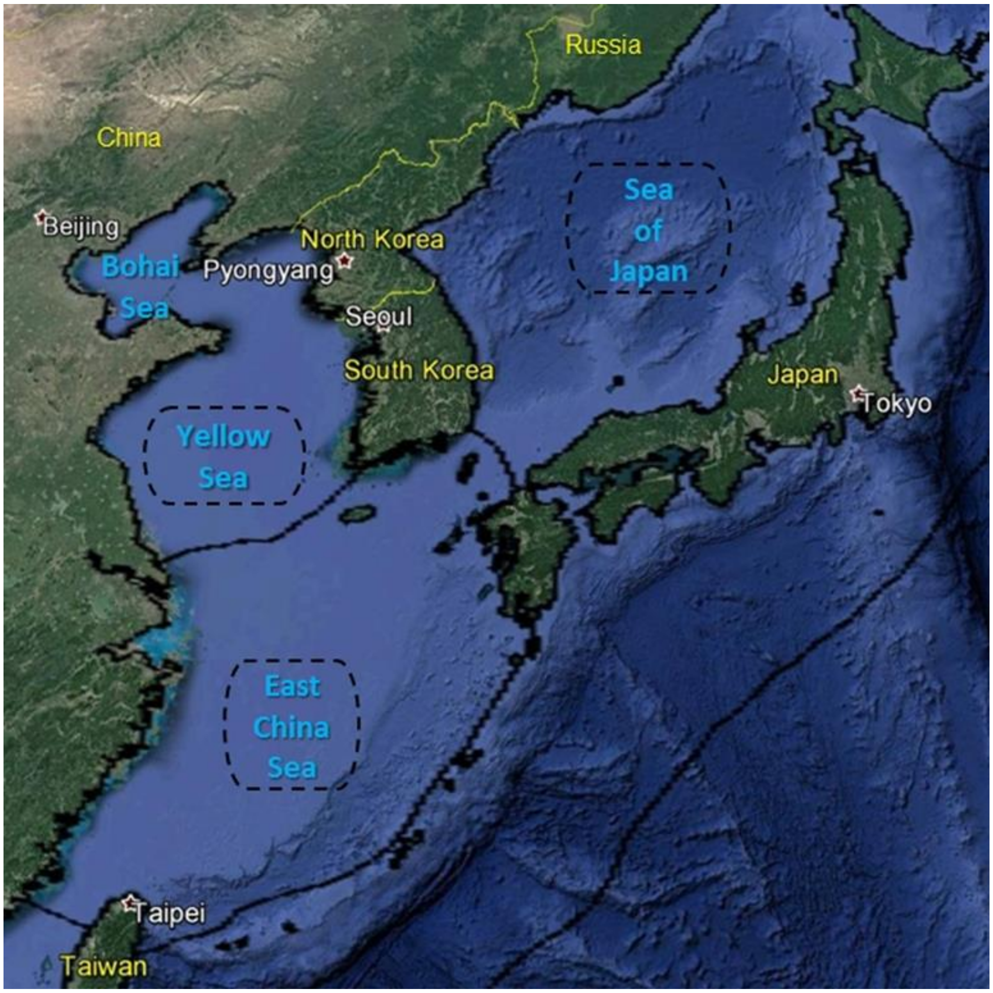


Figure 1. Geographic study region.

The four East Asian Marginal Sea (EAMS) basins, the Bohai Sea, the East China Sea, the Sea of Japan and the Yellow Sea. Three basins are also the name of Large Marine Ecoregions (LMEs, in dashed circles). LME boundaries are designated on the map with a black line.

The ecology and life history of *N. nomurai* is more well understood than most jellyfish species, due to the urgent need to mitigate for impacts of blooms (S. Sun et al., 2015; Uye, 2008, 2014). *N. nomurai* have the largest known medusae by biomass (Uye, 2014). The largest recorded *N. nomurai* medusa reached 2 m in bell diameter and 200 t wet weight (Kawahara et al., 2013; Uye, 2014). Medusae occupy the shallow, semi-enclosed basins of the EAMS, including the Bohai Sea, the East China Sea, the Sea of Japan and the Yellow Sea (Figure 1). *N. nomurai* medusae can stray into the Pacific Ocean around Honshu and Hokkaido islands, but there has never been recruitment detected among those that made it to the Pacific Ocean (Uye, 2014).

N. nomurai has a one-year metagenic life cycle consisting of an asexual benthic phase (i.e., polyp) and a sexual pelagic phase (i.e., medusa; Figure 2). The dormant, benthic podocyst is one feature of the *N. nomurai* asexual phase. Podocysts are buds produced by polyps, and have a protective chitinous coating (Ikeda et al., 2011; Kawahara et al., 2013). Podocysts can regenerate into new, viable polyps, which can strobilate and create more podocysts (Ikeda et al., 2011). One polyp can create several podocysts, and podocysts have been shown to maintain viability for more than six years in the lab (Kawahara et al., 2013). Polyps have the capacity to produce multiple ephyra, and thus the benthic life stages contribute greatly to the pelagic population of *N. nomurai*. Podocysts may be an important key in determining a bloom year for *N. nomurai*, with their high longevity and fecundity and the ability to remain dormant for years (Kawahara et al., 2013). Additionally, studies of other scyphozoan species have shown that podocysts are of fundamental importance in contributing to whether a species blooms or not (Arai, 2009). Triggers for *N. nomurai* podocyst excystment are not fully understood, but in the lab, physical abrasion of the chitinous coating resulted in 100% excystment (Kawahara et al., 2013). Other factors that could be triggers for excystment include low salinity, low dissolved oxygen (DO), and burial in organic-rich mud (Kawahara et al., 2013).

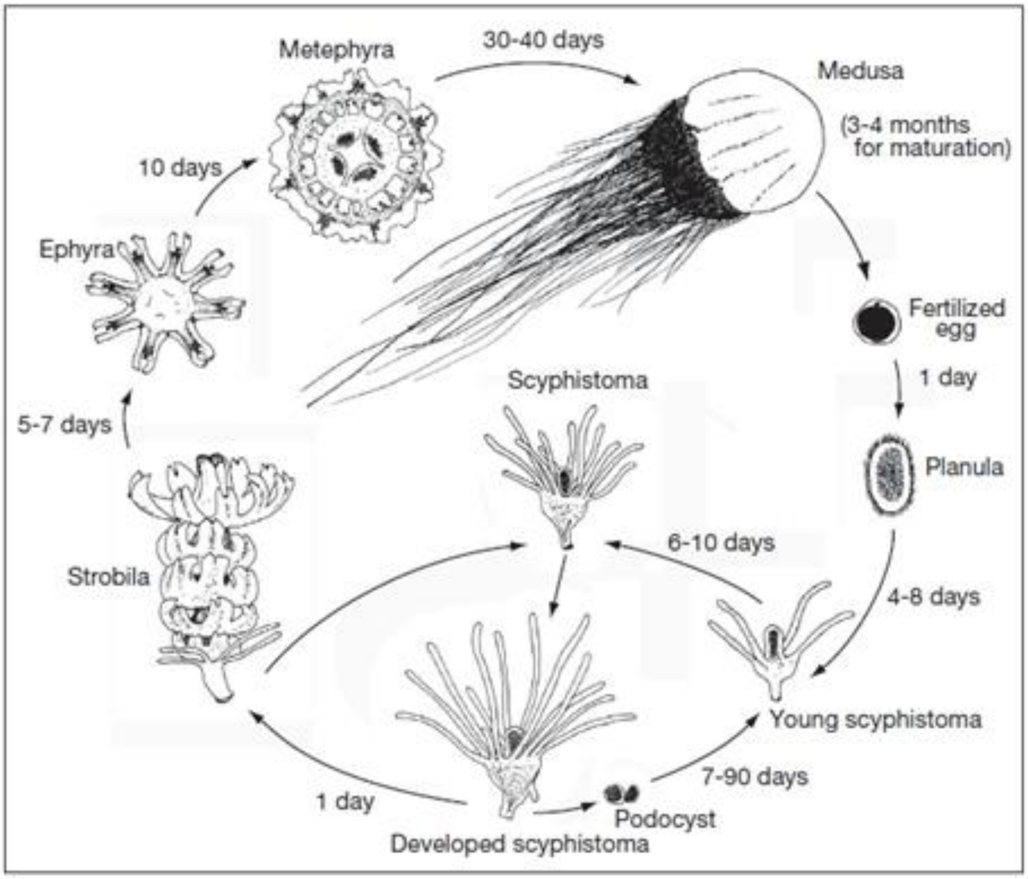


Figure 2. Life cycle of *Nemopilema nomurai*.

Pelagic stages are from “ephyra” through “fertilized egg”. Scyphistomae are referred to as “polyps” in this study. Adapted from Kawahara et al. (2006).

The medusa life stage occurs in the East China Sea (ECS), the Bohai Sea (BS) and the Yellow Sea (YS) from May – August, and from approximately August – November in the Sea of Japan (SOJ) if there is a bloom there (S. Sun et al., 2015; Uye, 2014). When there is a bloom in Japan, adult medusae in the Sea of Japan are advected there through the Tsushima Strait with the Tsushima Current (Kitajima et al., 2015; Uye, 2008, 2014). In such a condition, as medusa density decreases in the ECS, BS and YS, density increases in the SOJ and subsequently along the Pacific coast of Japan (Uye, 2014). Adult individuals are absent from field surveys in the entire EAMS region during winter months (Uye, 2014). Geographic distribution of *N. nomurai* medusae thus varies with population size and bloom condition.

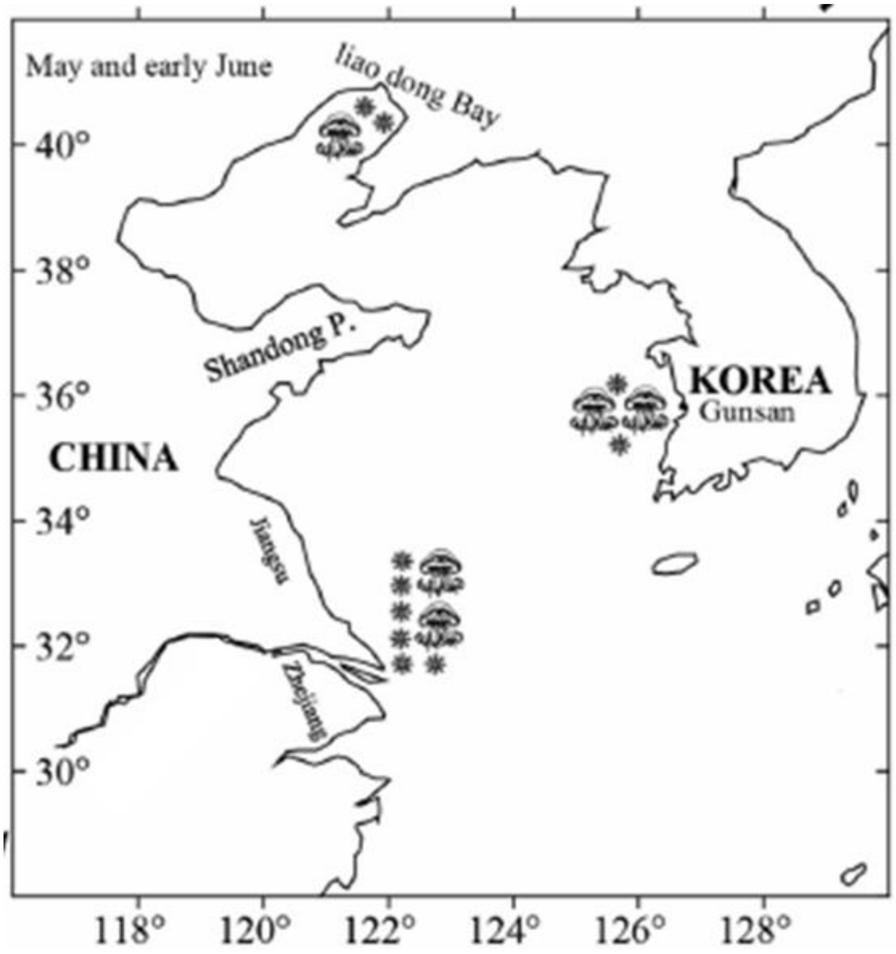


Figure 3. Seeding areas of *Nemopilema nomurai*.

Seeding areas are benthic habitat areas. Seeding areas are represented by medusa and ephyra symbols. One seeding area is confirmed near the Changjiang (Yangtze) River mouth, and others are theorized. Adapted from S. Sun et al. (2015).

Benthic conditions affect the benthic life stages of *N. nomurai*. While polyps have not been found in the field, benthic habitat areas (seeding areas) are inferred from ephyrae. *N. nomurai* ephyrae were recently documented in the ECS off Jiangsu and

Zhejiang provinces (S. Sun et al., 2015). The location of the ECS seeding area was corroborated by previously conducted studies using field surveys, circulation modeling, and population genetics (Hanzawa et al., 2010; S. Sun et al., 2015; Toyokawa et al., 2012). Other seeding areas are theorized at other locations, including along the Korean coast in the YS, and along the Chinese coast in the BS (Figure 3). Neither juveniles nor ephyrae have been detected in the SOJ. Recent genetic analysis showed that *N. nomurai* medusae in China show genetic similarity, suggesting that if there are multiple seeding areas there is likely connectivity between them (Dong et al., 2016).

Environmental conditions influence jellyfish blooms, and some environmental conditions may provide triggers for a bloom (Kawahara et al., 2013; Uye, 2014; Wei et al., 2015). It remains unclear, however, which environmental conditions are most influential, and whether there are conditions (factors) that specifically benefit *N. nomurai* as opposed to the other species. Despite *N. nomurai* having been more thoroughly studied than many other large bloom-forming scyphozoans, questions remain about the ecology of the species. Recent studies claim that several environmental factors have played an integral role in the increase in blooms since 2000 (Dong et al., 2010; Kawahara et al., 2013; Uye, 2014; Zhang, 2015). Those factors are rising sea temperature, eutrophication, overfishing and expansion of benthic habitat (Uye, 2014).This study focused on exploring the effects of environmental factors that have been overlooked and can have potential effects on the population size of *N. nomurai*, which include 1) aquaculture, 2) benthic anthropogenic structures, 3) fisheries, 4) bottom water conditions and 5) hypoxia. The remaining factors that have been identified as very likely contributors to determining bloom conditions (eutrophication, rising sea temperature) are, nonetheless, extremely important, but outside the scope of this study. For example, it has been suggested that sudden change in temperature is a trigger for strobilation (Wei et al., 2015; Zhang et al., 2012). Similarly, eutrophication is well documented in *N. nomurai* seeding areas (Purcell et al., 2007; Wang, 2006; Zhang, 2015). While studies have pointed to the importance of eutrophication and impact to the ecosystem such as lowering the mean trophic level (Zhang, 2015), few studies have quantitatively analyzed eutrophication and *N. nomurai* blooms. One study linked phytoplankton levels to eutrophication, and examined any relationship of those to *N. nomurai* blooms (Xu et al., 2013). A broad relationship was found, but no clear trigger or driver of blooms. Regardless, an intensive analysis of eutrophication and its impact on *N. nomurai* blooms is recommended for the future as it was outside the scope of this study.

Background

Aquaculture in East Asia

Aquaculture production in Asia, particularly in China, has grown exponentially in the past two decades, both in terms of facilities and production (Figure 4). Marine aquaculture requires structures that provide benthic habitat substrate for metagenic medusozoans (Duarte et al., 2013; Holst and Jarms, 2007; Purcell et al., 2007). Other anthropogenic structures besides those within aquaculture have also proliferated in recent decades and could similarly provide benthic habitat for *N. nomurai* (Dong et al., 2010; Halpern et al., 2008). This analysis focused on studying increases in anthropogenic benthic structure surface area as measured both by aquaculture production and by coastal population growth (as a proxy for structure-building) in order to evaluate the relationship between anthropogenic benthic habitat and *N. nomurai* occurrence.

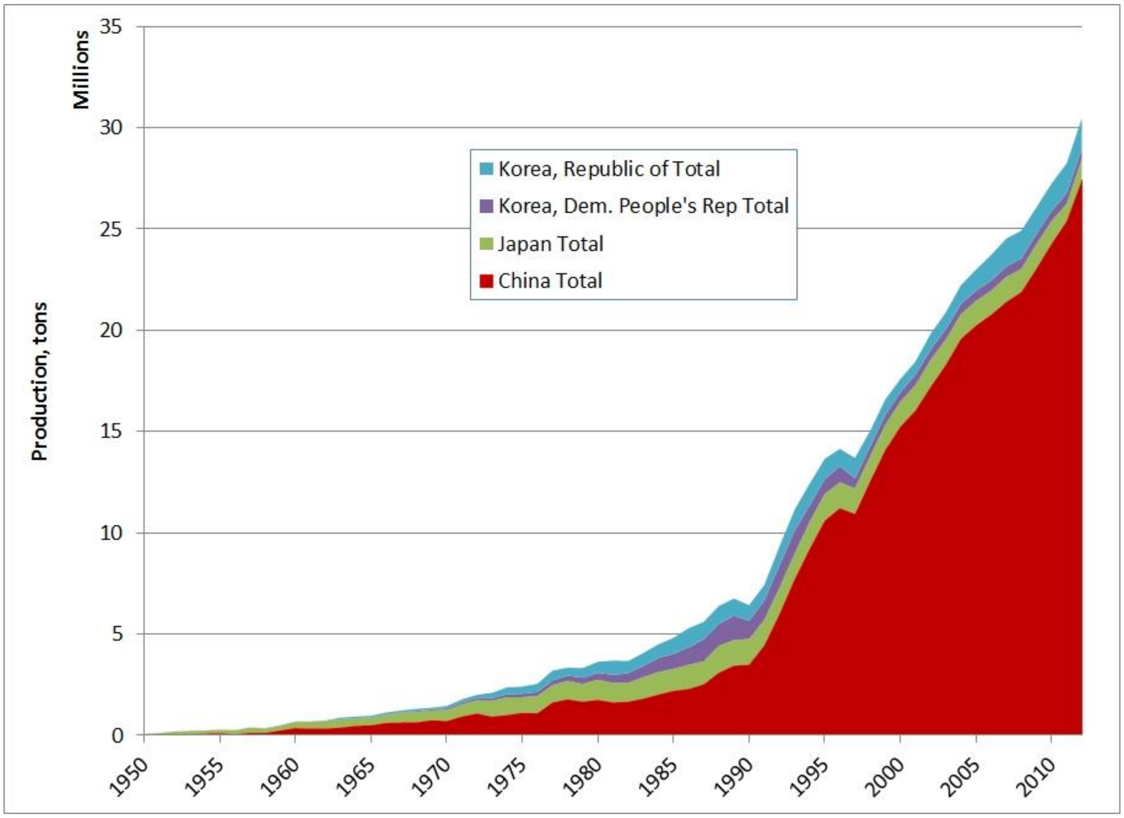


Figure 4. Marine aquaculture production by country.

Dataset includes all species groups on record. Data: FAO.

Aquaculture could affect *N. nomurai* occurrence in a number of ways in addition to the facilities themselves providing artificial benthic habitat. Cultured organisms could add to *N. nomurai* benthic habitat, such as kelp blades (*Laminaria japonica*) which have been shown to serve as benthic habitat for other bloom-forming jellyfish species (Kintner, 2016). In addition to habitat, feed for cultured organisms can also provide nutrients to jellyfish through waste production, excess, and by fueling the food chain. Finally, aquaculture of jellyfish (*Rhopilema esculentum*) could affect *N. nomurai* production. Jellyfish cultivation is part of the growing marine Asian aquaculture business (Dong et al., 2010). *R. esculentum* is a rhizostome very similar in morphology and physiology to *N. nomurai* (Omori & Kitamura, 2004). Given the similarities between the two species, jellyfish aquaculture and *N. nomurai* occurrence are likely to have ecological impacts on one another.

Benthic Structures

Surface area of hard substrate available as habitat for the benthic life stages of *N. nomurai* has increased in the EAMS in the form of anthropogenic structures in recent decades (Duarte et al., 2013; Kawahara et al., 2013; M. Sun et al., 2015; Uye, 2008; Zhang, 2015). Simultaneously, surface area of coral reefs and other naturally occurring benthic rocky terrain that might be suitable as *N. nomurai* habitat has dwindled in the region due to fisheries harvest, trawling, and commercial dredging (Chang et al., 2012; Zhang, 2015). Anthropogenic hard substrates include surfaces in developments such as ports and harbors, shoreline modification, energy production facilities, buoys and aquaculture facilities. The planulae of other species of jellyfish have been shown to preferentially settle and produce polyps on anthropogenic substrates, favoring them over naturally occurring materials (Holst and Jarms, 2007). An increase in benthic anthropogenic structures is important to analyze with respect to *N. nomurai* benthic habitat.

Bottom Conditions

Bottom environmental conditions such as temperature and salinity affect *N. nomurai*, and especially the asexual phase and the young ephyrae. *N. nomurai* tolerate a wider envelope of salinity than most other large-bodied jellyfish (except *R. esculentum*) in the EAMS region (Dong et al., 2015), although different *N. nomurai* life stages have different optimal salinity windows. In the benthic life stages, polyp growth, polyp survival and podocyst excystment are all affected by salinity (Dong et al., 2015). *N.*

nomurai polyps excel in growth and survival when salinity is 10 – 30, while podocyst production and excystment are optimized within a much narrower range: 20 – 27.5 (Dong et al., 2015). Podocysts have also, however, been found to maintain viability even at abnormally low salinities (Kawahara et al., 2013), and thus the functional window for the suite of benthic life stages remains unclear. This study examined bottom salinity in relation to *N. nomurai* occurrence.

Temperature (and changes in temperature patterns) have been shown to affect *N. nomurai* ecology in a multitude of ways including affecting survival, growth, reproduction, distribution and feeding at various life stages (Purcell et al., 2007; M. Sun et al., 2015; S. Sun et al., 2015; Wei et al., 2015; Xu et al., 2013). For example, polyps and podocysts overwintered and maintained viability under cold temperatures (2.5 – 15°C), and spring and summer polyps grew significantly larger when winter temperatures were warmer between 15 – 27.5°C (M. Sun et al., 2015). Temperature plays a key role in determining when *N. nomurai* might bloom and thrive, but bottom temperature has not been examined in the field in previous studies with respect to *N. nomurai* blooms. Temperature in seeding areas was analyzed for this study.

Fisheries

Some large, bloom-forming jellyfish have a cyclical relationship, often inversely proportional, with forage fish populations (Brotz et al., 2012; Dong et al., 2010; Robinson et al., 2014). *N. nomurai* influence the food web and trophic ecology, since their high growth rate and large medusa size requires an extensive supply of zooplankton prey (Uye, 2008). The closer the trophic levels of *N. nomurai* and another species, the more a bloom would likely affect the other species due to competition for prey. The trophic position of *N. nomurai* is partially determined by prey. *N. nomurai* medusae possess hundreds of tiny mouthlets (each <1 mm diameter) distributed along the oral arms, as opposed to a centralized mouth (Uye, 2014). Mouthlets restrict medusae food intake to micro- and mesozooplankton; relatively small particle intake sizes for a large-bodied medusa (Graham et al., 2003; Uye, 2008). Due to the small prey size, *N. nomurai* medusae occupy a trophic level similar to that of forage fish. *N. nomurai* and forage fish species often compete for the same food, and sometimes also for habitat (Kawahara et al., 2013; Robinson et al., 2014). Additionally, *N. nomurai* competes with forage fish through predation, as medusae ingest nutritionally valuable forage fish eggs (Purcell and Arai, 2001). A bloom of large size medusae can significantly impact a fish population that the bloom encounters (Jiang et al., 2008). Thus forage fish were prioritized for analysis in this study.

Fishing operations in general could impact *N. nomurai* occurrence through physical disturbance, eliminating prey resources, or harvesting species that compete for resources with *N. nomurai*. Other commercial harvest species of interest for this analysis were included if they met at least one of three selection criteria: those that share habitat or compete for resources with *N. nomurai*, those that are the target of set-net fisheries, or those that comprise a large percentage of the catch in the region within the past 20 years.

Hypoxia

Hypoxia, or low dissolved oxygen (DO), has been characterized in the field where *N. nomurai* seeding areas occur, but hypoxia has not been previously related to *N. nomurai* abundance. Eutrophication, or the process by which excess nutrients collect in a body of water, has been occurring in Chinese seas, and the ECS in particular, since the

1990’s (Dai et al., 2011; Purcell et al., 2007; Wang, 2006; Wei et al., 2007; Xu et al., 2013). Nutrient increase in the ECS is most pronounced in the summer, and is primarily the result of agricultural development in the Changjiang River watershed, although aquaculture operations and upwelling also contribute (Dai et al., 2011; Wei et al., 2007). Hypoxia often accompanies eutrophication, especially during strong stratification in the water column. In recent years, summer hypoxia has developed in the waters influenced by the Changjiang River plume (Ning et al., 2011; Wang, 2006; Wei et al., 2007), sometimes resulting in a dead zone similar in scope to that of the Mississippi River (Chen et al., 2007). The area of ECS hypoxia spatially coincides with confirmed *N. nomurai* seeding areas. Summer is the period of highest discharge throughout the year for the Changjiang River, and is the season when stratification is strongest in the ECS (Ning et al., 2011). Some jellyfish species benefit from hypoxia when they are tolerant to low DO conditions, and especially when they are more tolerant than other trophically-similar species such as forage fish (Brodeur et al., 2008; Purcell et al., 2001). Such a link is plausible for *N. nomurai*, since it was shown that podocysts of *N. nomurai* survived under hypoxic conditions, and successfully excysted in the lab once oxygen was plentiful again (Ikeda et al., 2011). While podocysts can survive low DO, hypoxia is still considered an environmental stressor for *N. nomurai* (Kawahara et al., 2013; Uye, 2014). Although hypoxia has been documented and measured in the summer in the ECS, ongoing field data regarding hypoxia in the basin is sporadic.

Objectives

The aim of the study was to answer the following questions:

1. Which factors analyzed have a significant statistical relationship with *N. nomurai* occurrence?
    a. If there is a relationship, what can be ecologically inferred from it, if anything?
2. Is the relationship between the factor and *N. nomurai* occurrence what was expected?

Of the various factors, several were expected to stand out as being most significant. Those expected to be especially noteworthy were kelp, shellfish and jellyfish aquaculture, jellyfish fisheries, and benthic structures. These factors were highlighted because they address surface area and availability of anthropogenic benthic habitat, which has not been analyzed before for *N. nomurai*. Also, since the jellyfish species in fisheries and aquaculture production is so similar to *N. nomurai*, the two jellyfish factors were expected to produce significant relationships. In addition to answering these questions, a final objective of the study was to generate a set of recommendations based on the findings of the analysis.

CHAPTER II – MATERIALS AND METHODS

Study Area and Data Collection

This study included data in all four of the East Asian Marginal Seas (EAMS) basins: the Bohai Sea (BS), the East China Sea (ECS), the Sea of Japan (SOJ) and the Yellow Sea (YS). Two datasets for *N. nomurai* were utilized. One dataset consisted of counts of *N. nomurai* medusae at the surface. These data were collected by researchers under the guidance of S.-i. Uye (Hiroshima University), via ships-of-opportunity. Researchers utilized passenger ferries traveling between Japan (Shimonoseki, Osaka and Kobe) and China (Qingdao, Shanghai and Tianjin). Surface (to 3 m depth) *N. nomurai* medusae were tallied during daylight hours from the deck (height = 15 m) in a 10 m wide lane, at five minute intervals (Uye, 2014). The surveys were conducted twice monthly, June – November inclusive, from 2006 – 2013. Density calculations were created for each five minute interval (count per m^2). Since the majority of these survey points were west of Japan, this dataset is also labeled as “China” geographically for the purposes of this analysis. These data are referred to herein as “ferry survey” data.

The second *N. nomurai* dataset was of estimate counts, reported by the Japanese Ministry of Agriculture, Fisheries and Forestry (MAFF). The data were obtained from the MAFF website (www.jafic.or.jp/kurage, in Japanese), with the assistance of researchers at Hiroshima University. The dataset consisted of reports of *N. nomurai* entrained in set-net fisheries across Japan. The data were sorted by day, prefecture, and geographic point location. These data cover coastal Japan only, and are labeled “Japan” geographically for the purposes of this analysis. The data are referred to as “MAFF fishery” data herein.

Ferry survey data were collected systematically using published protocols and contain presence-absence data as opposed to the MAFF fishery data which contained presence-only information. Neither dataset provided continuous coverage throughout the year, as both surveys were conducted in summer and autumn when *N. nomurai* medusae were most likely to be at peak abundance. Both datasets were summarized first by average count per month and then by average count per year. Factors were compared to *N. nomurai* data utilizing the finest scale resolution available based on the temporal frequency of the independent variable.

Aquaculture production data was obtained from the Fisheries and Agriculture Organization (FAO) of the United Nations. Data for jellyfish aquaculture was supplied by L. Brotz. FAO data (kelp, shellfish) were selected for only China, since the other countries in the EAMS region produced exponentially lower tonnage, and because coastal China is where the aquaculture analysis was focused. For shellfish aquaculture, a subset of the available taxa was utilized to include only the epibenthic species. Those groups selected from the umbrella FAO group “shellfish” were: Abalones, Cupped oysters, Marine molluscs [miscellaneous], Pen shells, Scallops, and Sea mussels. Within aquaculture, shellfish and kelp production were predicted to have a positive correlation with *N. nomurai* occurrence. Jellyfish production was predicted to have a negative (inverse) relationship with *N. nomurai* occurrence.

Other benthic structures in addition to aquaculture materials that could provide benthic habitat for *N. nomurai* include docks, buoys, piers, artificial reefs, oil and gas rigs, and breakwaters (Duarte et al., 2013). The proxy for anthropogenic structures was human population growth in coastal provinces, based on the assumption that more structures will be built as human population grows. Human population data was obtained from the National Bureau of Statistics of China (CNBS; National Bureau of Statistics of China, 2014). Records were reported from 1949 – 2014 inclusive. Data were summarized from only those coastal provinces in China that border known or potential *N. nomurai* seeding areas: Hebei, Jiangsu, Liaoning, Shandong, Shanghai, Tianjin, and Zhejiang. It was expected that increase in benthic structures (as indicated by an increase in human population) would correlate positively with the *N. nomurai* occurrence.

Bottom salinity (S), unitless, and temperature (T), °C, data were provided by Copernicus Marine Service Products (Copernicus). Bottom depths were selected from the global coverage dataset “Global Ocean 1/12° Physics Analysis and Forecast updated Daily”. Copernicus data were selected using a geographic bounding box encompassing the BS, ECS, and YS (115-128 E, 29-46 N), for the years 2006 – 2014 inclusive. The data were then summarized by day, location and depth. The values assigned to the greatest depth for each location were identified and retained, while other values were discarded. Possible depth values at each location were 0, 10, 20, 30, 50, 75, 100, 125, and 150 m. Retained bottom depths ranged from 10 – 150 m. S and T were averaged to monthly and then yearly values. Bottom conditions, both S and T, were expected to have significant and non-linear relationships with *N. nomurai* occurrence. The expectation was based on the theory of a bounded window *N. nomurai* where conditions are optimal for benthic life stages (Zhang et al., 2012).

Fisheries catch data were obtained from the Sea Around Us (Pauly and Zeller, 2015a). Sea Around Us (SAU) utilizes methods to create catch reconstruction numbers for each species in each year (and region). SAU baseline data come from FAO nominal catch numbers as reported by each country. Nominal catch contains landings data (mT) which are then converted to catch tonnage for on-vessel processing (FAO, 2015a). Nominal catch does not include bycatch or quantities discarded after catching (FAO, 2015a). SAU uses FAO nominal catch in country-specific Exclusive Economic Zones, and converts nominal catch data into reconstructed catch using known discards and bycatch "anchor points", combined with local expert consultation (Pauly and Zeller, 2015b). SAU data were summarized for three Large Marine Ecoregions (LME's): ECS, YS (includes the Bohai Sea basin; see Figure 1), and SOJ. Within fisheries, 13 taxa were analyzed. The catches of nine species (including all the forage fish) were predicted to have a positive correlation relationship with *N. nomurai* occurrence. Those species predicted to be positively correlated were anchovy (*Engraulis japonicus*), chub mackerel (*Scomber japonicus*), flying squid (*Todarodes pacificus*), herring (*Clupea pallasii pallasii*), horse jack mackerel (*Trachurus japonicus*), jellyfish (*Rhopilema esculentum*), Okhotsk mackerel (*Pleurogrammus azonus*), Pacific saury (*Cololabis saira*), sardine (*Sardinops sagax*) and shellfish (miscellaneous marine species). Largehead hairtail (*Trichiurus lepturus*) and shrimp (*Acetes japonicus*) catch were predicted to have negative correlation with *N. nomurai* occurrence. Finally, Alaskan pollock (*Theragra chalcogramma*) catch was predicted to have no significant relationship with *N. nomurai* occurrence, but was included because it is the species with the largest tonnage catch in the region yearly, and because it is targeted by set-net fisheries (FAO, 2015b).

Hypoxia time series data of dissolved oxygen (DO) for more than two years in the ECS were not available. The data points that were available for the relevant time period (2006 – 2014) were sporadic, from disparate studies. Summer monsoon activity was utilized instead as a proxy measure for hypoxia, assuming that more frequent and more intense monsoons would generate more mixing of the water column, and prevent stratification conditions in which hypoxia is most common (Wei et al., 2015; Wu et al., 2009). A second proxy for hypoxia was the index of intensity for summer monsoons, where an index value greater than zero indicated more intense storms (Wu et al., 2009). Data for summer monsoons were obtained from the International Best Track Archive for Climate Stewardship (IBTrACS) database (https://www.ncdc.noaa.gov/ibtracs/index.php) and filtered for the summer season (Apr – Sep), Western Pacific region. IBTrACS includes all storms with wind speed ≥ 35 knots. Storm intensity was obtained from the East Asian Summer Monsoon Index (EASMI). EASMI is based on wind speed at a pressure of 850 hPa, and is compiled from Asian monsoon data yearly during Jun – Aug (Wu et al., 2009). The index is calculated using the difference between zonal winds for a northern area of the ECS minus a southern area covering the South China Sea. EASMI consists of a yearly number between 2.5 and -2.5 where the greater the number, the stronger the monsoon intensity (Wu et al., 2009). It was expected that increased mixing in the summer induced by surface monsoon winds (as indicated by higher monsoon storm index values and higher number of storms), would correspond positively with *N. nomurai* abundance, because hypoxia is unlikely to occur in a well-mixed water column.

While “jellyfish bloom” does not equate to “jellyfish occurrence”, this study assumed that for *N. nomurai*, occurrence is an adequate proxy for a bloom. The delineation of *N. nomurai* bloom size for the present study was adapted from Uye (2014): large ≥ 1 medusa/100 m^2 (ferry survey data) and large ≥ 2,000 medusae average/set-net/day or ≥ 50 medusae average/set-net/year (MAFF fishery data). Small blooms were defined as 0.1 - 1 medusa/100 m^2 (ferry survey data) and 5 – 49 medusae average/set-net/year (MAFF fishery data). Analyses of ferry survey data in the present study were conducted using occurrence counts rather than density calculations, although density was used to define “large bloom”, “small bloom” and “no bloom” years.

Data Analysis

All statistical tests were performed in R software (R Core Team, 2013). Relative occurrence (high or low) of *Nemopilema nomurai* was evaluated first with correlation, then with Generalized Linear Models (GLM) and Generalized Additive Models (GAM). Correlations for Pearson’s product moment (r) were performed for each combination of *N. nomurai* dataset monthly and annual mean values, with each of the 21 factors. *N. nomurai* abundance was assessed using ferry survey data, since the MAFF fishery data reported presence-only. To evaluate the response of *N. nomurai* abundance to changes in the independent variable, GLM was performed with monthly and annual mean *N. nomurai* values. Non-linear trends were characterized using GAM tests and the annual mean values from the *N. nomurai* ferry survey data. GAM analysis was carried out using the cubic spline function, “identity” (i.e., Gaussian) family, with degrees of freedom (df) set to three. Significance was tested at $\alpha = 0.05$. Akaike Information Criterion (AIC) score, the score of relative model fitness, was tabulated for GLM and GAM tests. The lowest AIC score was the best fit model, and other tests were compared to that best fit. The delta AIC (ΔAIC) is the [AIC score – minimum AIC score] for a suite of tests, and was calculated for the suite of GLM and the suite of GAM tests. P-value was relied on more than AIC score to determine significance, because the AIC score was most likely skewed by small sample size. Significance was $p \leq 0.05$, and marginally significant findings were $0.05 \leq p \leq 0.10$. Marginal significance is discussed herein as significant. Marginal significance was specified as $0.05 \leq p \leq 0.10$ because the factors utilized low sample sizes (maximum $n = 9$). With $p = 0.10$, there is a 10% chance of making a Type I error (an incorrect rejection of the null hypothesis). Since aim of the tests was not to prove causality, but to provide recommendations for future research direction and to identify potentially important factors, high Type I error and the higher risk of false acceptance of the test hypothesis was accepted. Thus marginal significance was defined as $0.05 \leq p \leq 0.10$.

Dominant relationship "type" was designated for significant or marginally significant relationships. A decision tree was utilized to determine type. Pearson's r designated the direction (positive, negative) of a linear trend. If the GLM and GAM test for the same pair of variables was significant or marginally significant, or if the GLM was significant or marginally significant and the GAM was insignificant, the relationship type was delineated as linear and positive or negative, based on the direction indicated by the Pearson's r. If the GLM was insignificant, and the GAM was significant or marginally significant, the relationship type was delineated as non-linear.

CHAPTER III – RESULTS

Correlation Analysis

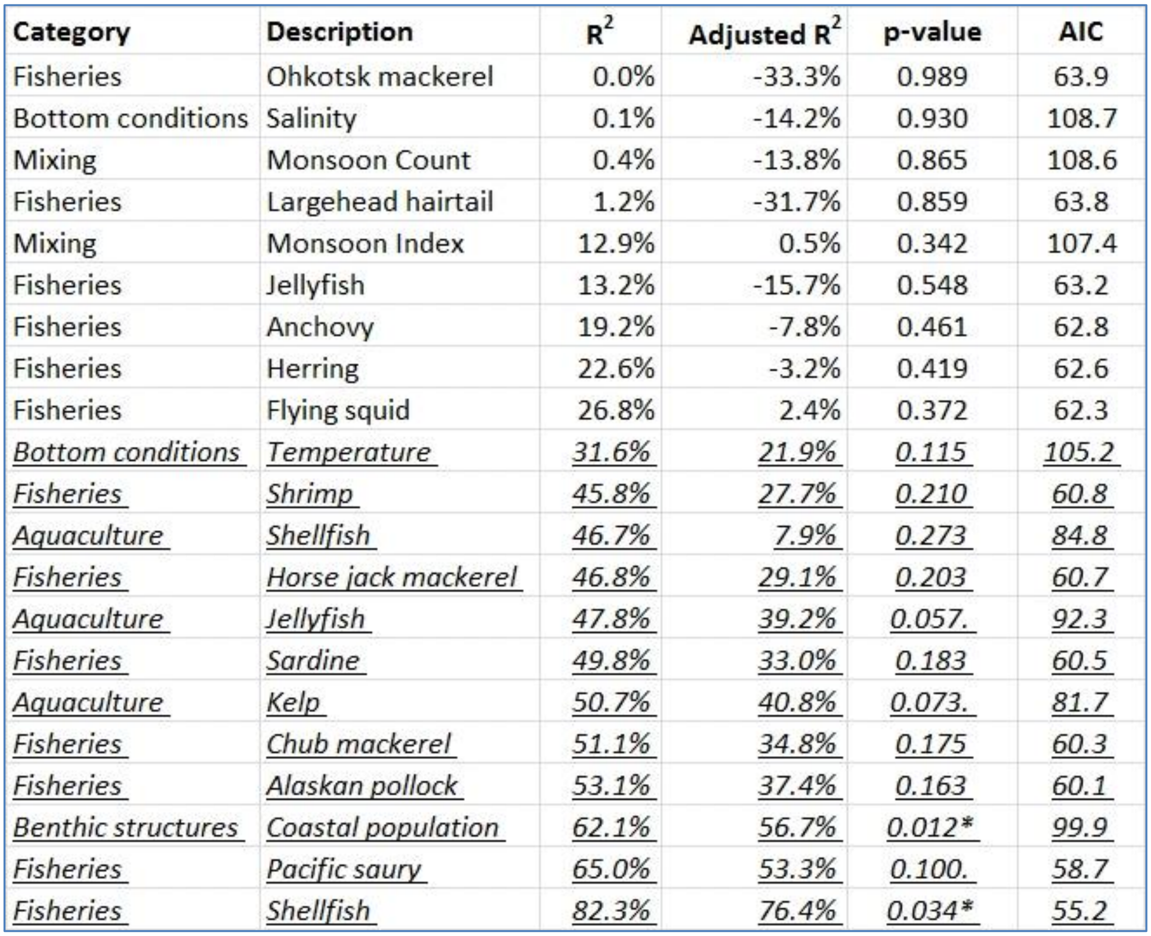
The correlation analysis detected eight factors with a significant or marginally significant correlation ($p \leq 0.10$) to ferry survey *N. nomurai* data (Table A1). There were four factors with a significant or marginally significant correlation to the MAFF fishery *N. nomurai* data (Table A2). The correlation between the two *N. nomurai* datasets using annual mean were significantly positively correlated (p-value = .002, r = .907), resulting in the lowest p-value of any correlation test (Table A1).

GLM and GAM Analysis

Generalized Linear Model (GLM) fitting of each variable with *N. nomurai* ferry survey data produced five significant or marginally significant relationships (Table 1). The five significant linear relationships were: kelp and jellyfish aquaculture, shellfish and Pacific saury fisheries, and benthic structures: coastal population. Shellfish and Pacific saury fisheries had, in addition to significant p-values, ΔAIC scores lower than the mean ΔAIC (Table 2). Shellfish and Pacific saury correlations were positive and negative, respectively (Table 1). Kelp and jellyfish aquaculture production were both negatively linearly correlated to *N. nomurai* occurrence. All of the statistically significant or marginally significant GLM tests had a goodness-of-fit (R^2) greater than 25% (Table 2). Several other factors resulted in R^2 values higher than 25% (underlined and italicized in Table 1).

Table 1

GLM test results.



Category	Description	R^2	Adjusted R^2	p-value	AIC
Fisheries	Ohkotsk mackerel	0.0%	-33.3%	0.989	63.9
Bottom conditions	Salinity	0.1%	-14.2%	0.930	108.7
Mixing	Monsoon Count	0.4%	-13.8%	0.865	108.6
Fisheries	Largehead hairtail	1.2%	-31.7%	0.859	63.8
Mixing	Monsoon Index	12.9%	0.5%	0.342	107.4
Fisheries	Jellyfish	13.2%	-15.7%	0.548	63.2
Fisheries	Anchovy	19.2%	-7.8%	0.461	62.8
Fisheries	Herring	22.6%	-3.2%	0.419	62.6
Fisheries	Flying squid	26.8%	2.4%	0.372	62.3
Bottom conditions	*Temperature*	*31.6%*	*21.9%*	*0.115*	*105.2*
Fisheries	*Shrimp*	*45.8%*	*27.7%*	*0.210*	*60.8*
Aquaculture	*Shellfish*	*46.7%*	*7.9%*	*0.273*	*84.8*
Fisheries	*Horse jack mackerel*	*46.8%*	*29.1%*	*0.203*	*60.7*
Aquaculture	*Jellyfish*	*47.8%*	*39.2%*	*0.057.*	*92.3*
Fisheries	*Sardine*	*49.8%*	*33.0%*	*0.183*	*60.5*
Aquaculture	*Kelp*	*50.7%*	*40.8%*	*0.073.*	*81.7*
Fisheries	*Chub mackerel*	*51.1%*	*34.8%*	*0.175*	*60.3*
Fisheries	*Alaskan pollock*	*53.1%*	*37.4%*	*0.163*	*60.1*
Benthic structures	*Coastal population*	*62.1%*	*56.7%*	*0.012**	*99.9*
Fisheries	*Pacific saury*	*65.0%*	*53.3%*	*0.100.*	*58.7*
Fisheries	*Shellfish*	*82.3%*	*76.4%*	*0.034**	*55.2*

Note: Generalized Linear Model (GLM) results for each variable, with *Nemopilema nomurai* ferry survey data. Data sorted by R^2, with $R^2 \geq 25.0\%$ underlined and italicized. Significance values indicated by p-value "." ≤ 0.10; "*" ≤ 0.05.

Three factors resulted in a significant, non-linear relationship (where the GLM was not significant). All of those factors were in the fisheries category: chub mackerel, Okhotsk mackerel and jellyfish fisheries (Table 2; Figure 5).

Examining significance of the tests through AIC score, the tests with the lowest AIC numbers did not necessarily result in a significant p-value (Table 2). The ΔAIC values were examined with respect to the ΔAIC mean. The GAM ΔAIC values show more synonymy between p-value significance and AIC score than GLM ΔAIC. Of seven GAM tests that have significant or marginally significant p-value, five of those also have ΔAIC lower than the mean (Table 2). However, the distribution of low ΔAIC was limited to the fisheries category, for both GLM and GAM tests. In total, eight factors tested resulted in statistically significant or marginally significant relationships, regardless of dominant type (Table 2).

Table 2

Correlation, GLM, and GAM test results.

Category	**Factor**	**n**	**Pearson's r**	**GLM R^2**	**GLM p-value**	**GLM AIC**	**GLM ΔAIC** $\bar{x}$ = 20	**GAM R^2**	**GAM p-value**	**GAM AIC**	**GAM ΔAIC** $\bar{x}$ = 26	**Dominant type**
Aquaculture	Jellyfish	8	(0.692)	47.8%	0.057.	92	37	39.1%	0.057.	92	45	linear, negative
Aquaculture	Kelp	7	(0.712)	50.7%	0.073.	82	26	45.5%	0.108	81	34	linear, negative
Aquaculture	Shellfish	7	(0.482)	46.7%	0.273	85	30	7.9%	0.273	85	38	
Benthic structures	Coastal population	9	(0.788)	62.1%	0.012*	100	45	58.9%	0.019*	100	52	linear, negative
Bottom conditions	Salinity	9	(0.035)	0.1%	0.930	109	53	27.5%	0.215	105	58	
Bottom conditions	Temperature	9	0.562	31.6%	0.115	105	50	21.8%	0.115	105	58	
Fisheries	Alaskan pollock	5	(0.728)	53.1%	0.163	60	**5**	37.4%	0.162	60	**13**	
Fisheries	Anchovy	5	0.438	19.2%	0.461	63	**8**	33.9%	0.386	60	**13**	

Category	Factor	n	Pearson's r	GLM R^2	GLM p-value	GLM AIC	GLM ΔAIC $\bar{x}$ = 20	GAM R^2	GAM p-value	GAM AIC	GAM ΔAIC $\bar{x}$ = 26	Dominant type
Fisheries	Chub mackerel	5	(0.715)	51.1%	0.175	60	5	86.3%	0.066.	53	5	non-linear
Fisheries	Flying squid	5	0.517	26.8%	0.372	62	7	26.5%	0.427	61	14	
Fisheries	Herring	5	(0.475)	22.6%	0.419	63	7	-3.2%	0.419	63	15	
Fisheries	Horse jack mackerel	5	0.684	46.8%	0.203	61	5	29.1%	0.202	61	14	
Fisheries	Jellyfish	5	(0.363)	13.2%	0.548	63	8	**95.2%**	**0.023***	**47**	0	non-linear
Fisheries	Largehead hairtail	5	0.134	1.2%	0.859	64	9	-31.7%	0.859	64	17	
Fisheries	Okhotsk mackerel	5	(0.009)	0.0%	0.989	64	9	83.6%	0.083.	53	6	non-linear
Fisheries	Pacific saury	5	(0.806)	65.0%	0.100.	59	3	53.3%	0.099.	59	11	linear, negative
Fisheries	Sardine	5	0.705	49.8%	0.183	60	5	36.6%	0.224	60	13	
Fisheries	Shellfish	5	0.907	**82.3%**	**0.034***	**55**	0	76.4%	0.033*	55	8	linear, positive

Category	Factor	n	Pearson's r	GLM R^2	GLM p-value	GLM AIC	GLM ΔAIC $\bar{x}$ = 20	GAM R^2	GAM p-value	GAM AIC	GAM ΔAIC $\bar{x}$ = 26	Dominant type
Fisheries	Shrimp	5	0.677	45.8%	0.210	61	**6**	27.7%	0.209	61	**14**	
Hypoxia	Monsoon Count	9	0.096	0.4%	0.865	109	53	-5.1%	0.751	108	61	
Hypoxia	Monsoon Index	9	0.360	12.9%	0.342	107	52	7.7%	0.438	107	60	

Note: Correlation, Generalized Linear Model (GLM), and Generalized Additive Model (GAM) tests against *N. nomurai* occurrence (ferry survey data). AIC values are separate for the GLM and GAM results. Significance values indicated by p-value "." ≤ 0.10; "*" ≤ 0.05. Delta AIC (ΔAIC) is [AIC - minimum AIC]. Degrees of freedom (df) for GLM and GAM tests was set to three. ΔAIC numbers in blue are those below the mean, and values in black are those above the mean. Black bolded values denote the factor with the lowest AIC score of its group (GLM or GAM).

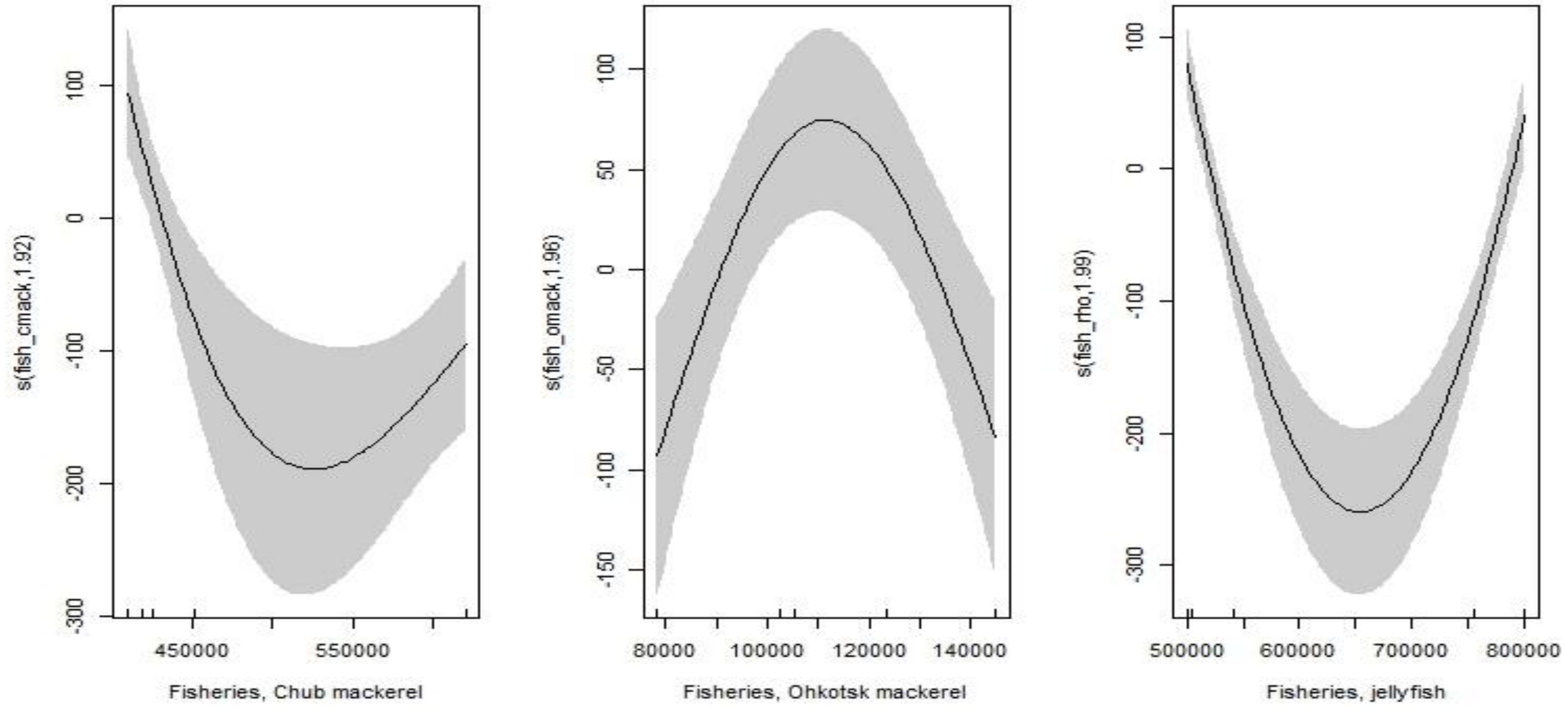


Figure 5. Residual GAM curves for three species.

Spline curves of Generalized Additive Model (GAM) relationship residuals between *N. nomurai* occurrence and species catch (mT). See Table 2 for p-values and ΔAIC.

CHAPTER IV – DISCUSSION

Most of the relationships expected did not occur in statistical testing. The majority of the factors (13) resulted in insignificant tests with *N. nomurai* occurrence. Overall, there is support or marginal support for relationships between benthic structures, jellyfish aquaculture, jellyfish fisheries, chub mackerel and Okhotsk mackerel and *N. nomurai* occurrence. There is also evidence that the datasets available limited the results, and more analysis is necessary to either verify or refute the relationships found in this study. The relationships found do not necessarily imply a mechanistic relationship, and the ecological mechanisms behind each relationship also need to be investigated further.

Aquaculture

The results of this study showed marginally significant relationships between *N. nomurai* abundance and jellyfish (*Rhopilema esculentum*) and kelp aquaculture (Table 2). For both aquaculture factors, the relationship was negative linear type. Jellyfish aquaculture was the only aquaculture category factor that resulted in the relationship with *N. nomurai* occurrence that was expected. The jellyfish result implies that the lower the tonnage of *R. esculentum* produced, the higher the occurrence of *N. nomurai* medusae. However, the significant relationship does not prove clearly that if *R. esculentum* aquaculture production increases then *N. nomurai* blooms will become less intense or less frequent. Rather, the relationship points to a possible ecological connection and suggests future research into this connection. This inference is further supported by species similarities, including unresolved taxonomy, similarity in trophic level and similar habitat needs between *R. esculentum* and *N. nomurai* (Dong et al., 2010; Omori and Nakano, 2001).

Kelp aquaculture production resulted in a significant negative linear relationship with *N. nomurai* occurrence. Kelp production was expected to result in an opposite (positive) relationship with *N. nomurai* occurrence, based on the assumption that kelp and its associated grow-out structures would provide benthic habitat for *N. nomurai*. If there was more benthic habitat, and all other factors were equal, there should be more *N. nomurai* medusae that arise due to increased numbers of strobilating polyps. Instead, this analysis does not provide support for the inference that kelp aquaculture facilities are an effective source of benthic *N. nomurai* habitat. The results suggest that, if anything, kelp production coincides with depressed *N. nomurai* occurrence. One reason for this could be disturbance; kelp takes less than a full year to grow to harvest, and the growing season is winter (Jiang et al., 2015). Kelp would be harvested by May, before the peak *N. nomurai* strobilation season in May-June. If polyps did grow on kelp or on kelp aquaculture structures, yearly rotating kelp harvest could physically disturb benthic *N. nomurai* growth, or remove the benthic growth from its habitat.

Shellfish aquaculture production was insignificant in relation to *N. nomurai* occurrence. The finding of no significance with shellfish aquaculture is illuminating because it lends support to the idea that possibly neither shellfish nor kelp aquaculture operations are encouraging *N. nomurai* population success. In fact, some by-products of both kelp and shellfish aquaculture could create adverse conditions for *N. nomurai* benthic life stages. Flow-through (open water) shellfish and kelp aquaculture facilities are often paired together in rotation (Jiang et al., 2015; Zhang et al., 2009). Rates of deposition of organic matter have been found to be six times higher in large scale kelp and shellfish mariculture areas than control areas, resulting in abnormally high rates of biodeposition and leading sometimes to anoxic sediments. *N. nomurai* would be susceptible to strain from such low oxygen environments. The viability of podocysts maintained through low oxygen events suggests the possibility of podocyst formation or dormancy as a stress response of *N. nomurai* in the benthic life stages. Under environmental stress, podocysts might be produced from polyps instead of polyps growing, multiplying, strobilating and giving rise to pelagic life stages, in a low DO environment. Or, existing dormant podocysts might simply be more likely to remain dormant during low DO events. Regardless, if low DO was exacerbated by kelp or shellfish aquaculture, then the higher rates of aquaculture production of those taxa could relate to lower numbers of *N. nomurai* medusae because of an impact on the benthic life stages of *N. nomurai*.

Fisheries

Several fisheries factors tested resulted in noteworthy results. Those factors were jellyfish, shellfish, and three species of forage fish (Pacific saury, chub mackerel, and Okhotsk mackerel).

Non-forage Fish

Jellyfish. Jellyfish (*R. esculentum*) catch analysis resulted in a significant non-linear relationship to *N. nomurai* occurrence (Table 2). These results did not support the expectation that *N. nomurai* occurrence would increase when *R. esculentum* catch was high. In that case, high *R. esculentum* catch would leave fewer jellyfish to compete with *N. nomurai* medusae, and *N. nomurai* would flourish. Instead, the results showed a non-linear relationship. Non-linear relationship could still represent habitat and prey competition, although competition is not clearly indicated unless there is resource limitation, which there is no proof of in this case. Interpretation of the relationship is difficult, since competition was not measured or quantified in this study. The non-linear relationship suggests there is an ecological interaction between *N. nomurai* and *R. esculentum*, a claim which is also supported by the findings from the aquaculture analysis.

Additionally, there is a possibility that *N. nomurai* are mistakenly or intentionally harvested and processed for consumption. The *R. esculentum* fishery became overfished in the 1990's and 2000's, and a supplementation program was implemented to boost yearly catch, with limited success (Brotz, 2011; Dong et al., 2010) *R. esculentum* is the most commonly exploited species in terms of catch and has the highest market value of any edible jellyfish (Armani et al., 2013; Omori and Nakano, 2001). However, *N. nomurai* are also edible (Omori and Nakano, 2001), and recent genetic analysis of jellyfish products sold in grocery stores in Europe showed that up to 90% of the products surveyed had been mislabeled as *R. esculentum* when the food product was actually *N. nomurai* (Armani et al., 2013). In the case of a jellyfish fishery collapse, there would be an absence of *R. esculentum* medusae available, and harvesters might choose to land *N. nomurai* if those medusae were available instead. Furthermore, neither of the *R. esculentum* data sources for this analysis distinguishes species in their jellyfish catch category, making species composition of the landings or catch numbers impossible to quantify. Continued analysis of *N. nomurai* and *R. esculentum* occurrence and harvest patterns are needed to verify the ecological relationships between the large rhizostomes in the EAMS.

Shellfish. Shellfish catch resulted in a significant positive linear relationship with *N. nomurai* occurrence. A trend based on shells providing benthic habitat for *N. nomurai* benthic life stages was expected, and the resulting relationship was opposite of this. The analysis lends support to an ecological link between shellfish harvest and *N. nomurai* abundance ($p = 0.03$, $R^2 = 82.3\%$), but the nature of the link is unclear. There was not species-specific information available for shellfish catch, and there could have been a percentage of the target shellfish fishery species that would provide benthic habitat substrate for *N. nomurai*.

The shellfish aquaculture and fishery analyses both suggest a trend where more shellfish organic matter corresponds to lower *N. nomurai* occurrence. Could activities involved in shellfish harvest stimulate *N. nomurai* production? This could be the case if, as in aquaculture, shellfish growth creates organic matter that suffocates the benthos, and the removal of the shells removes the strain. Or the physical shellfish harvest could disturb podocysts and other benthic life stages. Podocysts have been shown to excyst when the chitinous covering has been physically abraded (Kawahara et al., 2013). Shellfish harvest could feasibly disturb the substrate and abrade the chitinous covering of nearby podocysts during dredging and thus stimulate *N. nomurai* population growth.

The *N. nomurai* ferry survey timespan coincides with a decrease in shellfish harvest (in a shift from harvest to aquaculture production), which could also explain the numerical relationship (Figure 6). However, without catch-per-unit-effort (CPUE) data or population surveys, it is impossible to know the actual abundance of uncultivated shellfish, since the catch could have decreased but the effort also decreased, and the population remained the same. Further studies are needed to uncover, evaluate, and validate the relationship between shellfish and *N. nomurai* occurrence, and any mechanism by which shellfish harvest could stimulate *N. nomurai* population growth.

Forage Fish

Catches of seven forage fish species were analyzed for this study, and three of those resulted in marginally significant relationships: Pacific saury, chub mackerel and Okhotsk mackerel. In the *N. nomurai* habitat range, forage fish populations and catches have fluctuated, sometimes dramatically, in recent decades (Essington et al., 2015; Jiang et al., 2008; Robinson et al., 2014). No clear signal seems to be revealed between forage fish as a group and *N. nomurai* occurrence from this analysis, but relationships between *N. nomurai* and individual species suggests the potential for ecological connections. Some forage fish species are known to complement bloom-forming jellyfish with inverse population patterns, but those fluctuations tend to occur on a longer time scale than the scope of this study (Essington et al., 2015; Robinson et al., 2014). There could be such relationships between *N. nomurai* occurrence and forage fish species, and future studies with time series of population data, spanning several decades, would allow evaluation of those patterns. Other explanations may be possible for the notable relationships.

The relationship between Pacific saury (saury) catch and *N. nomurai* occurrence was linear and negative (Table 1). The statistical relationship was expected to be positive, based on an expected inverse relationship reflecting competition or resource limitation between saury and *N. nomurai* occurrence. The results suggest an opposite effect where saury and *N. nomurai* presences could complement each other. When fisheries catch is high, saury are removed from the ecosystem. High saury catch corresponds with low *N. nomurai* occurrence in a marginally significant linear relationship (Figure A37), $R^2 = 65.0\%$, $p = 0.10$. Beneficial conditions for saury abundance could be similar to the beneficial conditions for *N. nomurai* medusae abundance, which could in turn result in both species being numerous (low saury catch, high *N. nomurai* occurrence) in similar conditions. However, an argument for complementarity rests on many assumptions, including the assumption that catch of saury is representative of the saury population. Catch value alone, without CPUE or other population monitoring information, does not indicate abundance or population. Thus complementarity of saury and *N. nomurai* abundance is hypothesized as a result of this study, and should be analyzed further, in the future.

Chub mackerel and Okhotsk mackerel catch resulted in marginally significant non-linear relationships with *N. nomurai* occurrence. For both species, the relationship with *N. nomurai* occurrence was predicted to be negatively correlated, and thus the resulting relationships were unexpected.

Chub mackerel is a small, abundant forage fish commonly harvested in the EAMS region (Figure 7). Chub mackerel is a primarily coastal schooling fish, with a diet of ichtyoplankton and zooplankton (FAO, 2015c). Results of the correlation and GLM showed that when catch of chub mackerel was low, N. nomurai occurrence was high (Figure A30). This could be the result of chub mackerel spawning in coastal regions and providing prey for N. nomurai medusae. When more chub mackerel eggs are present, there should be more food for N. nomurai medusae. However, another explanation is that chub mackerel are fished in Japan using set-nets, and set nets are the fishery gear type most impacted by N. nomurai blooms in Japan (Uye, 2008, 2014). In a bloom, medusae can clog a set net (preventing the net from catching the target species), and also damage fish that are co-entrained in the net (Uye, 2008, 2014). N. nomurai medusae, during bloom years, thus might have impacted the fishery, instead of the implications of the statistical model which suggested the reverse where chub mackerel catch influenced N. nomurai occurrence. Catches of chub mackerel have declined since the 1990's relative to previous years (Ishida et al., 2009), and a deterrent to fishing, such as N. nomurai clogging the nets and disrupting fishing, could have a large relative impact if there are few fish to catch in the first place. It is plausible that N. nomurai abundance levels (and blooms) are influencing the chub mackerel catch, and not the other way around.

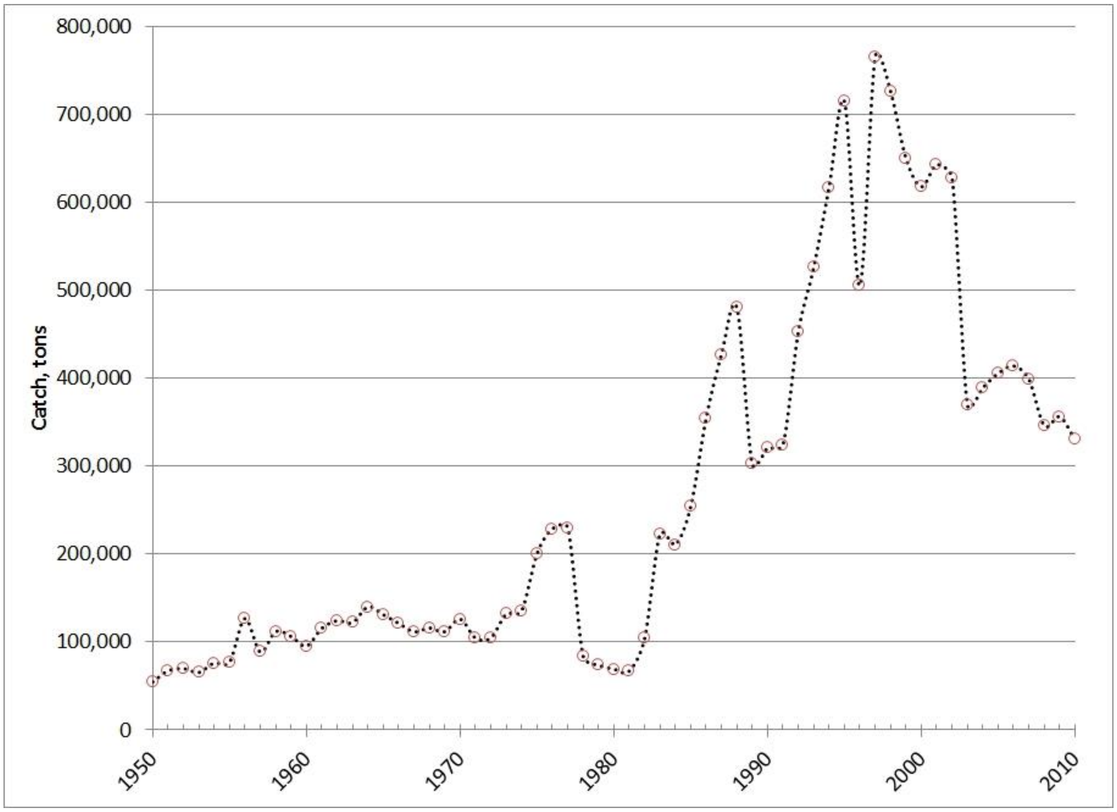


Figure 6. Shellfish fisheries harvest catch.

Catch plotted in mT, for China, East Asian Marginal Seas, from 1950 – 2010. The overall drop in shellfish harvest after 1995 coincides with the shift from harvest to mariculture (Cao et al., 2015). Data: Sea Around Us.

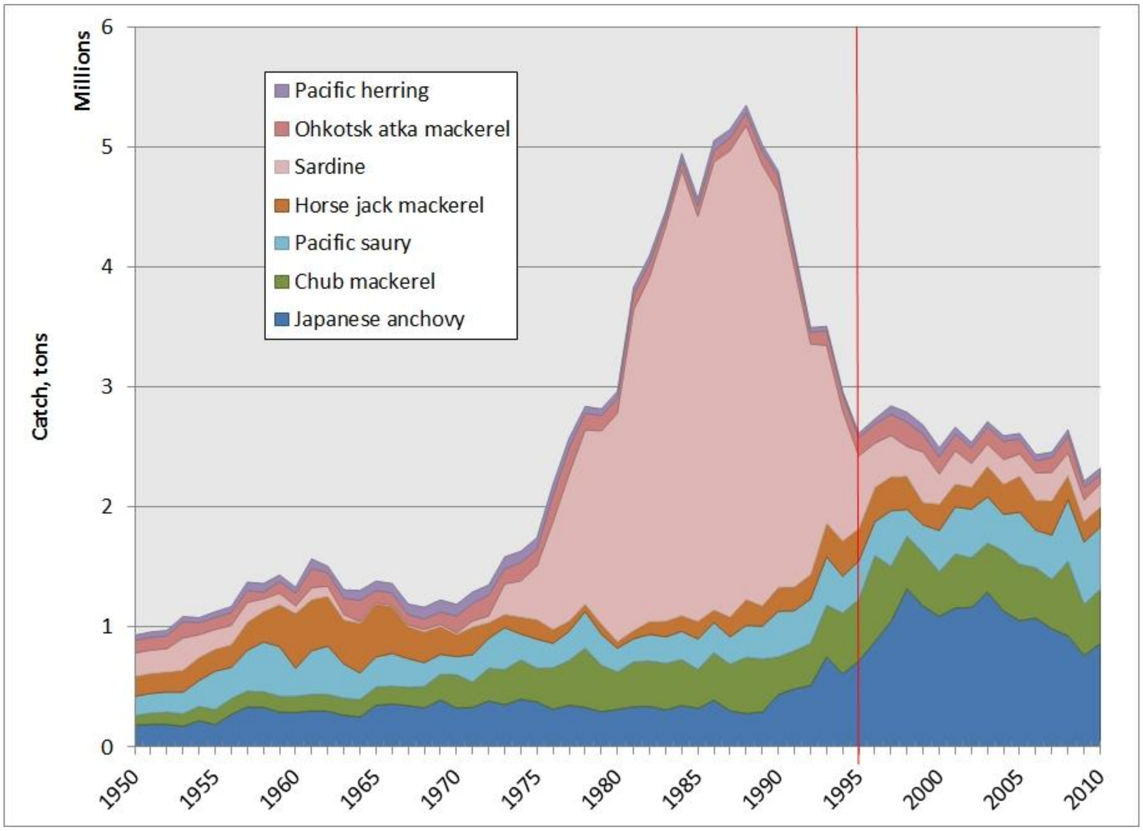


Figure 7. Forage fish species catch reconstruction.

Forage fish in the East Asian Marginal Seas from 1950 – 2010 inclusive. Red line indicates the year 1995, when *N. nomurai* blooms became more frequent. Data: Sea Around Us.

Okhotsk mackerel make up a relatively low component of the catch in the EAMS region among the taxa analyzed in this study (Figure 8). However, the GAM relationship is significant (R^2 = 83.6%, p = 0.08; Figure 5). The linear trend between Okhotsk mackerel and *N. nomurai* is near constant (Figure A36), and the non-linear relationship is the only significant or marginally significant test result of the three tests performed (Table 2). The non-linear relationship could be a result of competition for resources influenced by other factors. For example, Okhotsk mackerel spawns in coastal areas with rocky or gravel substrate (FAO, 2015d), which is ideal habitat for *N. nomurai* polyps. If *N. nomurai* and Okhotsk mackerel were to utilize the same benthic habitat, the two species would compete for food and habitat resources. Predation could also play a role. As with other forage fish species, Okhotsk mackerel eggs could provide ideal food for medusae. The significant non-linear relationship suggests some link between the two species, warranting further investigation in the future.

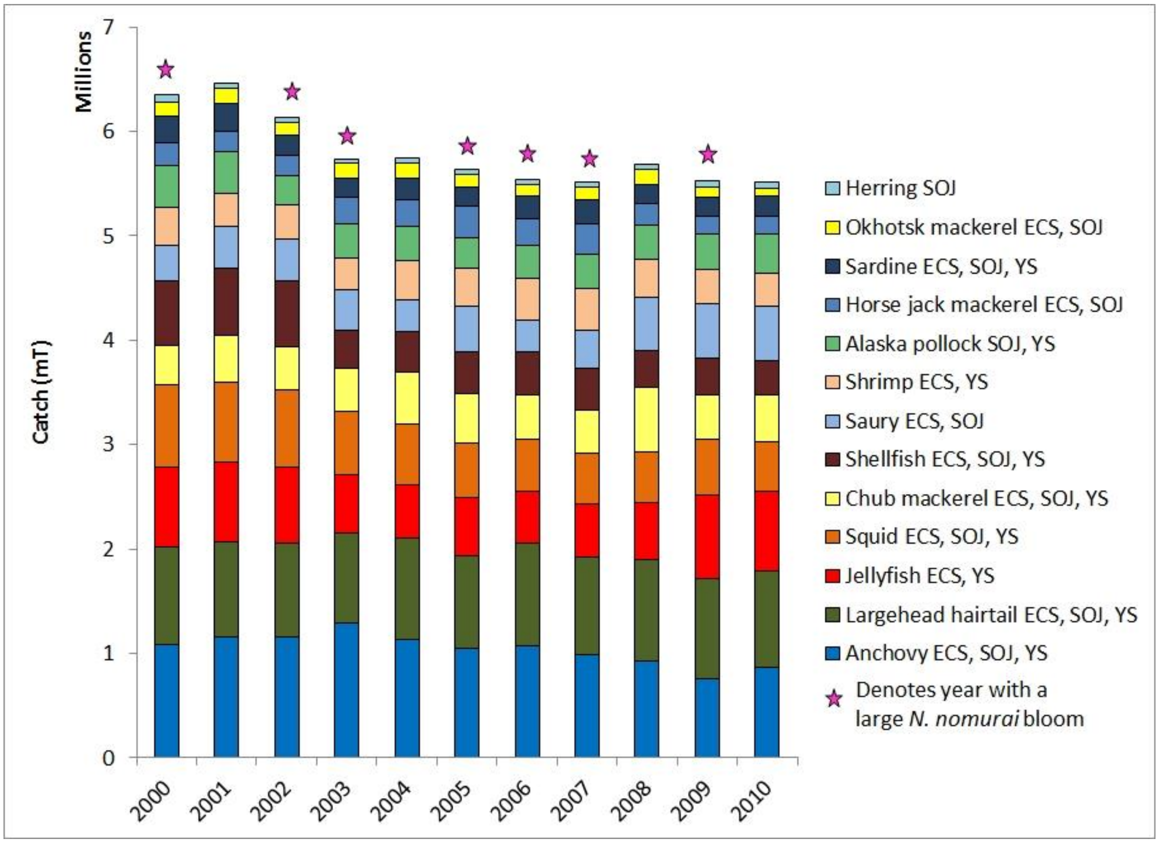


Figure 8. Fisheries catch 2000 – 2010.

All fisheries species and taxa of interest for this study, with catch basin LME indicated. Species displayed are sorted by lowest to highest mean catch per year for the decade. ECS = East China Sea, SOJ = Sea of Japan, YS = Yellow Sea. YS includes the Bohai Sea. Blue shades indicate forage fish. Data: Sea Around Us.

Benthic Structures

Benthic structures resulted in a significant, negative linear relationship with *N. nomurai* occurrence (Table 2). This was the opposite direction of the expected relationship, where the expectation was based on the assumption that an increase in anthropogenic structures would result in more *N. nomurai* benthic habitat. It was also assumed that coastal human population was an appropriate proxy for anthropogenic benthic structures, since increasing human population would correspond with an increase in coastal development. The results suggest that there could have been too many assumptions involved in using human population growth as a proxy for anthropogenic benthic habitat creation. Alternatively, this relationship could be evidence that *N. nomurai* benthic life stages are not utilizing anthropogenic coastal structures as habitat. Recent increase in human population growth in coastal China has coincided with reef destruction and decline of other naturally occurring hard substrates (Zhang, 2015). Thus *N. nomurai* might not be utilizing anthropogenic structures as successfully as naturally occurring hard substrate, and the decrease in natural substrate habitat decreased over the time period analyzed. Another possibility is that new benthic habitat takes time to colonize, and the time series could not detect the corresponding growth. Or, these results could occur in response to excess pollution that could accompany increases in human population, which would then suppress *N. nomurai* occurrence. Increased human population could result in higher levels of localized jellyfish harvest, and *N. nomurai* would be susceptible. It seems likely that some combination of factors is responsible for the coincident decrease of *N. nomurai* occurrence with human coastal population increase. Meanwhile, the question of whether benthic anthropogenic structures create habitat for *N. nomurai* remains unresolved. The results of this analysis show support for a negative linear link between *N. nomurai* and coastal human population growth, but the relationship and the mechanism for such a link needs further investigation.

Limitations

Several data limitations were evident in the study. The time series duration of *N. nomurai* data and the time series duration of fisheries category data, along with the resulting limitation for GAM analysis, are examples. Limitation of one dataset could have broad reaching impacts, and limitation of the *N. nomurai* data utilized would impact the entire analysis.

Some results of the analysis could be artifacts of the distribution of the *N. nomurai* dataset. The beginning year of data for both the ferry survey and the MAFF fishery datasets was 2006, which was a strong bloom year with the highest average medusa counts occurring in that year, for both datasets (Figure 9; Figure 10). Examining the trend over two decades, there are five “large” or “small” bloom years preceding 2006 that are thus not captured in the present analysis (Figure 11).

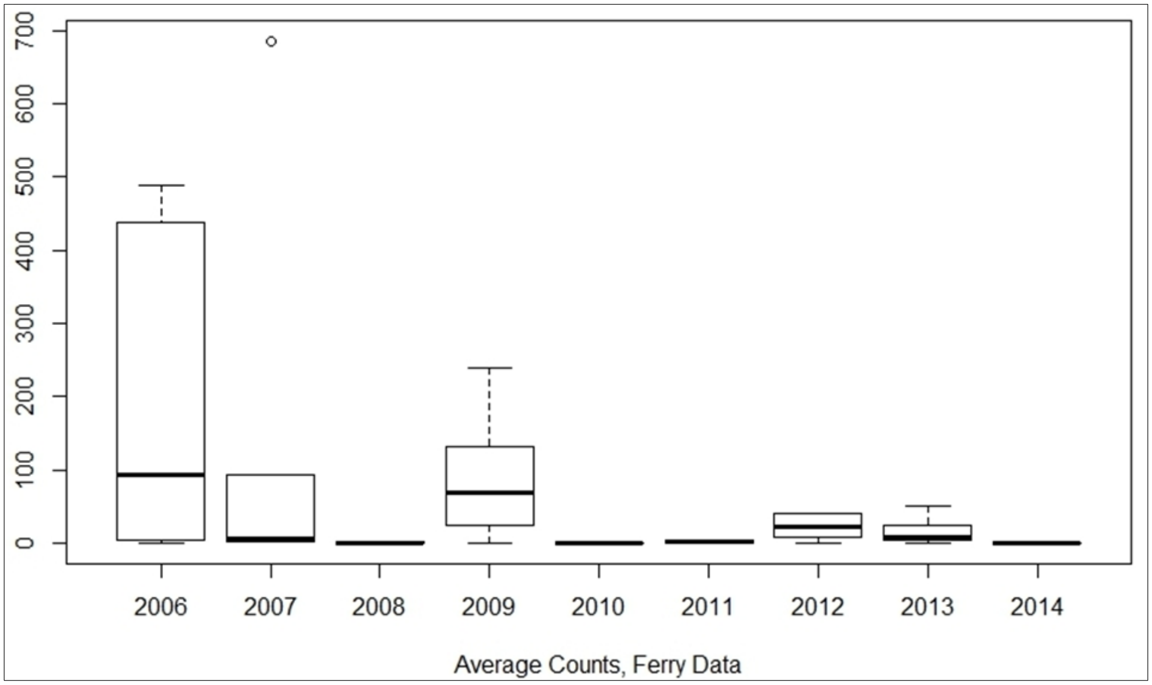


Figure 9. Boxplot of ferry survey *Nemopilema nomurai* data.

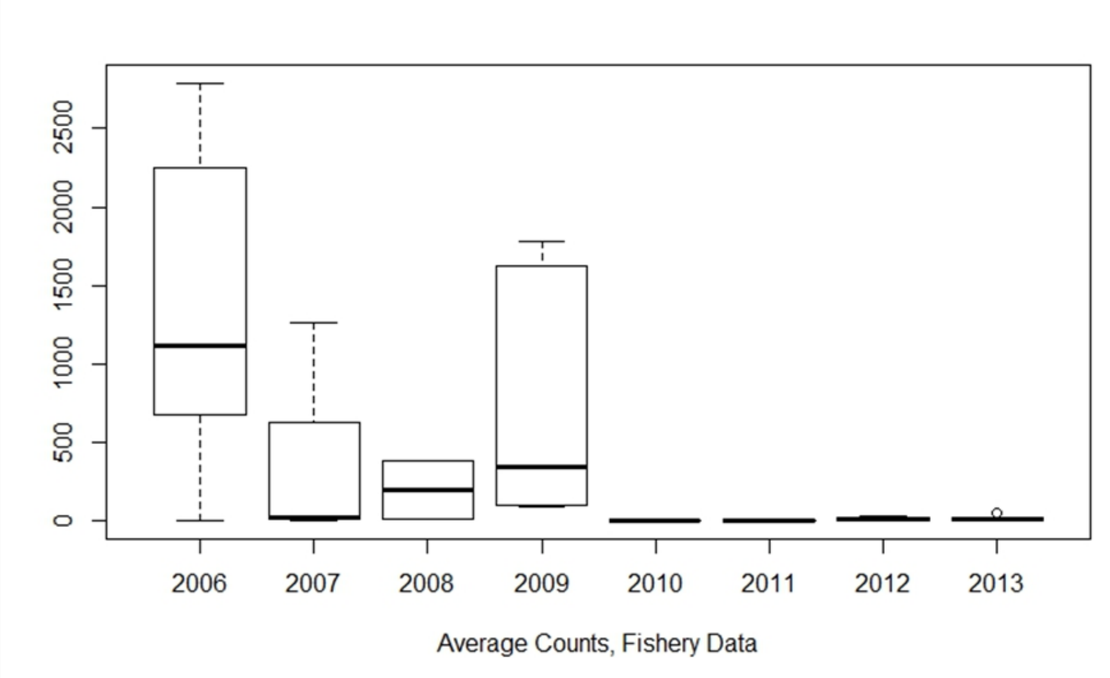


Figure 10. Boxplot of MAFF fishery survey *Nemopilema nomurai* data.

Several factors in the analysis exhibited significant or marginally significant linear relationships with *N. nomurai*, contrary to their expected trend. Other factors exhibited no significant relationship where one was expected. Unexpected trends could be a product of the limitations of the data, such as small sample size. The largest possible annual dataset time series was n = 9. The recommended degrees of freedom (df) is df ≤ n-2 (Zar, 2009), and thus the maximum df was seven. However, most of the environmental factors had time series of shorter duration than nine, and the df went down summarily. The fisheries data time series was the shortest for all the factors at n = 5 (Table 2). For those, the df was set to 3 (n-2). In some cases, the actual df was more than 3.5 (Table A2), which could result in a better-than-actual fit for the model.

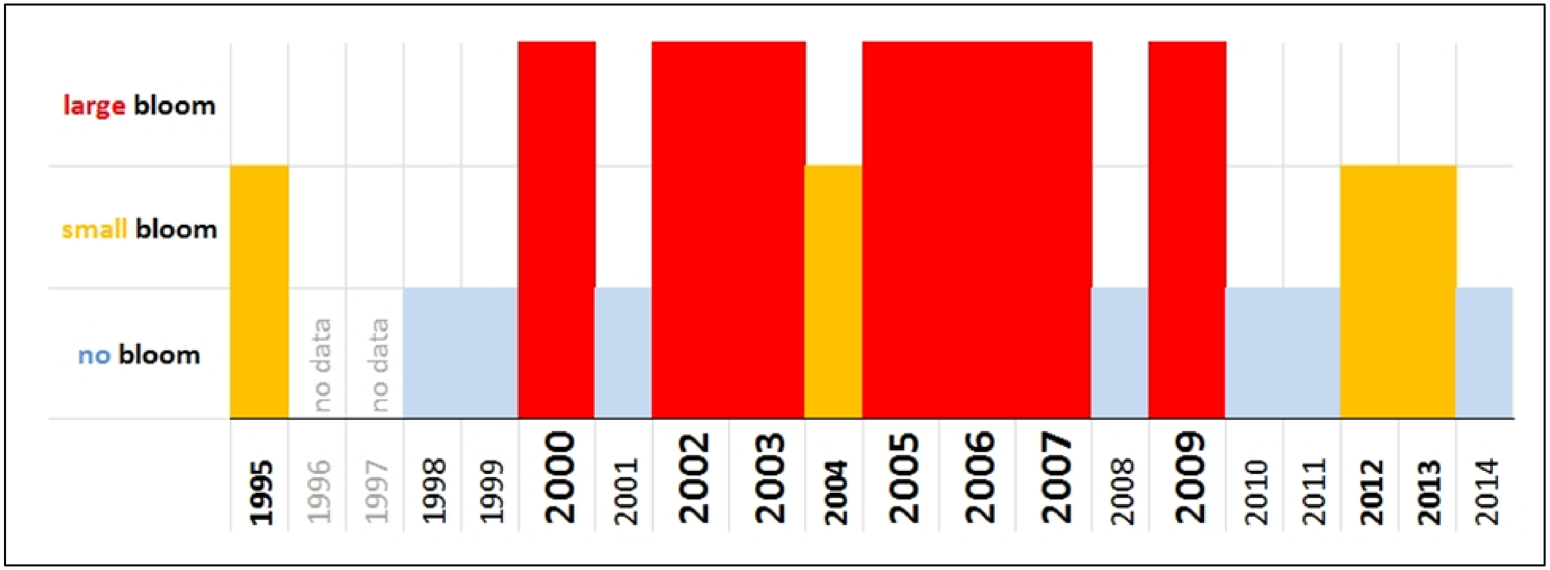


Figure 11. Blooms of *Nemopilema nomurai* since 1995.

Figure was constructed with reports from various studies (i.e., Dong et al., 2010; Kitajima et al., 2015; Purcell et al., 2007; Xu et al., 2013; Zhang et al., 2012) and Uye ferry surveys. “Small” is any reported bloom with either unspecified size or density <1 individual /100 m^2, and “No bloom” is density <0.1 individual /100 m^2.

Results of the fisheries category factors suggest a data limitation signal, because ΔAIC values for fisheries were all below the mean ΔAIC, while none of the other ΔAIC scores were below the mean (Table 2). One possible reason for the lack of expected outcomes for the fisheries category factors is that the time series data were too short to adequately capture a relationship between the catch and *N. nomurai* occurrence.

The scale of the factors was an issue as well. Forage fish species, for example, have been shown to have cyclical relationships with other jellyfish species often on a decadal (or longer) scale, not on the annual cycle documented in this analysis (Robinson et al., 2014). And forage fish populations have also been shown, independent of jellyfish, to vary on a decadal scale (Essington et al., 2015). Similarly, climate patterns as captured by the EASMI index are also known to operate on decadal scales (Alheit and Bakun, 2010; Purcell, 2005).

GAM analyses are useful for analyzing non-linear patterns, and also give the capability to analyze the best fit curve for several variables at a time (Boyce et al., 2002). However, multiple variable GAM analysis was not possible in this study due to the low degrees of freedom (df) necessary, and especially for the fisheries factors. The resulting combined df of several factors was too high to adequately evaluate the relationships. The restricted df for the analysis also contributed to interpreting a marginal significance of $p = 0.10$. Future analysis could employ a categorical analysis, using “small”, “medium”, or “large” bloom rating for *N. nomurai* each year, thus extending the *N. nomurai* scope of analysis. Ideally, however, quantitative surveys of *N. nomurai* abundance will continue, the time series datasets will expand, and the ecological factors affecting *N. nomurai* blooms will become increasingly more evident.

CHAPTER V – CONCLUSIONS

Aquaculture, benthic structures and jellyfish fisheries were predicted to be especially important, and did in fact have significant or marginally significant relationships with *N. nomurai* occurrence (except for shellfish aquaculture). However, the significant relationships were not always the expected dominant type. This study did not show definitively that aquaculture contributes to *N. nomurai* blooms, but the results suggest a link and warrant further investigation, especially because aquaculture facilities have been found to host benthic life stage individuals of other scyphozoan species (Holst and Jarms, 2007; Lo et al., 2008; Purcell et al., 2007). In addition, the benthic structures factor itself did not result in the expected relationship, challenging the assumption that anthropogenic structures are creating viable habitat for *N. nomurai* benthic life stages. In order to fully support the statistical evidence, field studies surveying aquaculture facilities for *N. nomurai* polyps, podocysts and ephyrae, especially of facilities for kelp and jellyfish, and especially in suspected seeding areas, are recommended to further refute the relationship.

Forage fish catch levels did not universally correlate inversely with *N. nomurai* occurrence. Despite some forage fish species catches exhibiting significant relationships, most of the forage fish examined resulted in no significant relationship. Examining longer time series data of forage fish catch, and also incorporating more detailed population data such as CPUE or stock assessments, is recommended. Fisheries species population information would help to illuminate ecological relationships between forage fisheries species and *N. nomurai* occurrence and blooms.

The results of this study do support the claim that there is an impact of fishing on the marine ecology of the EAMS. A concurrent analysis (stock assessment, combined with catch analysis) would create a more complete picture of the interactions of fisheries species with *N. nomurai*. While fishing and aquaculture are ancient practices in EAMS, the 20th century witnessed the arrival of large-scale harvest operations capable of extracting biomass in unprecedented quantities (Kleisner et al., 2013), and these operations have altered marine ecosystems (Essington et al., 2015; Zhang, 2015). This analysis did not disprove those findings, and it remains a plausible theory that fishing is altering ecosystems where *N. nomurai* occur and could influence blooms. In addition, a recent analysis showed that fishing of high trophic level organisms amplified forage fish population collapses (Essington et al., 2015), which suggests that the same mechanism could have created an ecological niche vacancy for *N. nomurai*.

The strongly significant negative linear relationship between benthic structures (yearly Chinese coastal human population) and *N. nomurai* occurrence was surprising. This result, counter to the expectation that benthic structures create *N. nomurai* habitat, could point to another relationship where greater coastal human population in seeding areas results in activity that inhibits *N. nomurai* occurrence. This relationship is important to analyze further. Isolating coastal development factors and analyzing those with respect to *N. nomurai* occurrence would be useful, as well as continued analysis of human coastal population on a longer time series.

This study verified that there is a statistical relationship between commercial jellyfish (*R. esculentum* aquaculture and fisheries) and *N. nomurai* occurrence. The implication is that there is also a relationship with *N. nomurai* blooms, although the mechanism of such a relationship is unresolved. Future studies are needed to evaluate the overlap between *R. esculentum* and *N. nomurai* production. One area in need of special attention is field verification of species composition of jellyfish landings. Ascertaining whether (and to what extent) *N. nomurai* are being harvested and sold as *R. esculentum* is essential as a next step. If the mislabeling of species in harvest is occurring at the scale suggested by Armani et al. (2012), then jellyfish fishing and CPUE could have extensive impact on the population or bloom condition of *N. nomurai*. For example, blooms that occur in Japan could be a result of lower harvest or CPUE in the East China Sea and Yellow Sea. Fishers might mistake which species they're landing. It is easy to imagine that the species could be confused in the field, or the incorrect material not identified upon landing, as the taxonomic designation of *N. nomurai* itself was only recently revised (Omori and Kitamura, 2004). *N. nomurai* was, until the revision, considered synonymous variously with both *Stomolophus meleagris* and *Stomolophus nomurai* by taxonomists, without any particular justification. *Stomolophus nomurai* is no longer an accepted epithet (Omori and Kitamura, 2004). *Stomolophus meleagris*, on the other hand, is in widespread use as it refers to the "cannonball jellyfish" that occurs in the North Atlantic and the Gulf of Mexico. All three genera: *Nemopilema*, *Rhopilema*, and *Stomolophus* are very similar morphologically, and member species have historically been lumped and split various times (Omori and Kitamura, 2004). Recent genetic analyses utilized identified primers (accession records are in Chinese) and verified the likelihood of one singular geographic population of *N. nomurai* (Dong et al., 2016), further demonstrating that genetic testing of samples could distinguish *Nemopilema* from *Rhopilema* specimens. The species composition of jellyfish landings could have implication for populations and abundance of both *N. nomurai* and *R. esculentum*. Despite any remaining questions, the present study strongly supports the assertions that *R. esculentum* and *N. nomurai* affect each other ecologically, and that their populations and production are intertwined.

Questions remain regarding whether hypoxia has an effect on *N. nomurai* populations. A time series of dissolved oxygen data for the Changjiang River outflow area water column would be extraordinarily useful. This time series, combined with time series data of nutrient loading and levels would allow us to assess the relative contribution of hypoxia and eutrophication to the area. Laboratory tests of how various *N. nomurai* life stages respond to nutrient levels would provide invaluable information as well.

Recommendations

A list of recommendations for data collection and future analysis was generated as a result of this study.

1. Sample and monitor the sediment (benthic habitat) near *N. nomurai* known and proposed seeding areas. Compare sampling with historical benthic maps to ascertain changes in natural benthic habitat for *N. nomurai*.
2. Sample aquaculture structures for polyps, especially near known seeding areas.

3. Obtain CPUE or stock assessment data for fisheries species including forage fish. Pursue future analyses with longer time series.
4. Grow *N. nomurai* polyps in conjunction with shellfish aquaculture facilities and measure the resulting growth and survival of *N. nomurai* benthic life stages. Monitor the nutrients and dissolved oxygen levels.
5. Perform settlement studies on *N. nomurai* planulae using natural and artificial substrates.
6. Calculate the species composition of jellyfish landings at representative locations over several years.
7. Create an *in-situ* dissolved oxygen time series for the Changjiang River outflow area, throughout the water column.
8. Obtain nutrient load data for the Changjiang River outflow area for a time series.

The continued monitoring of *N. nomurai* occurrences, especially in the East China Sea, the Yellow Sea and the Bohai Sea, is critical to expanding our understanding of the dynamics of *N. nomurai* blooms. Data such as those gathered by additional site-specific surveys including depth stratified sampling for *N. nomurai*, would be invaluable to fill gaps, and to illuminate further the ecological impact of *N. nomurai* occurrences. Each piece of the *N. nomurai* story is important to understanding the big picture, and contributes to our abilities to interpret and analyze jellyfish blooms around the world.

APPENDIX A – Supplemental Data Tables

Table A1.

Correlation table, ferry survey data

Time range	Interval	Category	y variable	r	p-value	CI	Data source	Geographic region
2006 - 2013	per year	Aquaculture	Jellyfish	(0.692)	0.057.	-0.939 to 0.025	FAO	China
2006 - 2012	per year	Aquaculture	Kelp	(0.712)	0.073.	-0.954 to 0.089	FAO	China
2006 - 2012	per year	Aquaculture	Shellfish	(0.482)	0.273	-0.906 to 0.425	FAO	China
2006 - 2014	per year	Benthic structures	Human population, China	(0.765)	0.016*	-0.948 to -0.205	CNBS	China
2006 - 2014	per year	Benthic structures	Human population, coastal China	(0.788)	0.012*	-0.953 to -0.260	CNBS	China: coastal provinces
2006 - 2014	per year	Benthic structures	Human population, coastal China seeding areas	(0.788)	0.012*	-0.953 to -0.260	CNBS	China: BS, ECS, YS provinces
2006 - 2014	monthly	Bottom conditions	Salinity	(0.093)	0.545	-0.376 to 0.206	Copernicus MEMS	BS, ECS, YS
2006 - 2014	monthly	Bottom conditions	Salinity, *N. nomurai* seeding areas	0.301	0.045*	0.008 to 0.546	Copernicus MEMS	Coastal ECS, YS

Time range	Interval	Category	y variable	r	p-value	CI	Data source	Geographic region
2006 - 2014	per year	Bottom conditions	Salinity, *N. nomurai* seeding areas	(0.035)	0.930	-0.683 to 0.644	Copernicus MEMS	Coastal ECS, YS
2006 - 2014	monthly	Bottom conditions	Temperature	(0.064)	0.678	-0.351 to 0.234	Copernicus MEMS	BS, ECS, YS
2006 - 2014	monthly	Bottom conditions	Temperature, *N. nomurai* seeding areas	(0.155)	0.309	-0.429 to 0.145	Copernicus MEMS	coastal ECS, YS
2006 - 2014	per year	Bottom conditions	Temperature, *N. nomurai* seeding areas	0.562	0.115	-0.163 to 0.893	Copernicus MEMS	Coastal ECS, YS
2006 - 2010	per year	Fisheries	Alaska pollock	(0.728)	0.163	-0.981 to 0.431	SAU	SOJ, YS
2006 - 2010	per year	Fisheries	Anchovy	0.438	0.461	-0.724 to 0.952	SAU	ECS, SOJ, YS
2006 - 2010	per year	Fisheries	Chub mackerel	(0.715)	0.175	-0.979 to 0.454	SAU	ECS, SOJ, YS
2006 - 2010	per year	Fisheries	Flying squid	0.517	0.372	-0.671 to 0.961	SAU	ECS, SOJ, YS
2006 - 2010	per year	Fisheries	Herring	(0.475)	0.419	-0.956 to 0.701	SAU	SOJ
2006 - 2010	per year	Fisheries	Horse jack mackerel	0.684	0.203	-0.400 to 0.977	SAU	ECS, SOJ

Time range	Interval	Category	y variable	r	p-value	CI	Data source	Geographic region
2006 - 2010	per year	Fisheries	Jellyfish	(0.363)	0.548	-0.943 to 0.764	SAU	ECS, YS
2006 - 2010	per year	Fisheries	Largehead hairtail, all	0.111	0.859	-0.855 to 0.905	SAU	ECS, SOJ, YS
2006 - 2010	per year	Fisheries	Largehead hairtail, China	0.134	0.830	-0.849 to 0.909	SAU	ECS, YS
2006 - 2010	per year	Fisheries	Okhotsk mackerel	(0.009)	0.989	-0.884 to 0.880	SAU	ECS, SOJ
2006 - 2010	per year	Fisheries	Pacific saury	(0.806)	0.100.	-0.987 to 0.264	SAU	ECS, SOJ
2006 - 2010	per year	Fisheries	Sardine	0.705	0.183	-0.468 to 0.979	SAU	ECS, SOJ, YS
2006 - 2010	per year	Fisheries	Shellfish	0.907	0.034*	0.124 to 0.994	SAU	ECS, SOJ, YS
2006 - 2010	per year	Fisheries	Shrimp	0.677	0.210	-0.510 to 0.976	SAU	ECS, YS
2006 - 2014	per year	Hypoxia	Monsoon count, all	(0.066)	0.865	-0.700 to 0.625	IBTRACS	Western Pacific
2006 - 2014	Apr - Sep	Hypoxia	Monsoon count, summer	0.096	0.805	-0.607 to 0.715	IBTRACS	Western Pacific

Time range	Interval	Category	y variable	r	p-value	CI	Data source	Geographic region
2006 - 2014	Jun - Aug	Hypoxia	Monsoon index	0.360	0.342	-0.400 to 0.826	EASMI	Western Pacific
2006 - 2013	per year	*N. nomurai*	MAFF fishery avg yr	0.907	0.002**	0.562 to 0.983		

Note: Pearson's product moment (r) correlation test results for all factors, against *Nemopilema nomurai* Uye ferry survey data. Significance values indicated by p-value "." ≤ 0.10; "*" ≤ 0.05, "**"≤ 0.01. China coastal provinces are: Fujian, Guangdong, Guangxi, Hainan, Hebei, Jiangsu, Liaoning, Shandong, Shanghai, Tianjin, and Zhejiang. Provinces bordering China's Bohai Sea (BS), East China Sea (ECS) and Yellow Sea (YS) are those used in *N. nomurai* seeding areas. *N. nomurai* seeding area provinces are: Hebei, Jiangsu, Liaoning, Shandong, Shanghai, Tianjin, and Zhejiang. SOJ = Sea of Japan. The region for salinity and temperature data was defined using bounded coordinates (31.5N, 36.5N) Latitude, (119.5E, 123.5E) Longitude, inclusive. Data sources are defined in Methods section.

Table A2.

Correlation table, MAFF fishery data

Time range	**Interval**	**Category**	**y variable**	**r**	**p-value**	**CI**	**Data source**	**Geographic region**
2006 - 2013	per year	Aquaculture	Jellyfish	(0.749)	0.032*	-0.951 to -0.094	FAO	China
2006 - 2012	per year	Aquaculture	Kelp	(0.721)	0.068.	-0.955 to 0.070	FAO	China
2006 - 2012	per year	Aquaculture	Shellfish	(0.416)	0.353	-0.890 to 0.491	FAO	China
2006 - 2013	monthly	Bottom conditions	Salinity	(0.108)	0.544	-0.430 to 0.239	Copernicus MEMS	BS, ECS, YS
2006 - 2013	monthly	Bottom conditions	Temperature	0.026	0.885	-0.315 to 0.361	Copernicus MEMS	BS, ECS, YS
2006 - 2010	per year	Fisheries	Herring	(0.211)	0.733	-0.922 to 0.825	SAU	SOJ
2006 - 2010	per year	Fisheries	Largehead hairtail, Japan	(0.026)	0.967	-0.888 to 0.876	SAU	SOJ
2006 - 2010	per year	Fisheries	Pacific saury	(0.843)	0.073.	-0.989 to 0.154	SAU	ECS, SOJ
2006 - 2010	per year	Fisheries	Shellfish	0.880	0.049*	-0.012 to 0.992	SAU	ECS, SOJ, YS
2006 - 2013	per year	Hypoxia	Monsoon count, all	(0.058)	0.892	-0.733 to 0.674	IBTRACS	Western Pacific

Time range	Interval	Category	y variable	r	p-value	CI	Data source	Geographic region
2006 - 2013	Apr - Sep	Hypoxia	Monsoon count, summer	(0.017)	0.968	-0.713 to 0.696	IBTRACS	Western Pacific
2006 - 2013	Jun - Aug	Hypoxia	Monsoon index	0.406	0.318	-0.418 to 0.864	EASMI	Western Pacific

Note: Pearson's product moment (r) correlation test results for factors against *N. nomurai* MAFF fishery data. Significance values indicated by p-value "." ≤ 0.10; "*" ≤ 0.05. Geographic location codes: BS = Bohai Sea, ECS = East China Sea, SOJ = Sea of Japan and YS =Yellow Sea. The region for salinity and temperature data was defined using bounded coordinates (31.5N, 36.5N) Latitude, (119.5E, 123.5E) Longitude, inclusive. Data sources are defined in Methods section.

Table A3.

GAM test results

Category	**Factor**	**n**	**GAM R^2**	**GAM Deviance Explained**	**GCV**	**GCV/ min. GCV**	**Actual df**	**GAM p-value**	**GAM AIC**	**GAM ΔAIC** $\bar{x}$ = 26
Aquaculture	Jellyfish	8	39.1%	47.8%	5,053	5.5	3.00	0.057.	92	45
Aquaculture	Kelp	7	45.5%	57.3%	5,599	6.0	3.30	0.108	81	34
Aquaculture	Shellfish	7	7.9%	23.3%	8,887	9.6	3.00	0.273	85	38
Benthic structures	Coastal population	9	58.9%	65.5%	3,256	3.5	3.28	0.019*	100	52
Bottom conditions	Salinity	9	27.5%	43.9%	6,228	6.7	3.80	0.215	105	58
Bottom conditions	Temperature	9	21.8%	31.6%	5,949	6.4	3.00	0.115	105	58
Fisheries	Alaskan pollock	5	37.4%	53.1%	8,157	8.8	3.00	0.162	60	13
Fisheries	Anchovy	5	33.9%	61.2%	11,017	11.9	3.65	0.386	60	13
Fisheries	Chub mackerel	5	86.3%	92.9%	2,580	2.8	3.92	0.066.	53	5
Fisheries	Flying squid	5	26.5%	54.0%	11,476	12.4	3.50	0.427	61	14
Fisheries	Herring	5	-3.2%	22.6%	13,454	14.5	3.00	0.419	63	15
Fisheries	Horse jack mackerel	5	29.1%	46.8%	9,239	10.0	3.00	0.202	61	14
Fisheries	Jellyfish	5	95.2%	97.6%	927	1.0	3.99	0.023*	47	0

Category	Factor	n	GAM R^2	GAM Deviance Explained	GCV	GCV/ min. GCV	Actual df	GAM p-value	GAM AIC	GAM ΔAIC $\bar{x}$ = 26
Fisheries	Largehead hairtail	5	-31.7%	1.2%	17,163	18.5	3.00	0.859	64	17
Fisheries	Okhotsk mackerel	5	83.6%	91.6%	3,138	3.4	3.96	0.083.	53	6
Fisheries	Pacific saury	5	53.3%	64.9%	6,091	6.6	3.00	0.099.	59	11
Fisheries	Sardine	5	36.6%	54.7%	8,684	9.4	3.14	0.224	60	13
Fisheries	Shellfish	5	76.4%	82.3%	3,078	3.3	3.00	0.033*	55	8
Fisheries	Shrimp	5	27.7%	45.8%	9,417	10.2	3.00	0.209	61	14
Hypoxia	Monsoon Count	9	-5.1%	12.8%	8,443	9.1	3.37	0.751	108	61
Hypoxia	Monsoon Index	9	7.7%	23.3%	7,399	8.0	3.35	0.438	107	60

Note: complete Generalized Additive Model (GAM) results table (Gaussian family). All tests were run with df set to 3. GCV is Generalized Cross Validation, or the R-software measure of goodness-of-fit of the model. Lowest relative GCV is the best fit. Delta AIC (ΔAIC) is calculated by [AIC - minimum AIC]. Significance values indicated by p-value "." ≤ 0.10; "*" ≤ 0.05.

APPENDIX B – Supplemental Generalized Additive Model (GAM) Figures

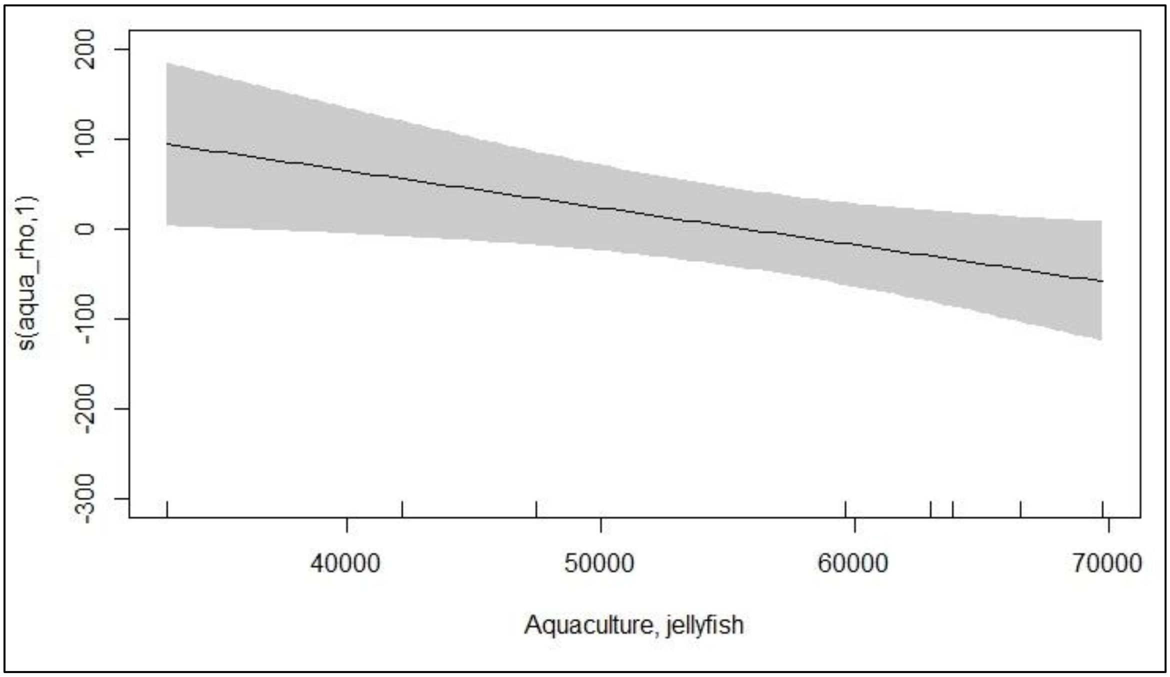


Figure A1. Aquaculture, jellyfish residual GAM spline relationship curve.

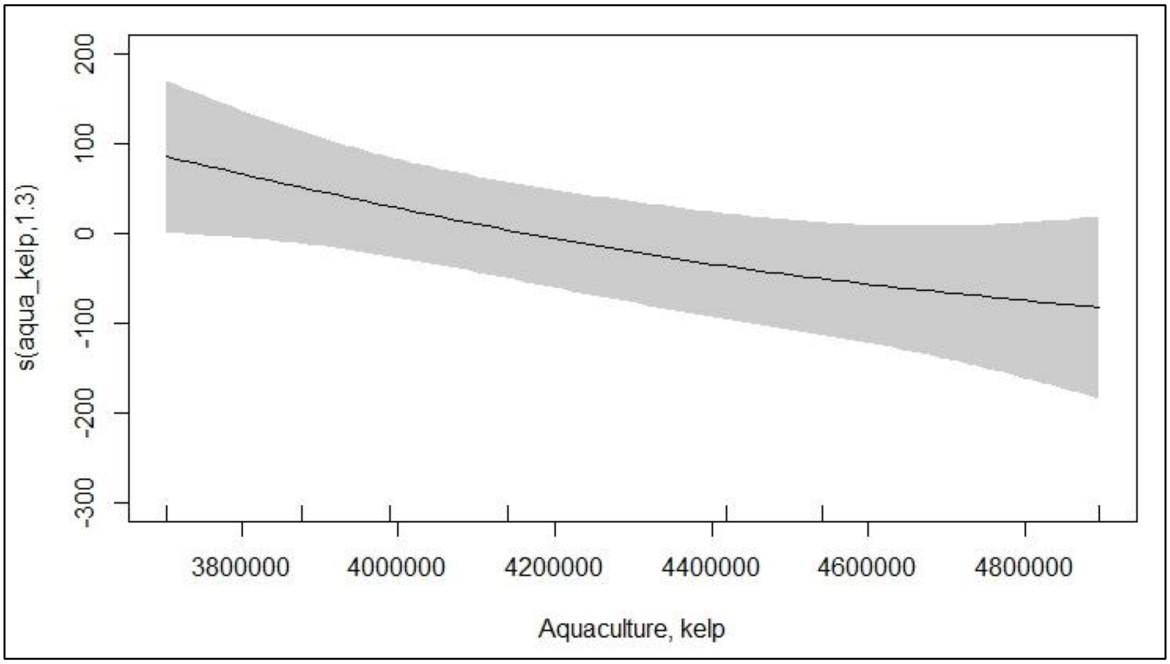


Figure A2. Aquaculture, kelp residual GAM spline relationship curve.

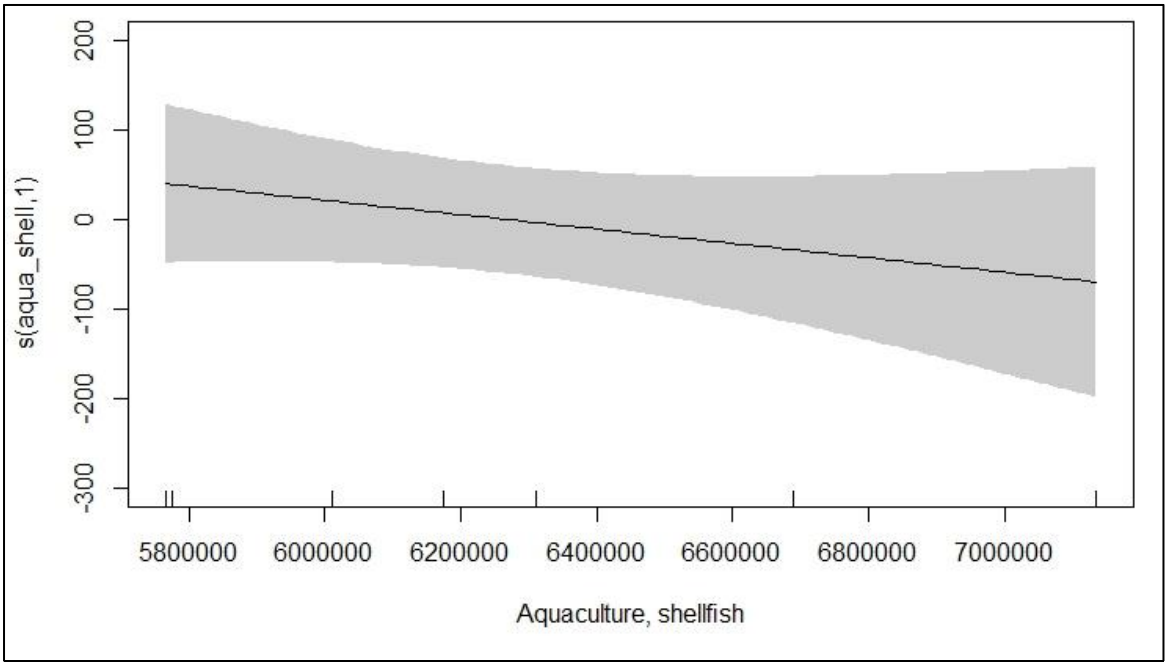


Figure A3. Aquaculture, shellfish residual GAM spline relationship curve.

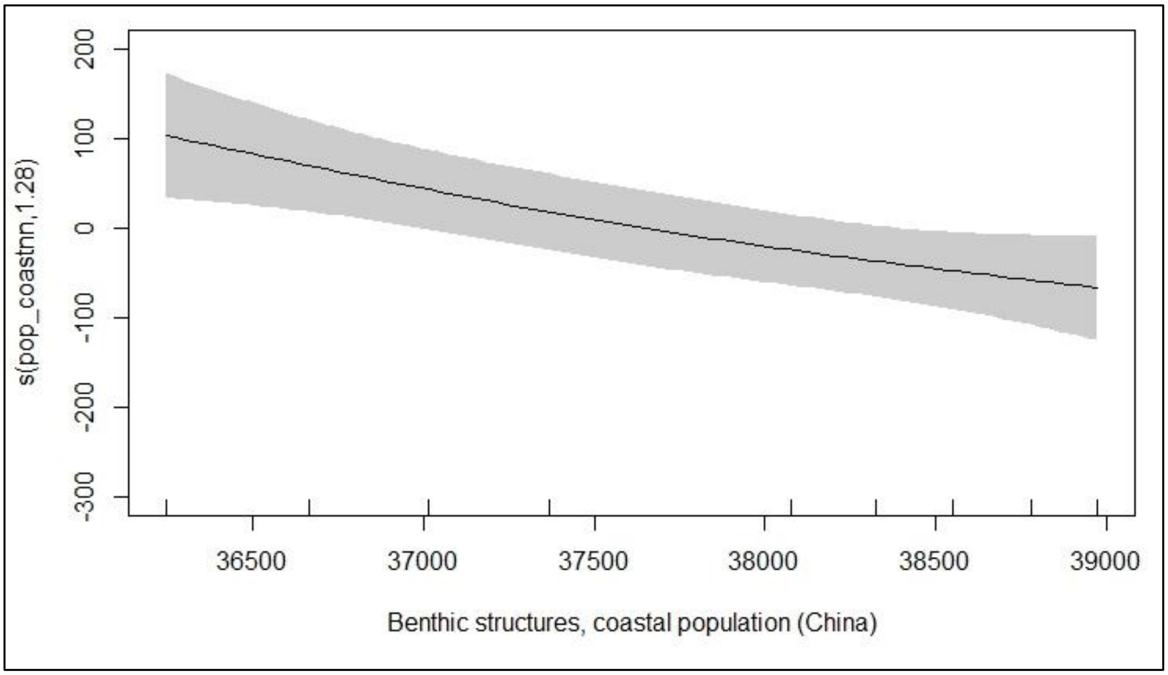


Figure A4. Benthic structures, coastal population residual GAM spline relationship curve.

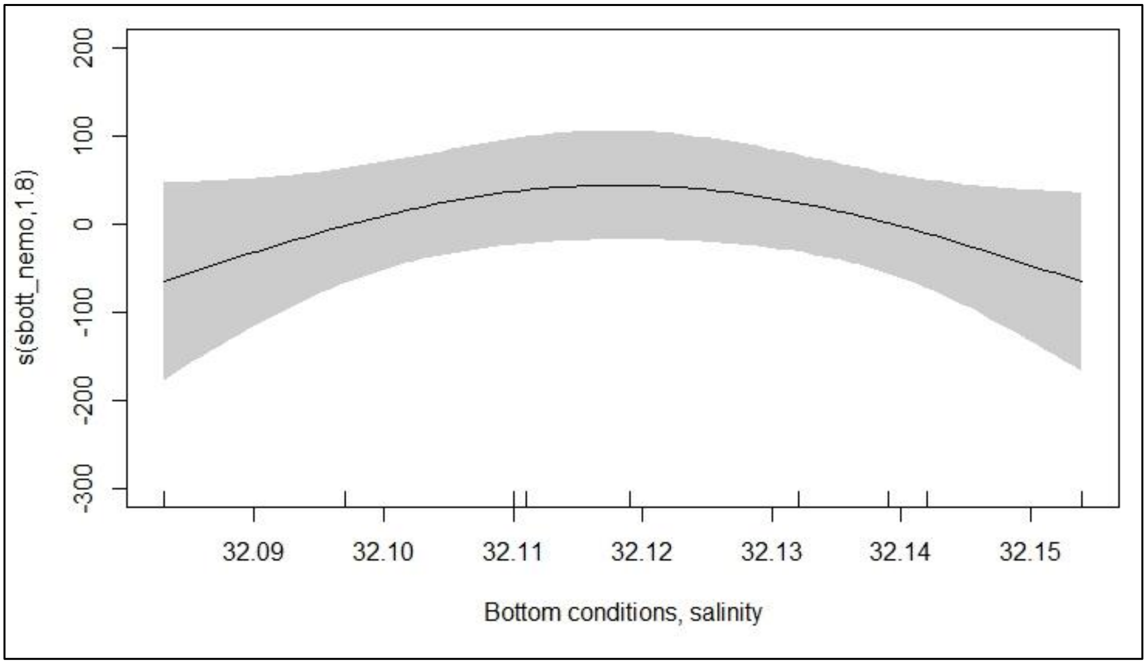


Figure A5. Bottom conditions, salinity residual GAM spline relationship curve.

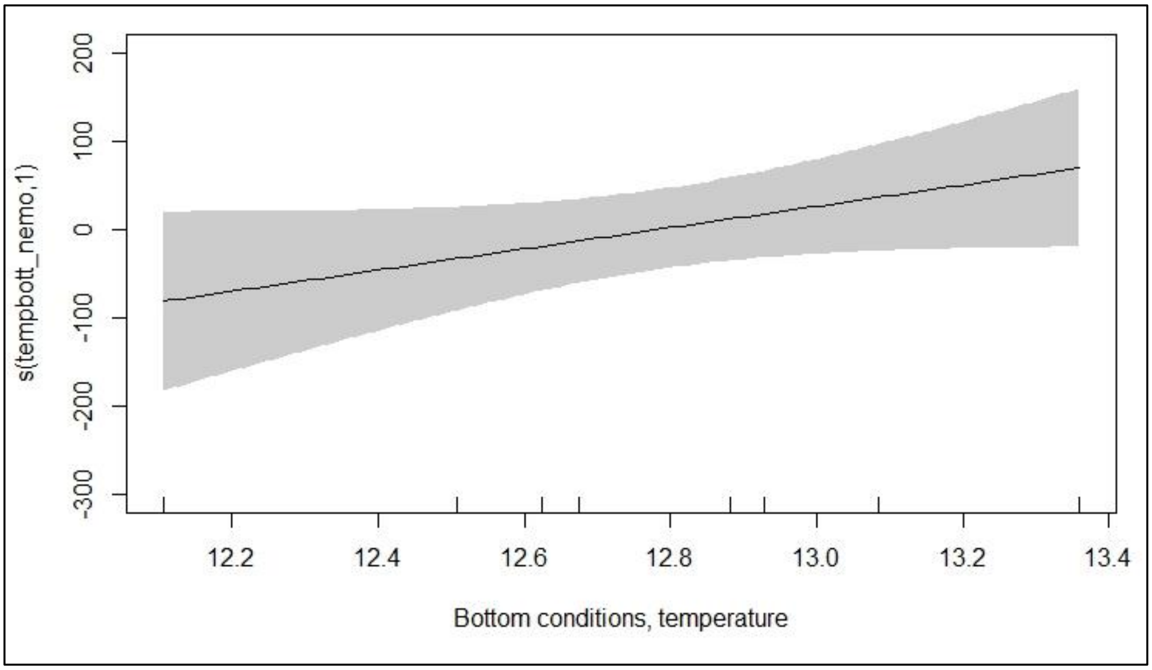


Figure A6. Bottom conditions, temperature residual GAM spline relationship curve.

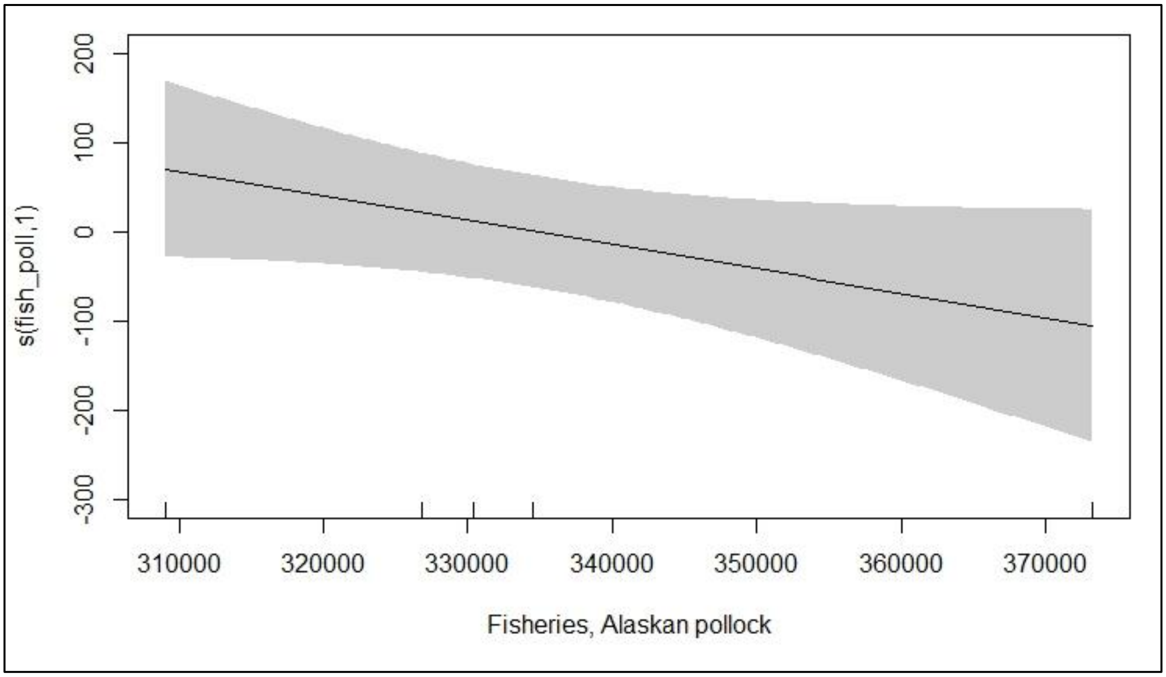


Figure A7. Fisheries, Alaskan pollock residual GAM spline relationship curve.

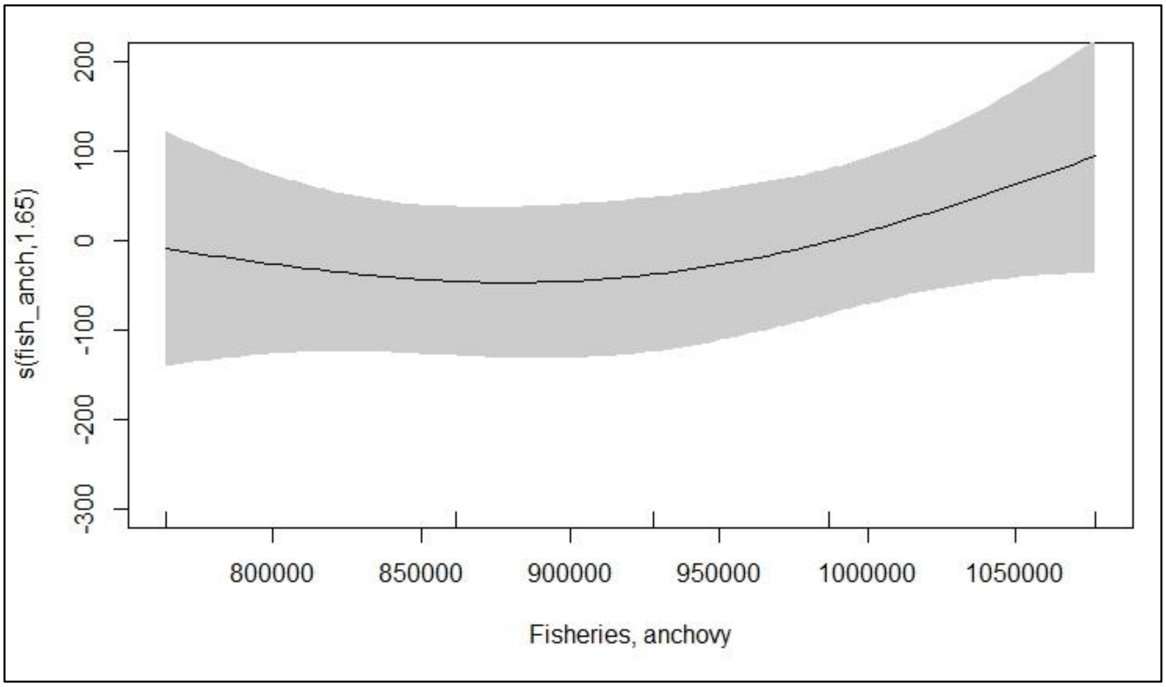


Figure A8. Fisheries, anchovy residual GAM spline relationship curve.

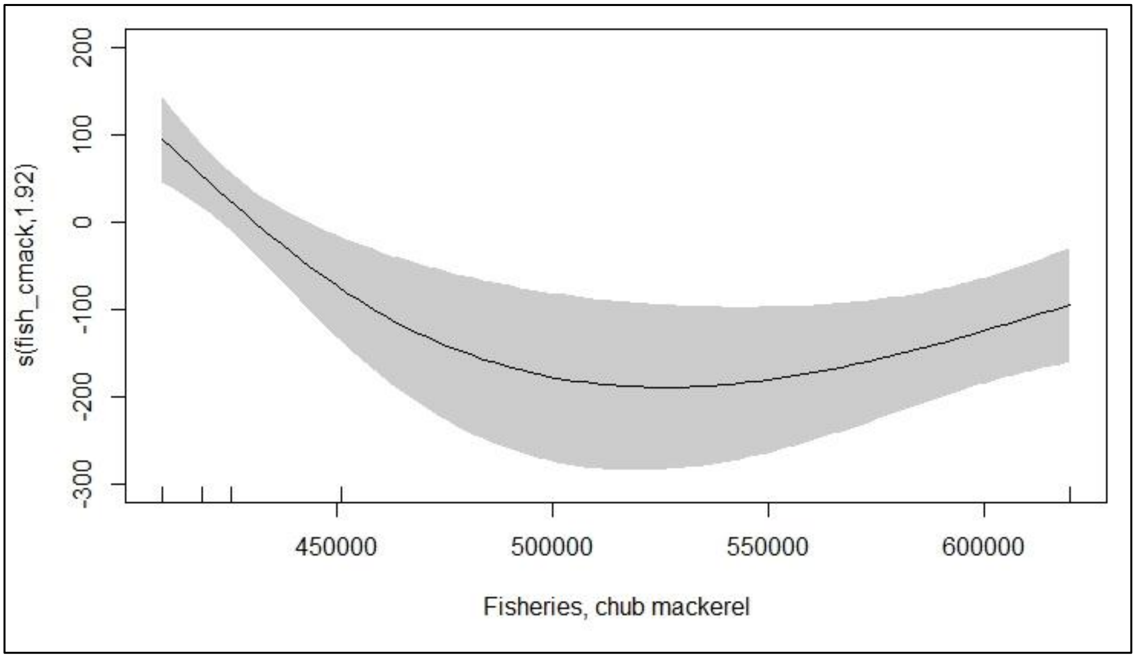


Figure A9. Fisheries, chub mackerel residual GAM spline relationship curve.

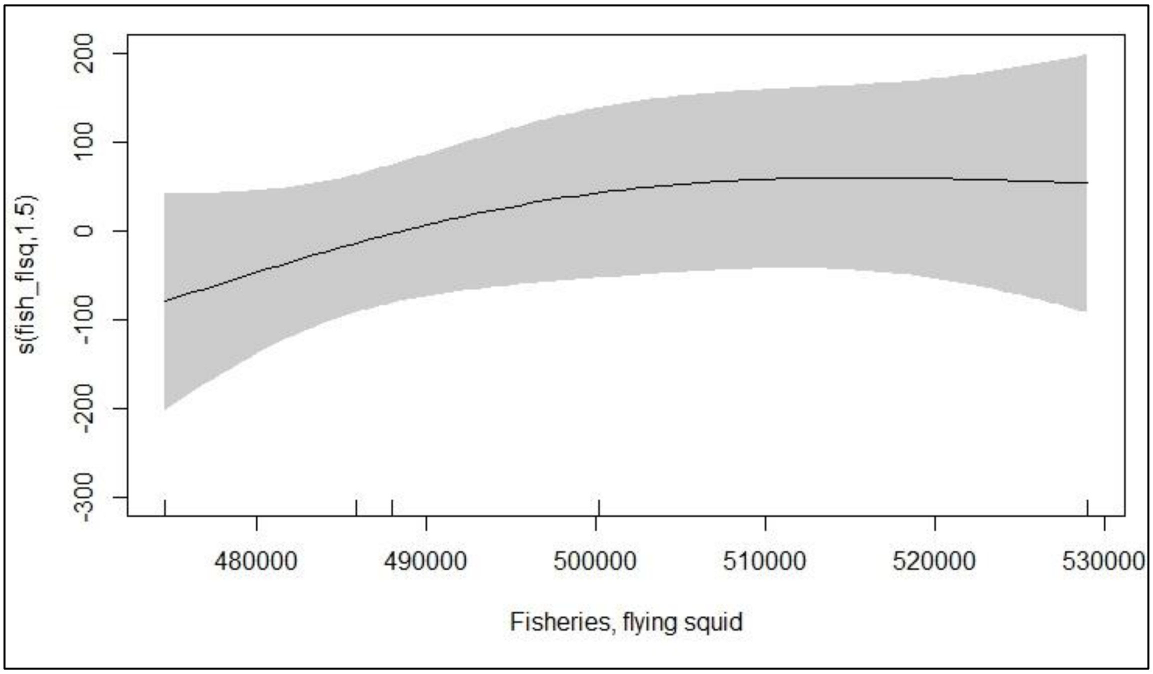


Figure A10. Fisheries, flying squid residual GAM spline relationship curve.

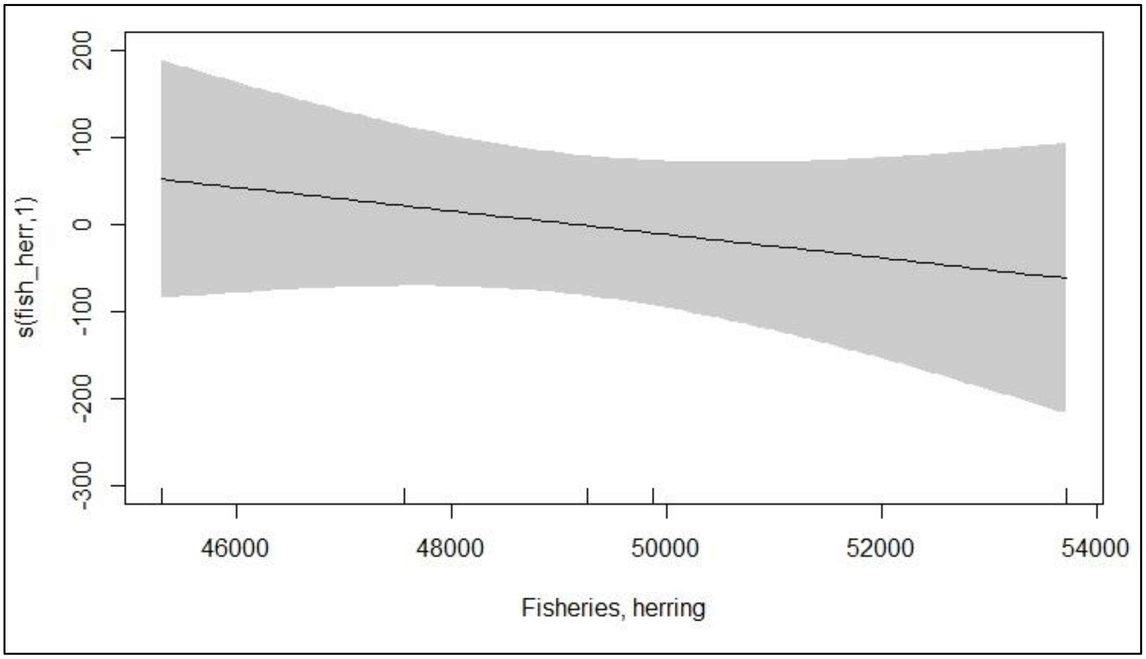


Figure A11. Fisheries, herring residual GAM spline relationship curve.

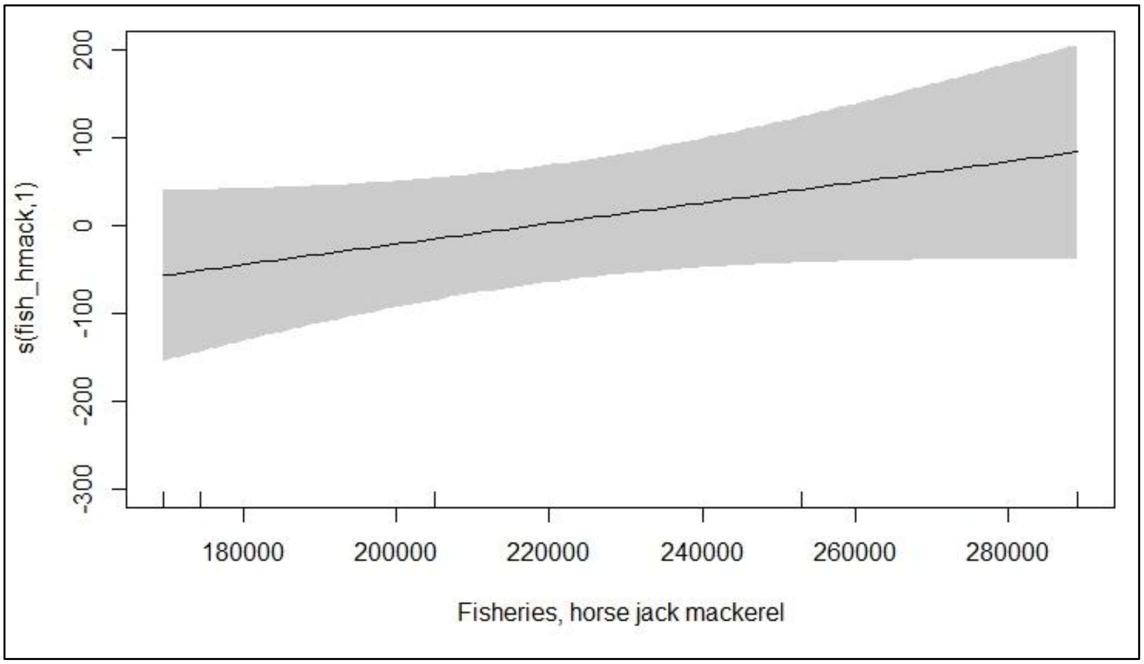


Figure A12. Fisheries, horse jack mackerel residual GAM spline relationship curve.

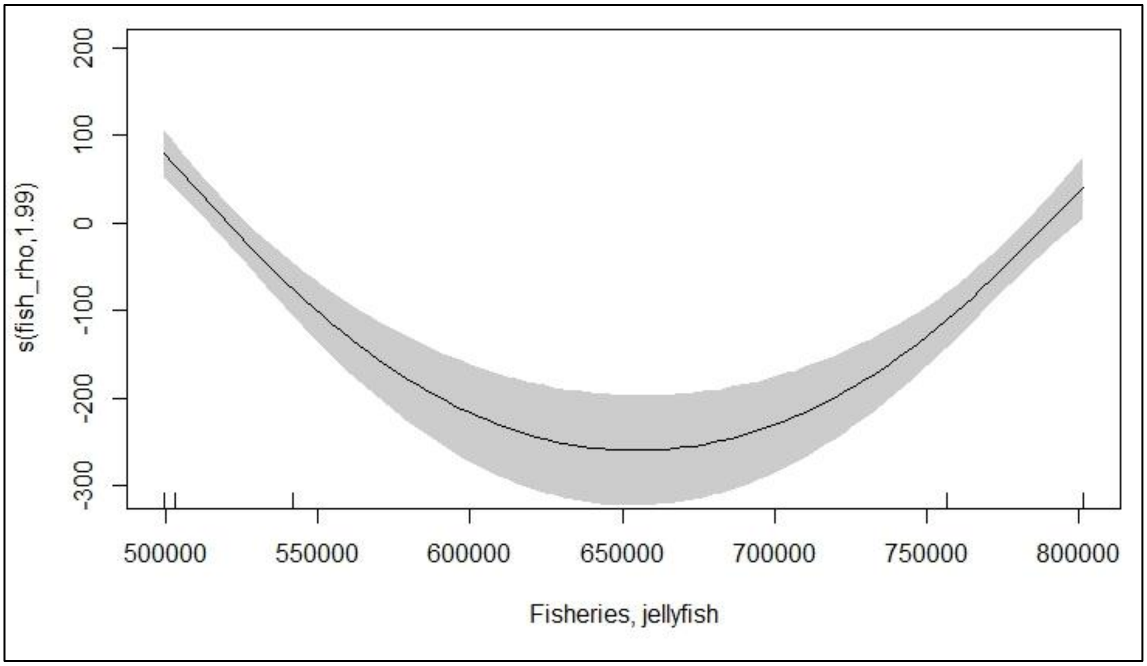


Figure A13. Fisheries, jellyfish residual GAM spline relationship curve.

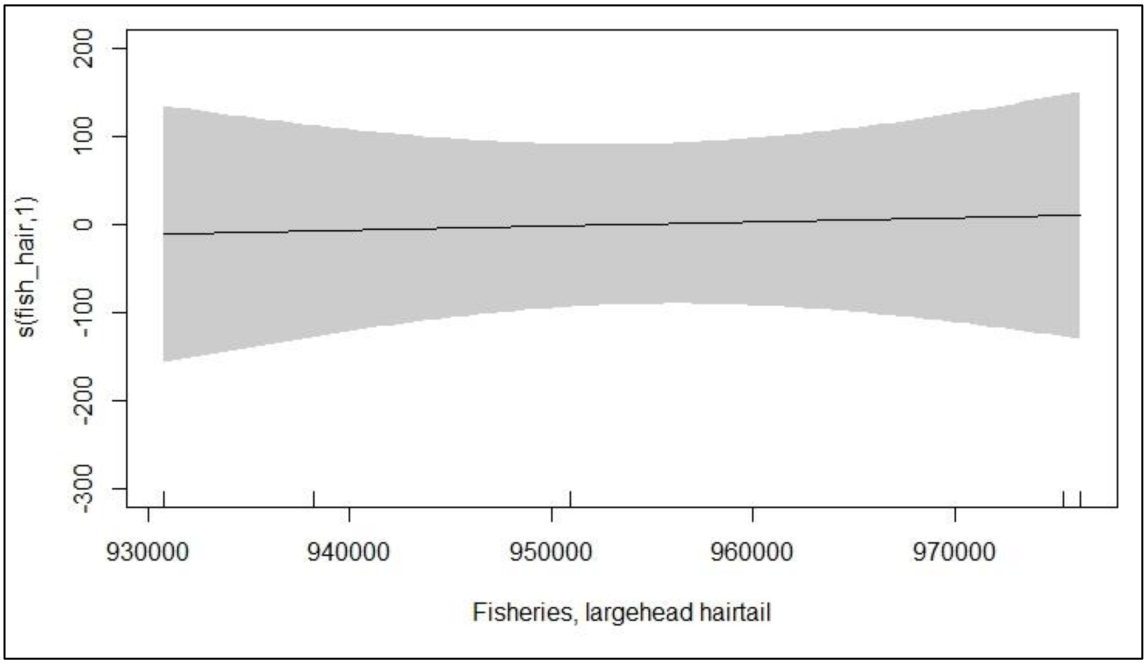


Figure A14. Fisheries, largehead hairtail residual GAM spline relationship curve.

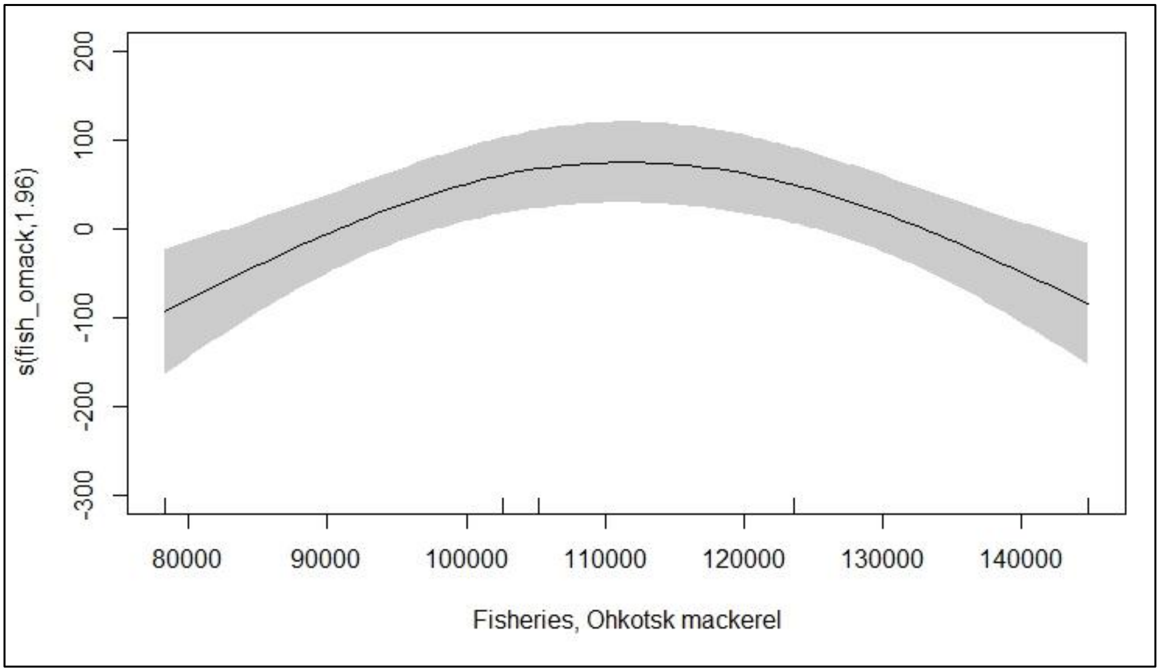


Figure A15. Fisheries, Okhotsk mackerel residual GAM spline relationship curve.

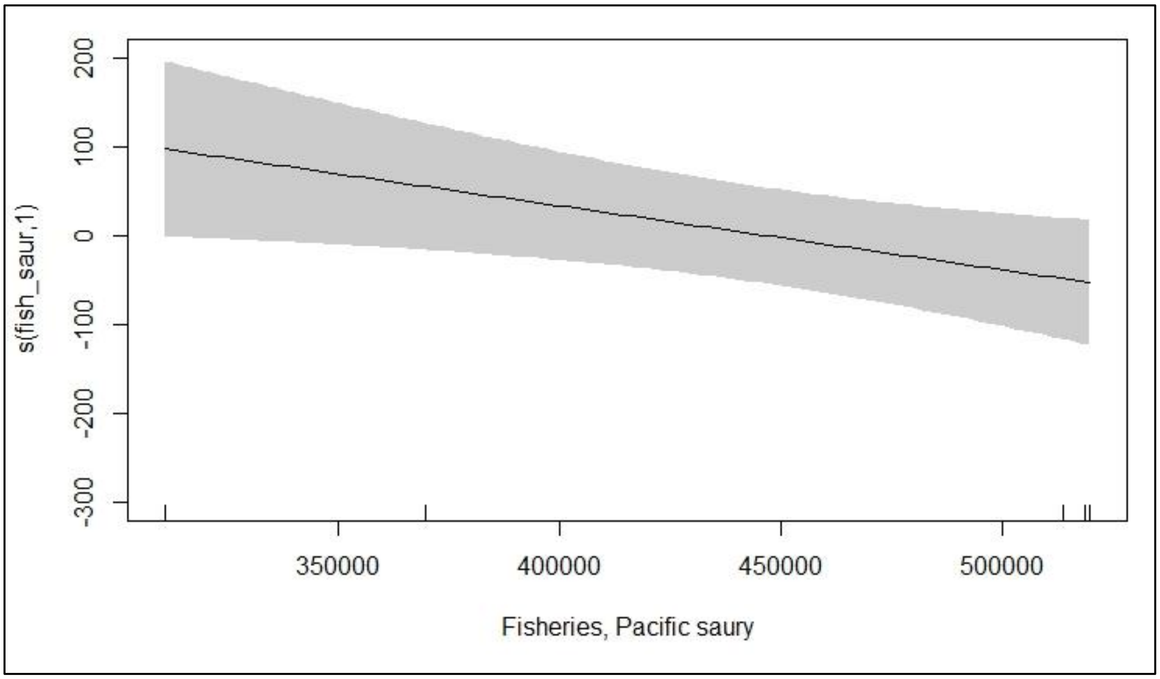


Figure A16. Fisheries, Pacific saury residual GAM spline relationship curve.

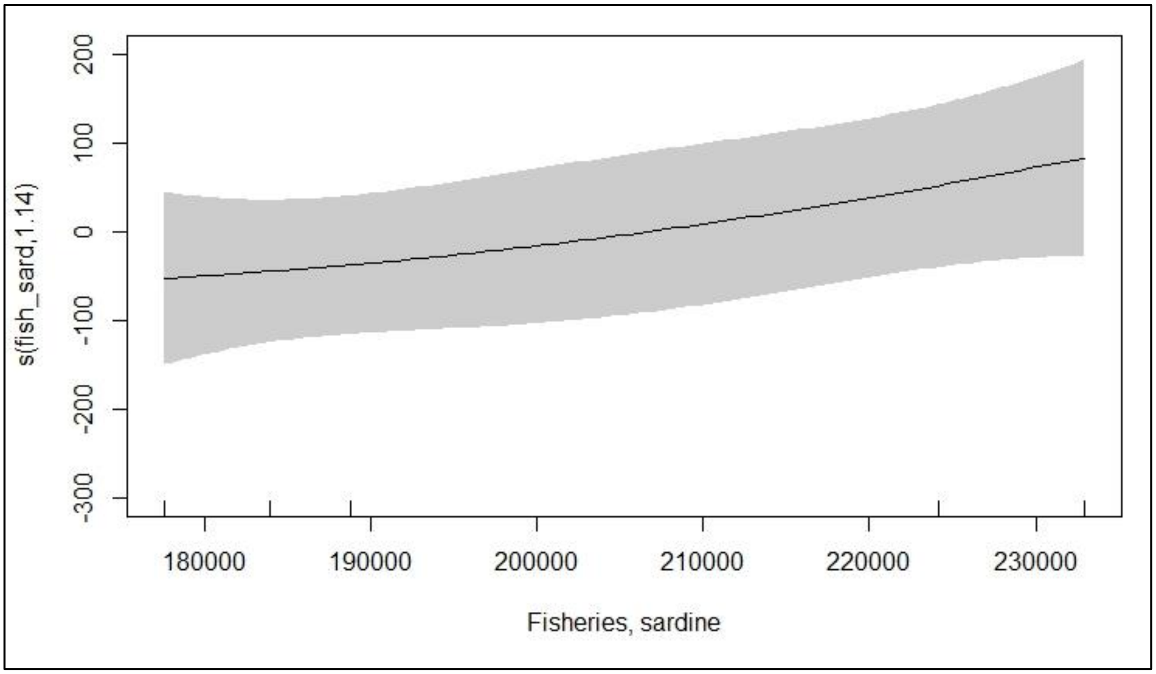


Figure A17. Fisheries, sardine residual GAM spline relationship curve.

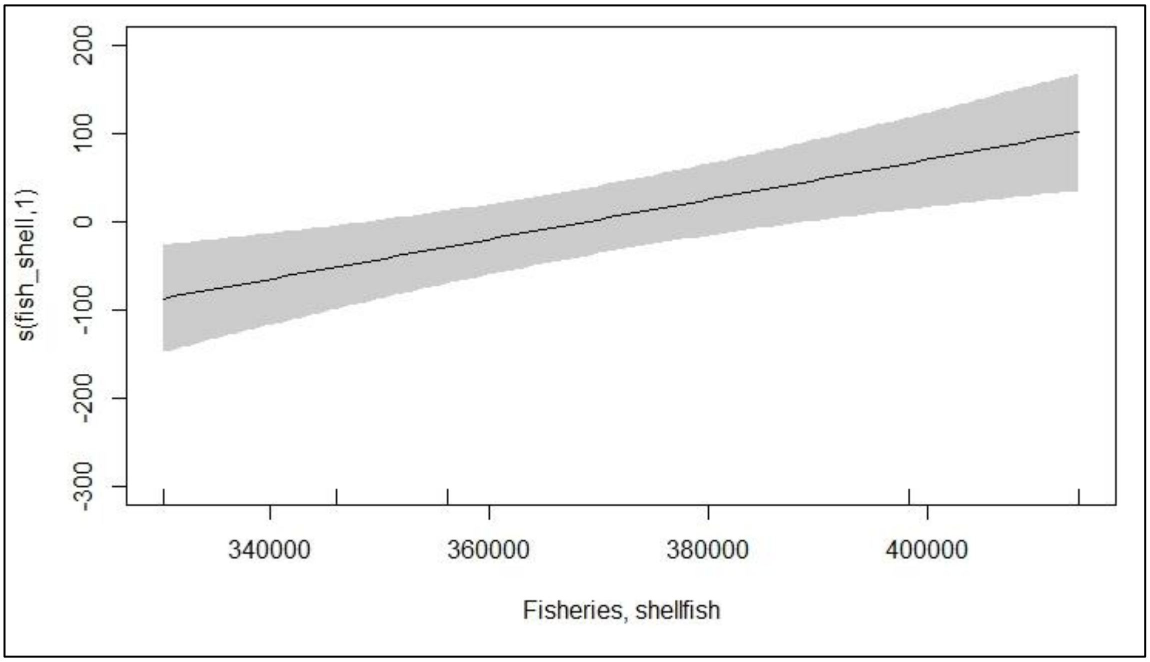


Figure A18. Fisheries, shellfish residual GAM spline relationship curve.

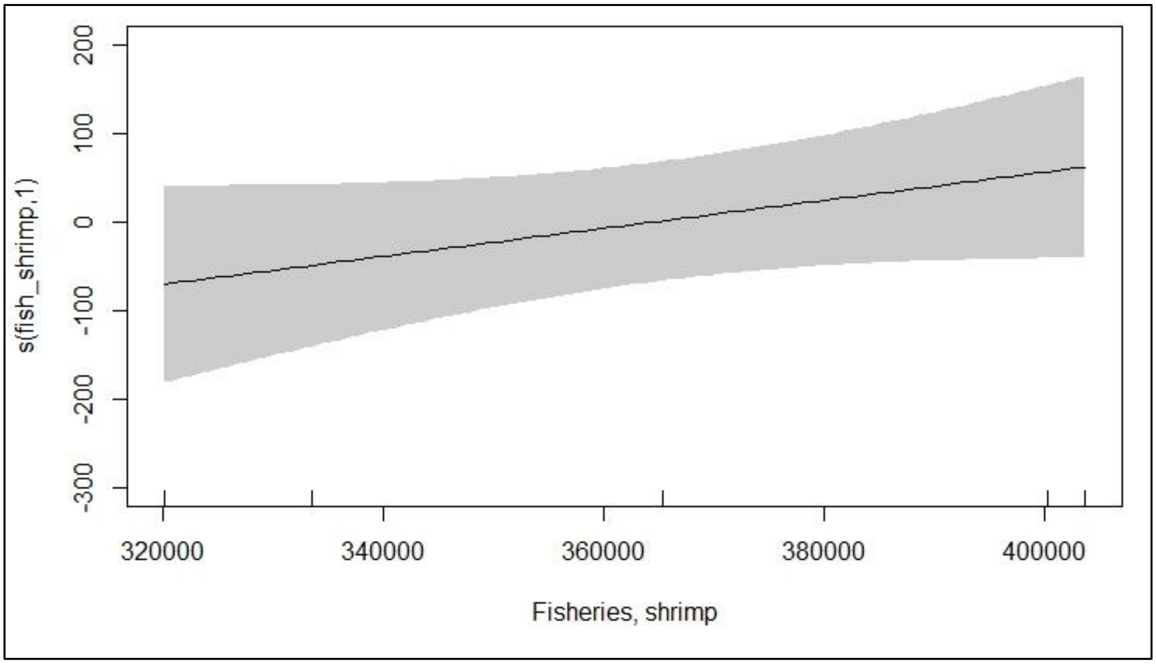


Figure A19. Fisheries, shrimp residual GAM spline relationship curve.

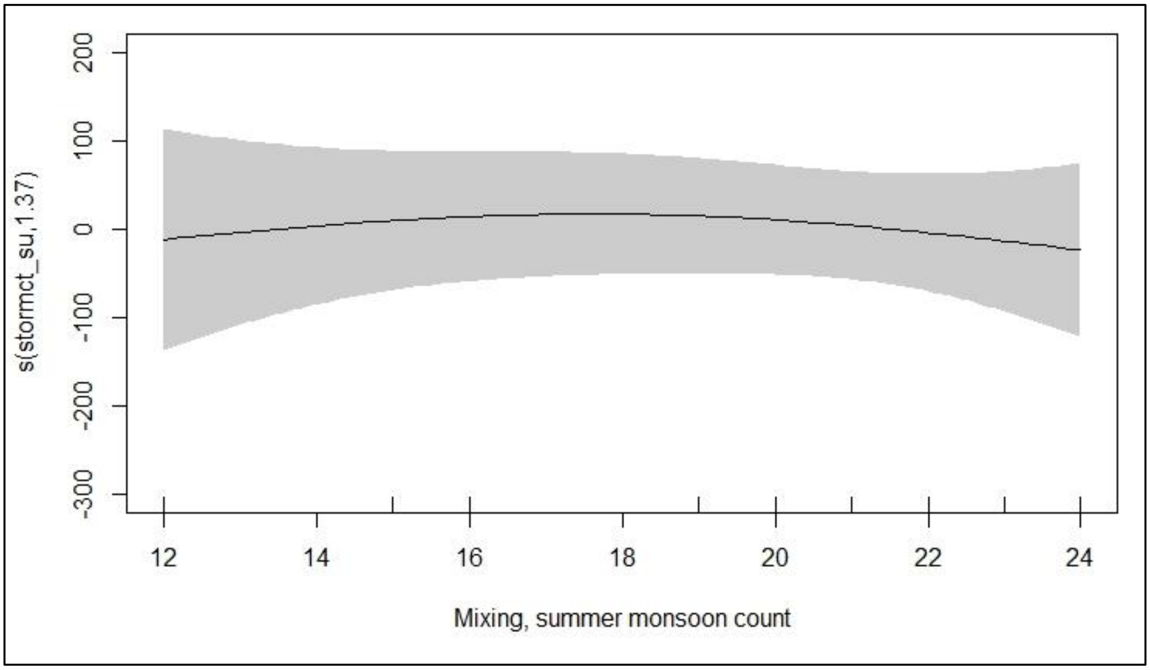


Figure A20. Hypoxia, mixing, storm count residual GAM spline relationship curve.

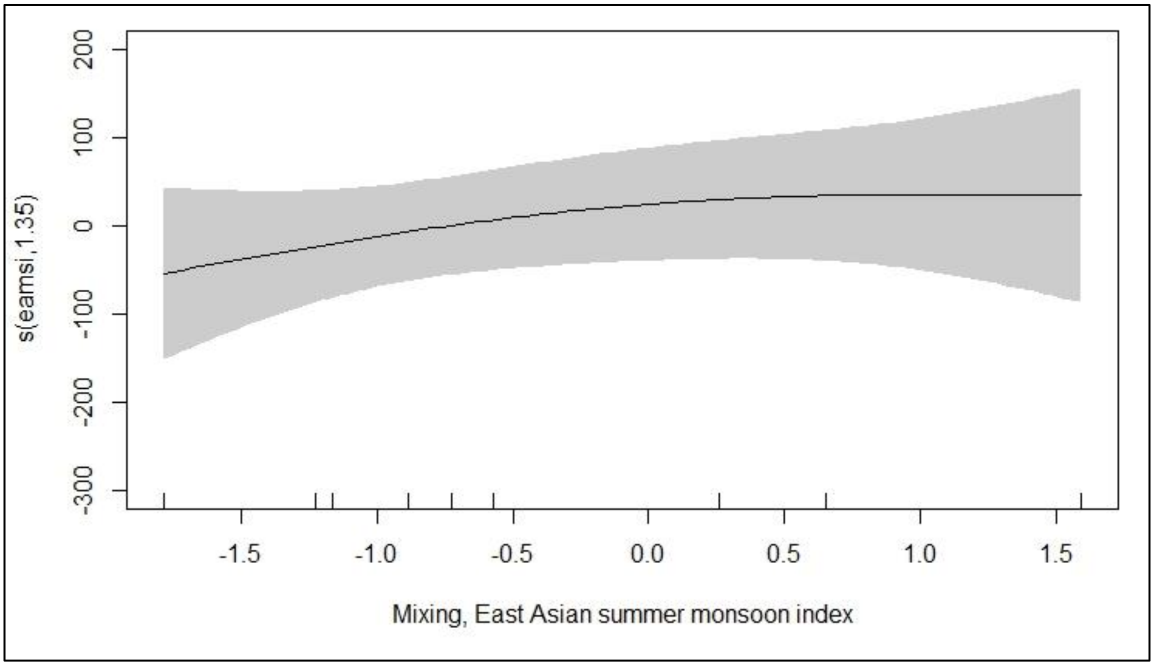


Figure A21. Hypoxia, mixing, storm intensity residual GAM spline relationship curve.

APPENDIX C – Supplemental Linear Regression Figures

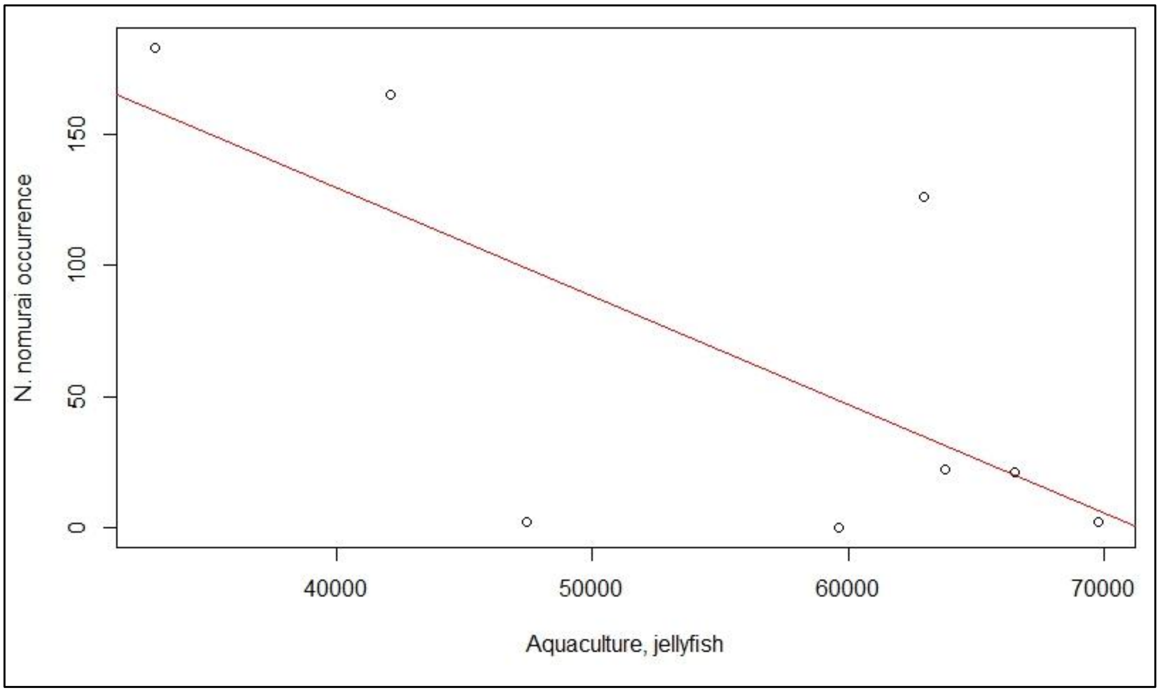


Figure A22. Aquaculture, jellyfish production linear regression.

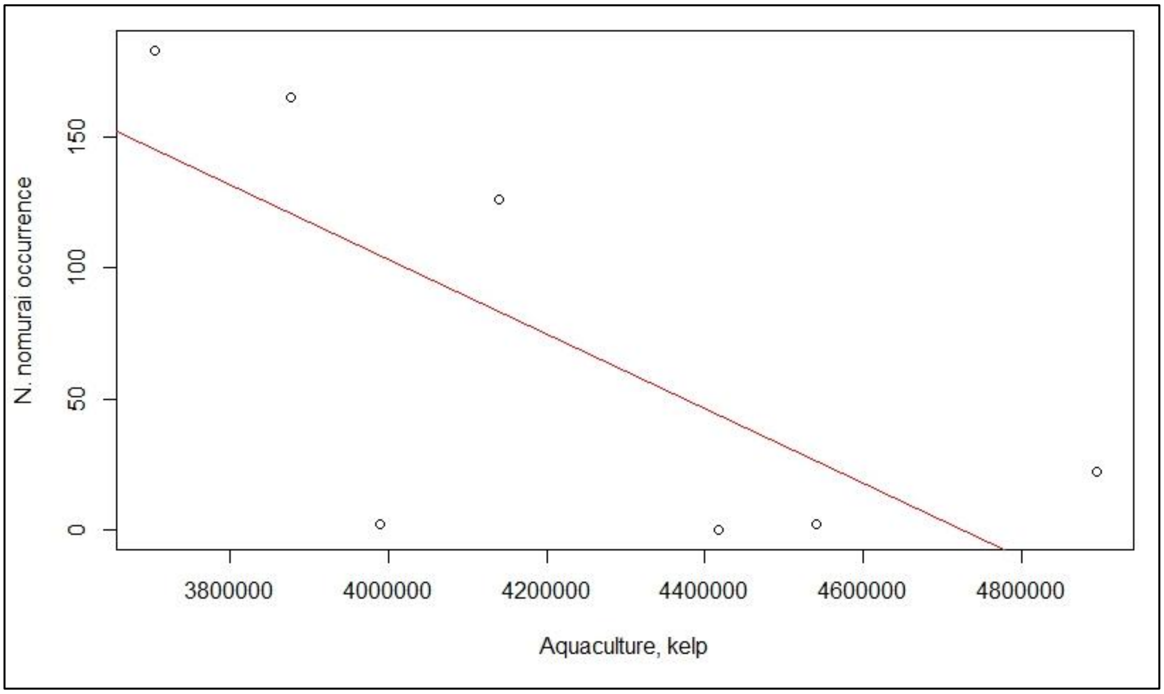


Figure A23. Aquaculture, kelp production linear regression.

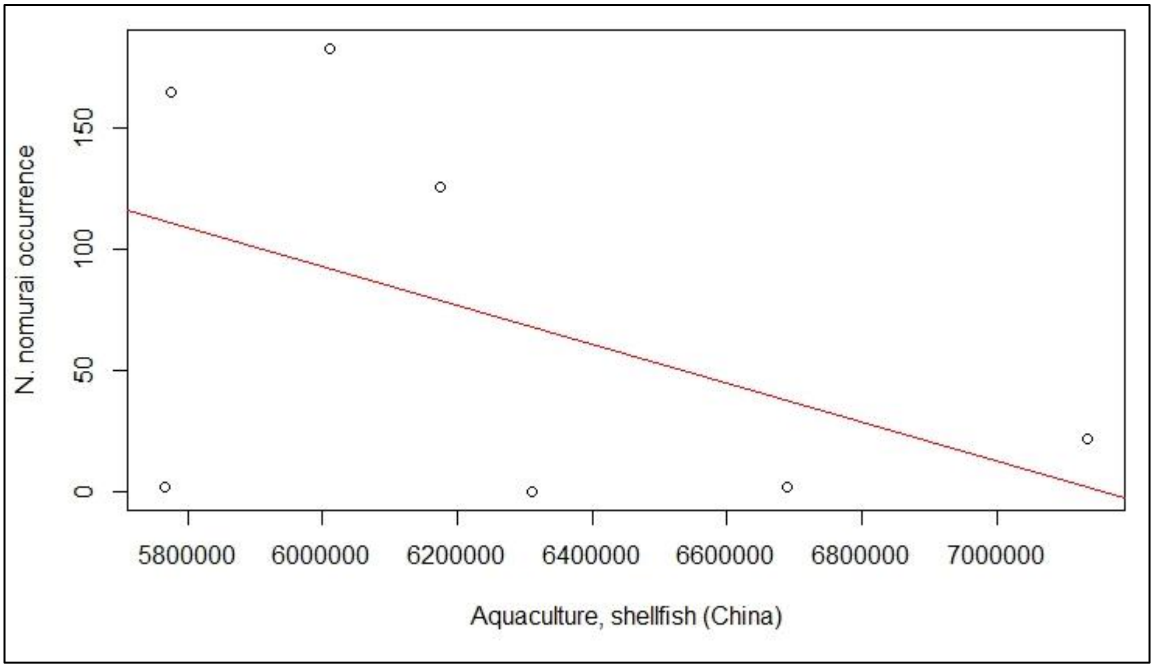


Figure A24. Aquaculture, shellfish production linear regression.

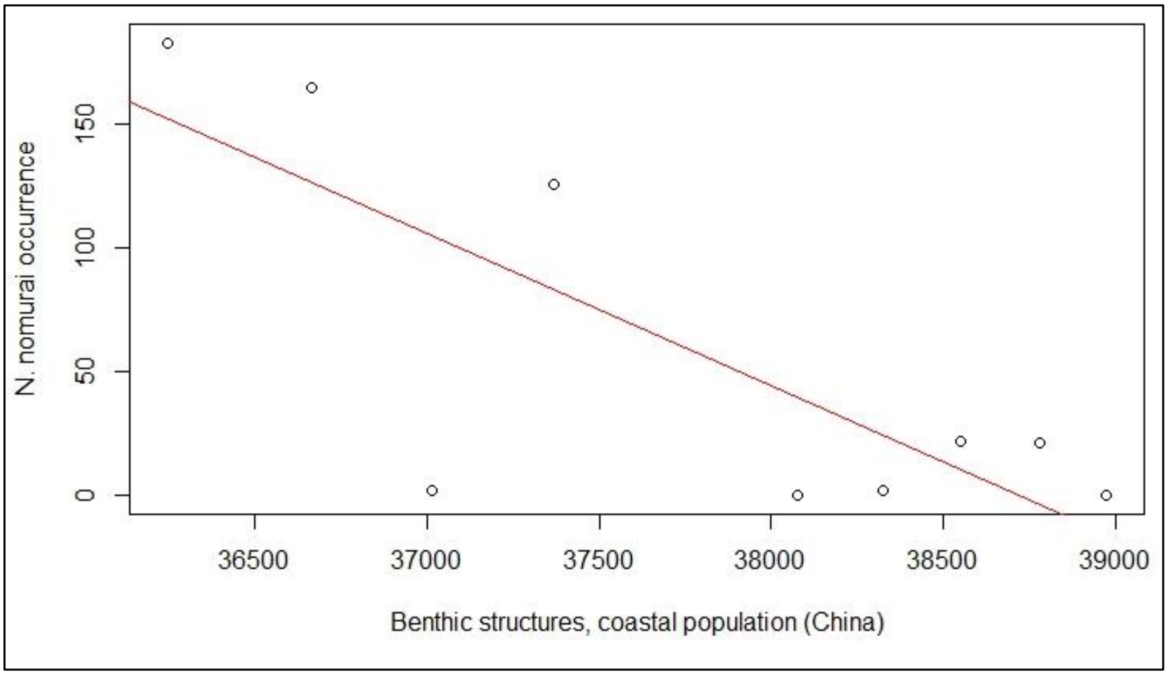


Figure A25. Benthic structures, coastal population linear regression.

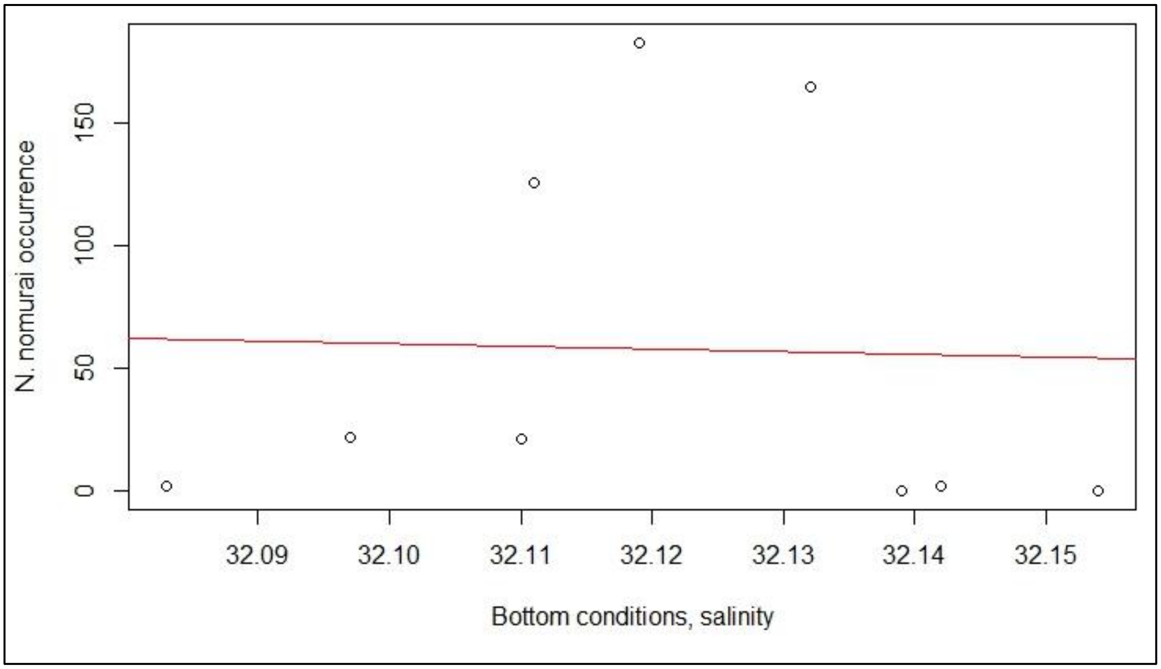


Figure A26. Bottom conditions, salinity linear regression.

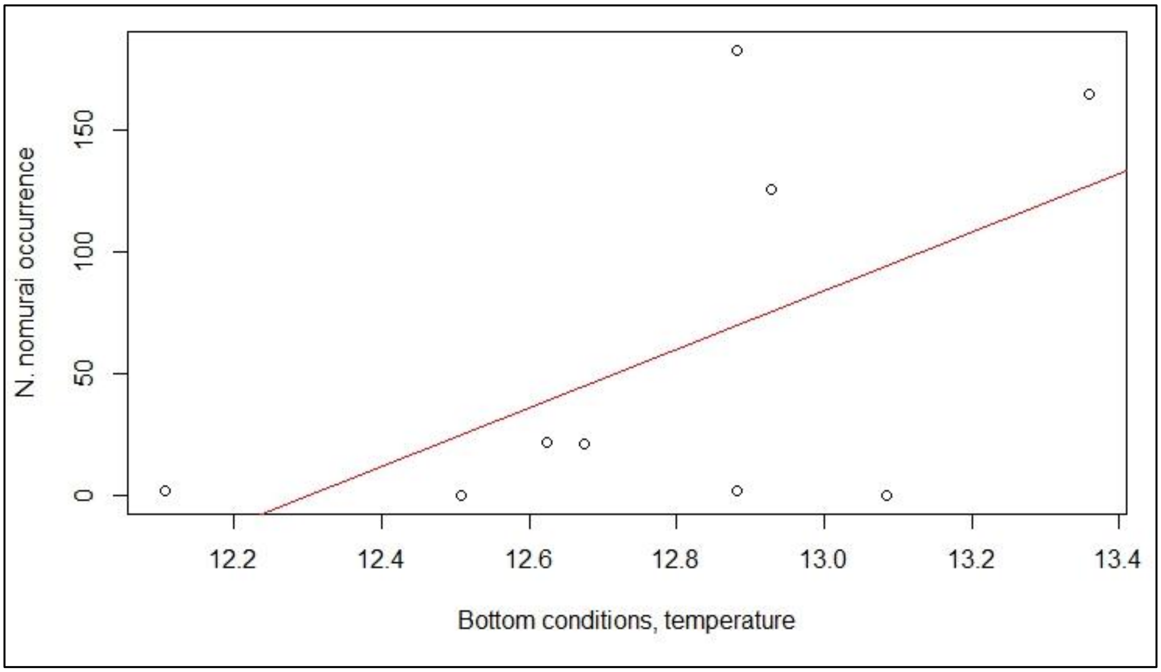


Figure A27. Bottom conditions, temperature linear regression.

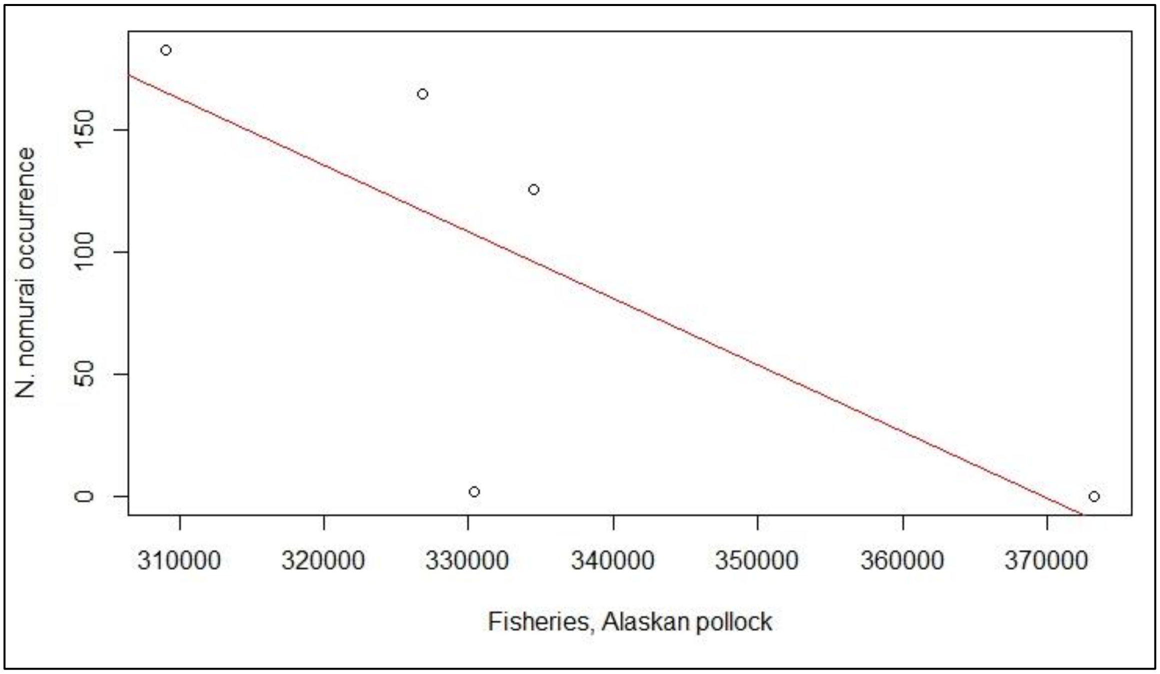


Figure A28. Fisheries, Alaska pollock catch linear regression.

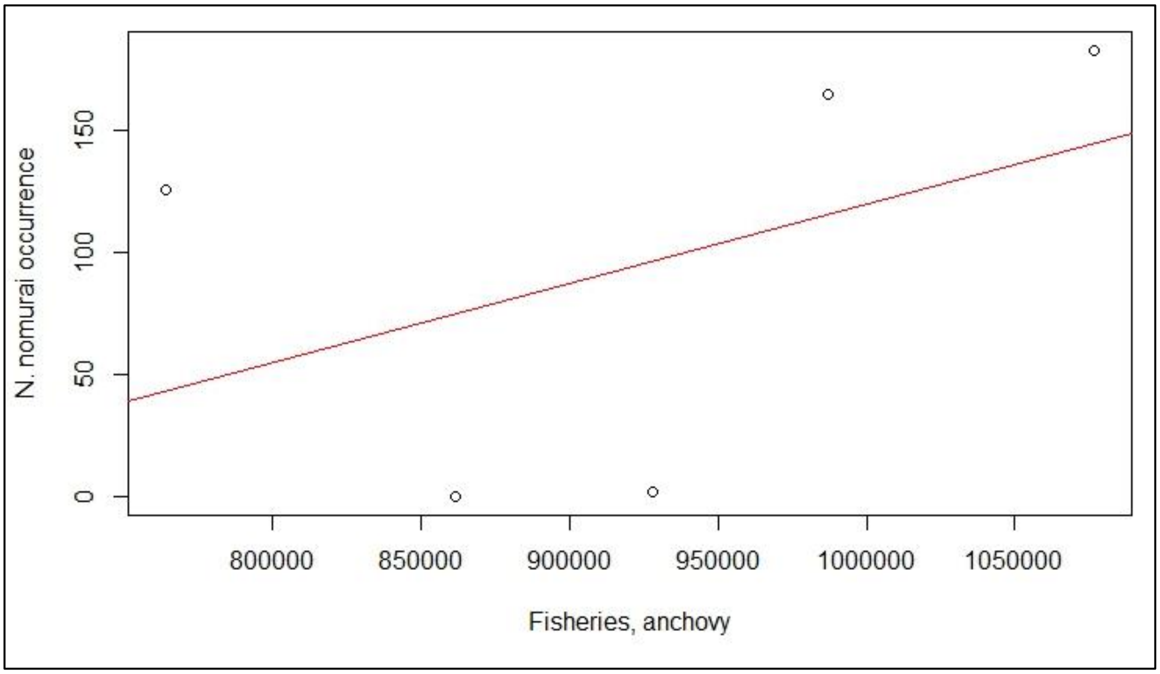


Figure A29. Fisheries, anchovy catch linear regression.

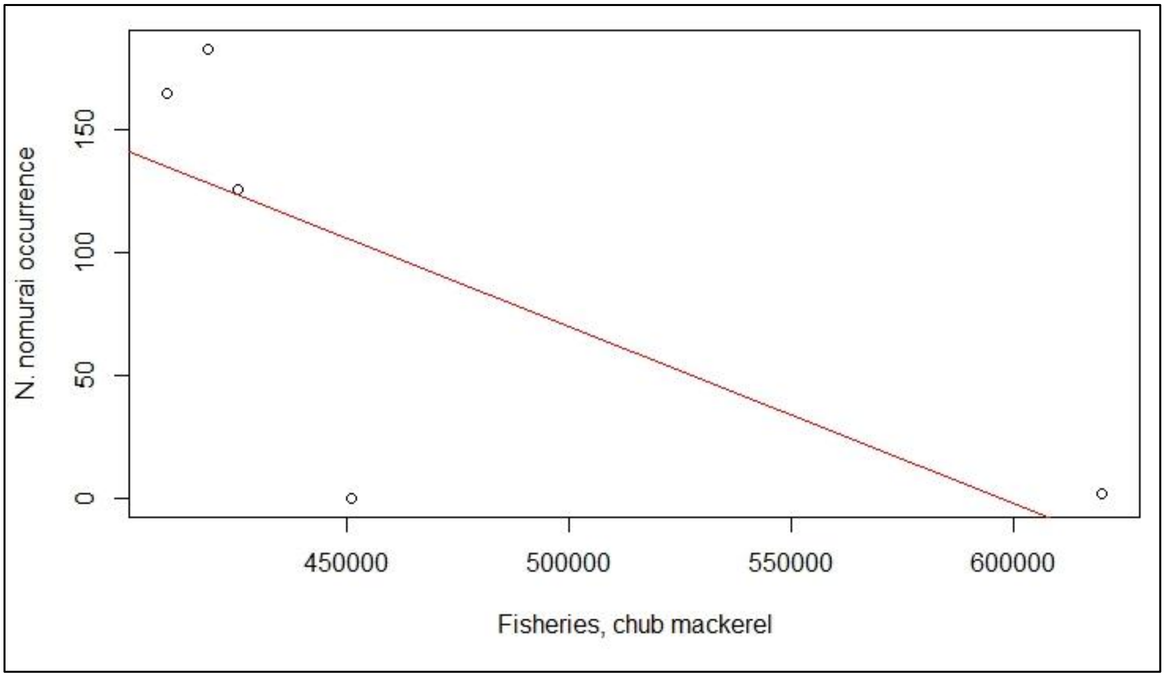


Figure A30. Fisheries, chub mackerel catch linear regression.

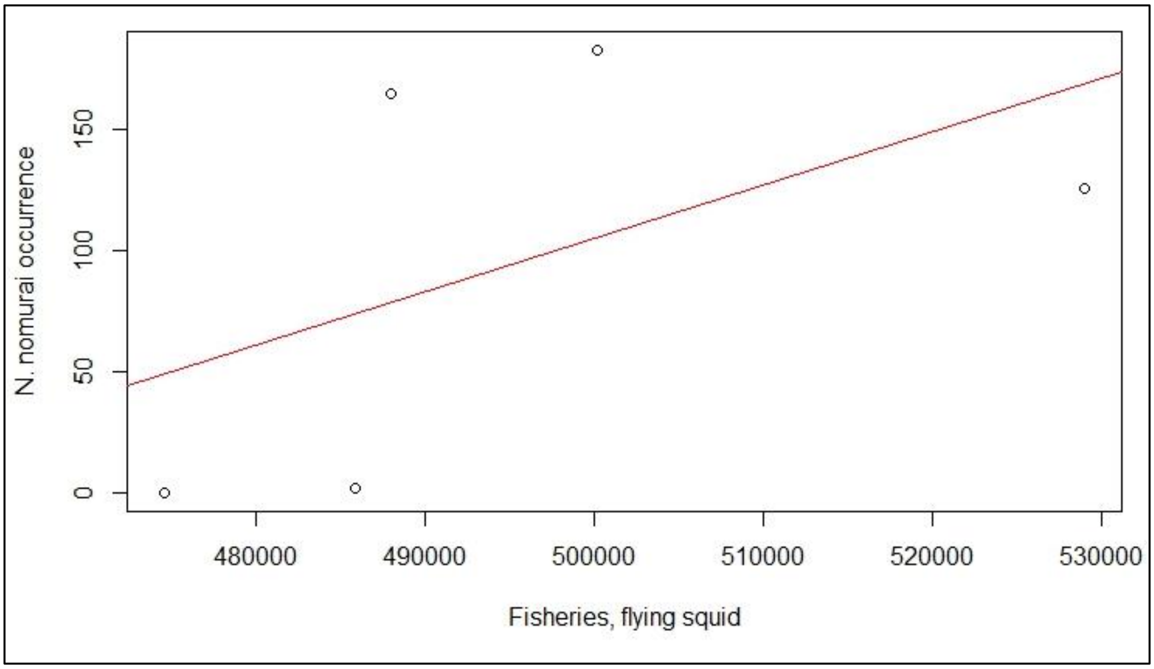


Figure A31. Fisheries, flying squid catch linear regression.

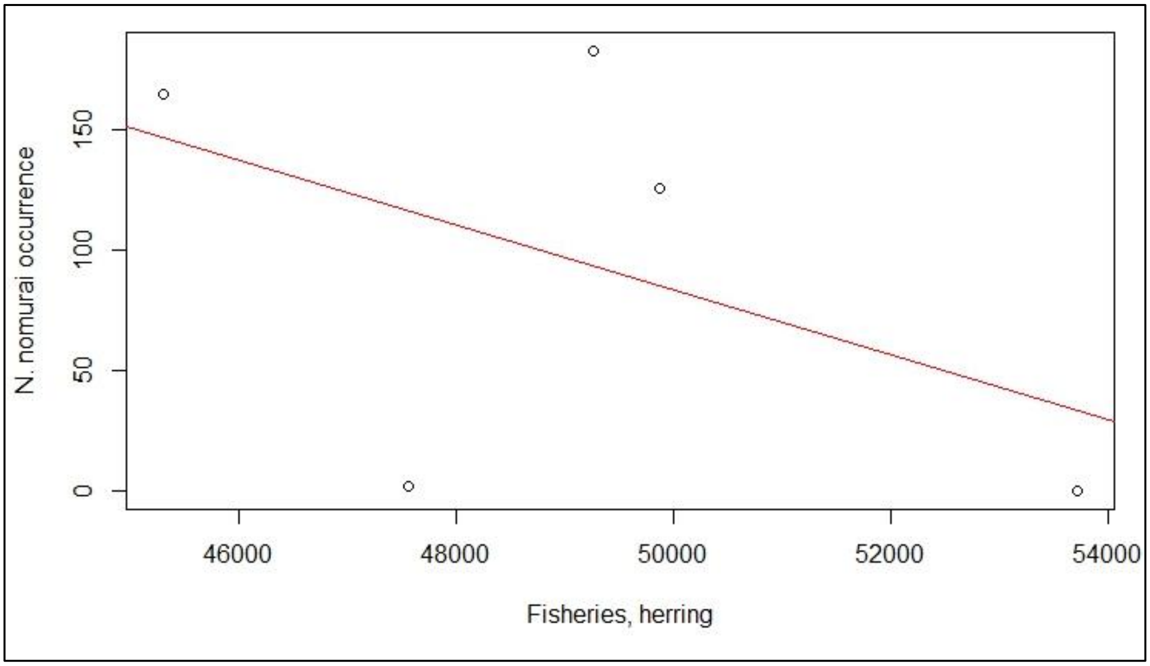


Figure A32. Fisheries, herring catch linear regression.

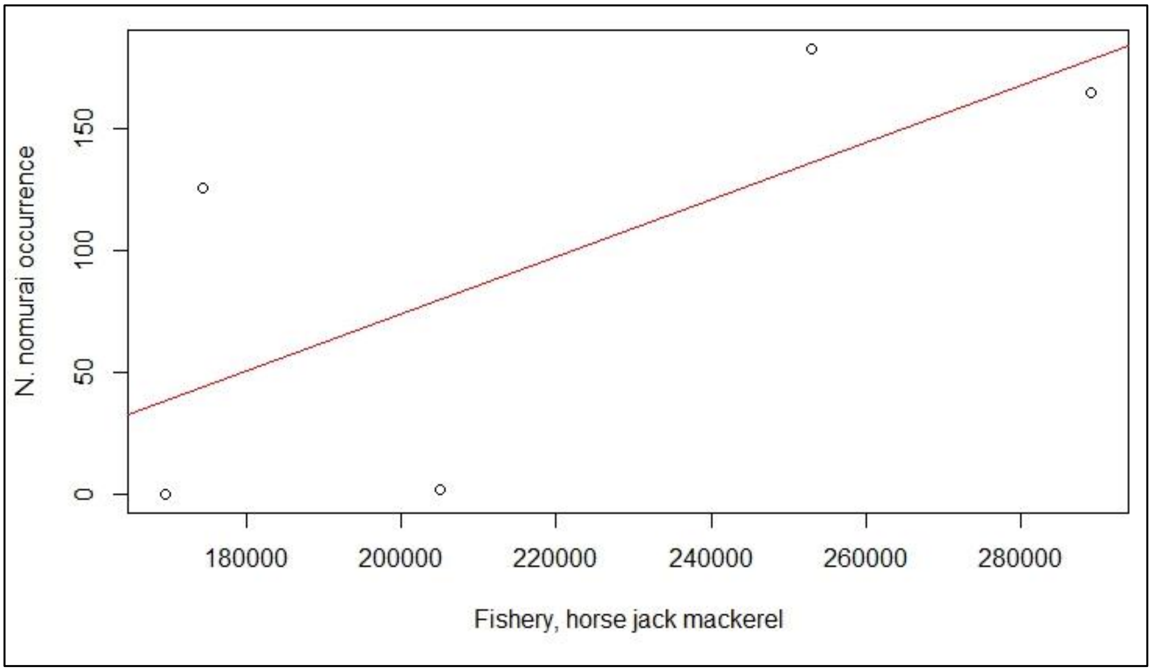


Figure A33. Fisheries, horse jack mackerel catch linear regression.

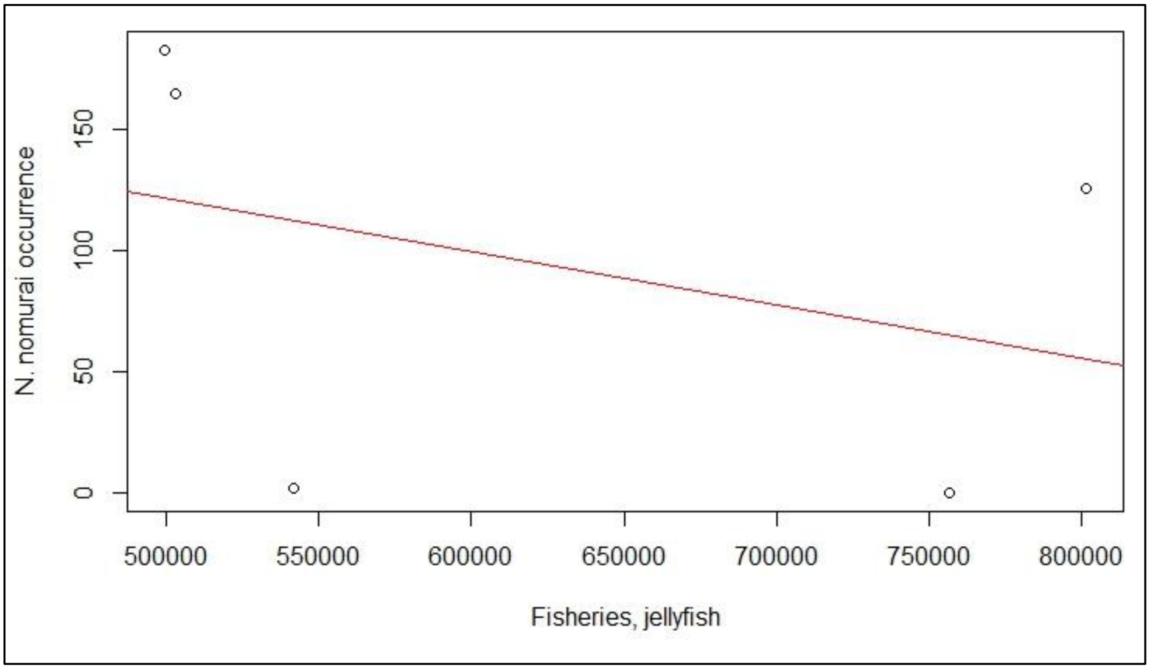


Figure A34. Fisheries, jellyfish catch linear regression.

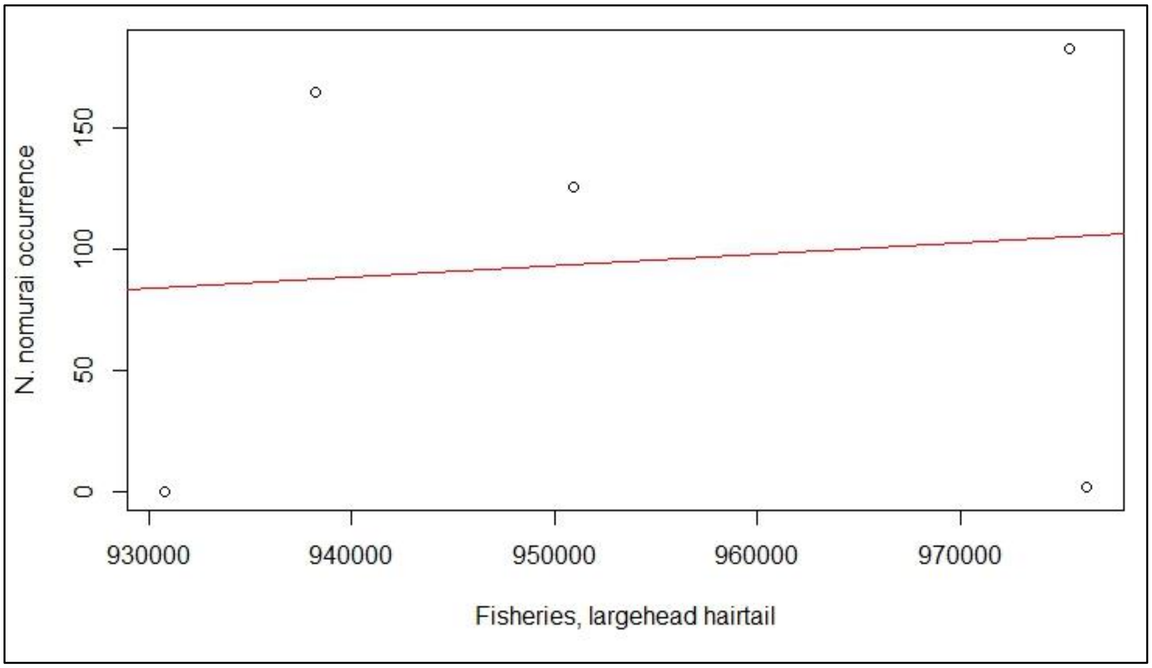


Figure A35. Fisheries, largehead hairtail catch linear regression.

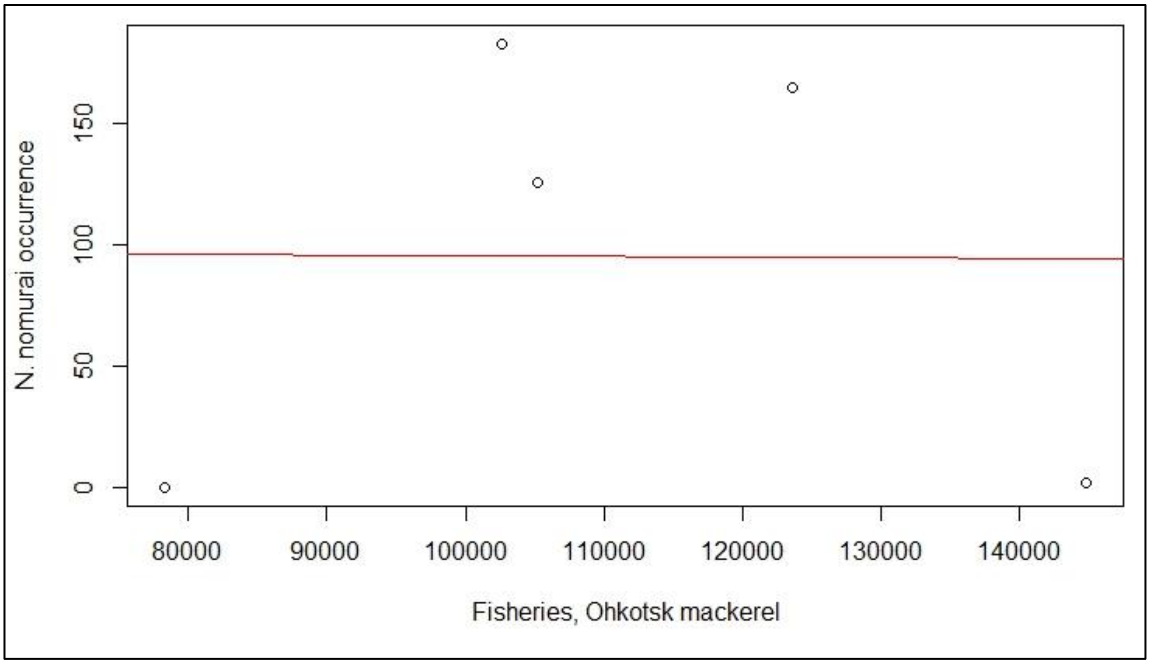


Figure A36. Fisheries, Okhotsk mackerel catch linear regression.

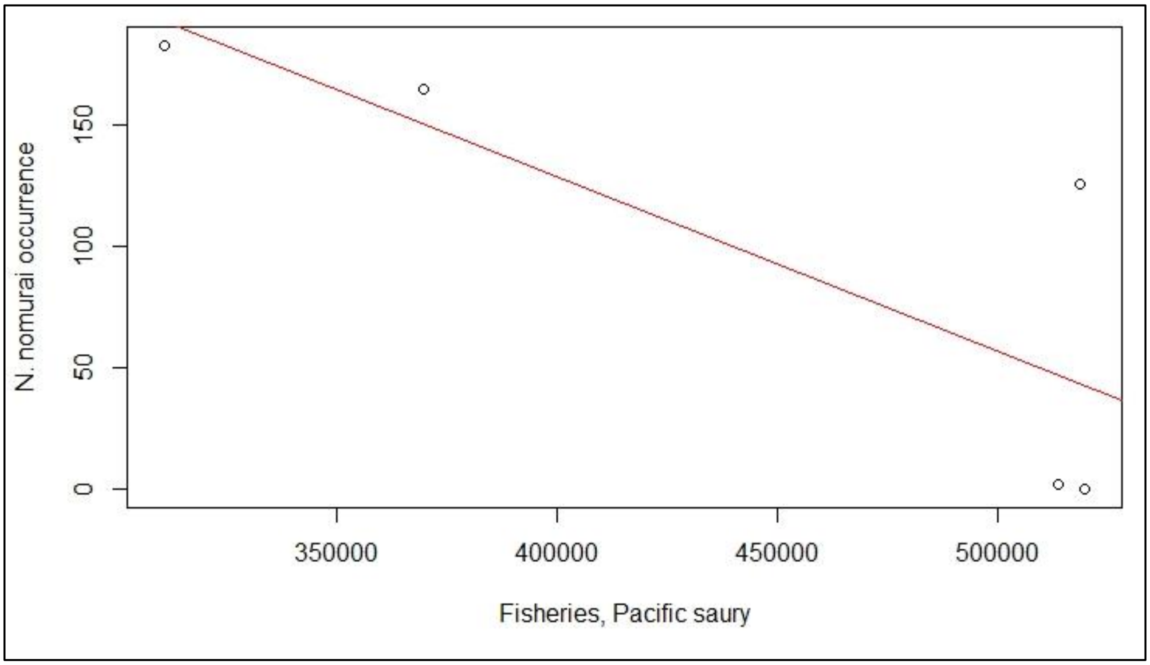


Figure A37. Fisheries, Pacific saury catch linear regression.

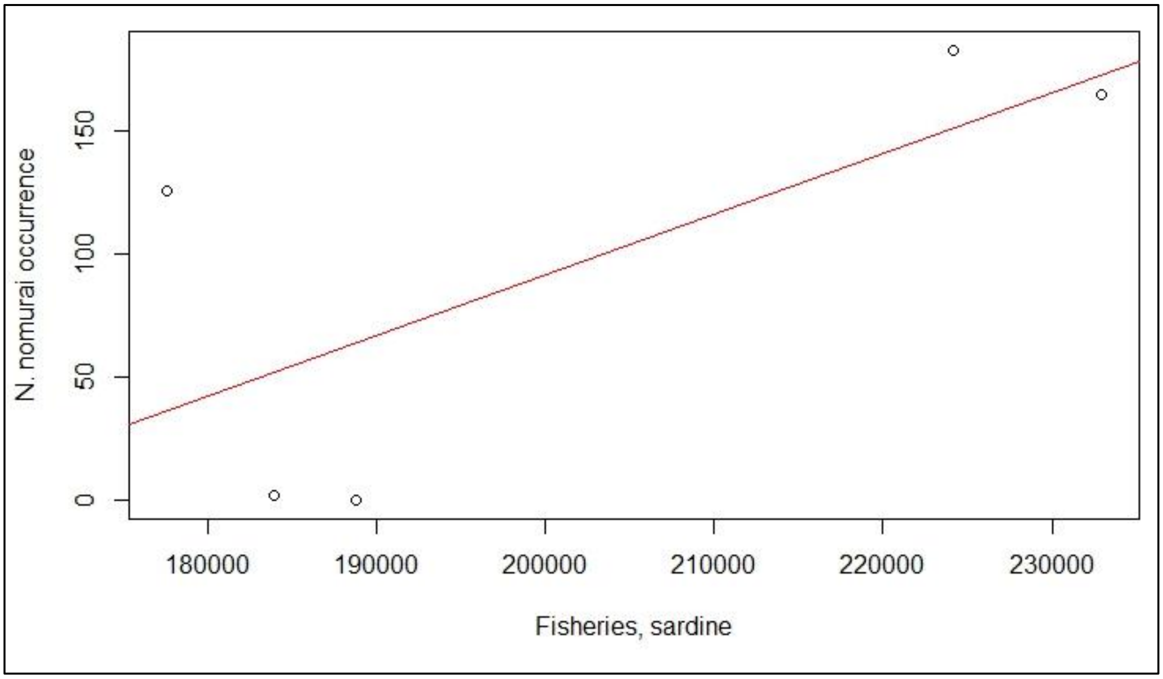


Figure A38. Fisheries, sardine catch linear regression.

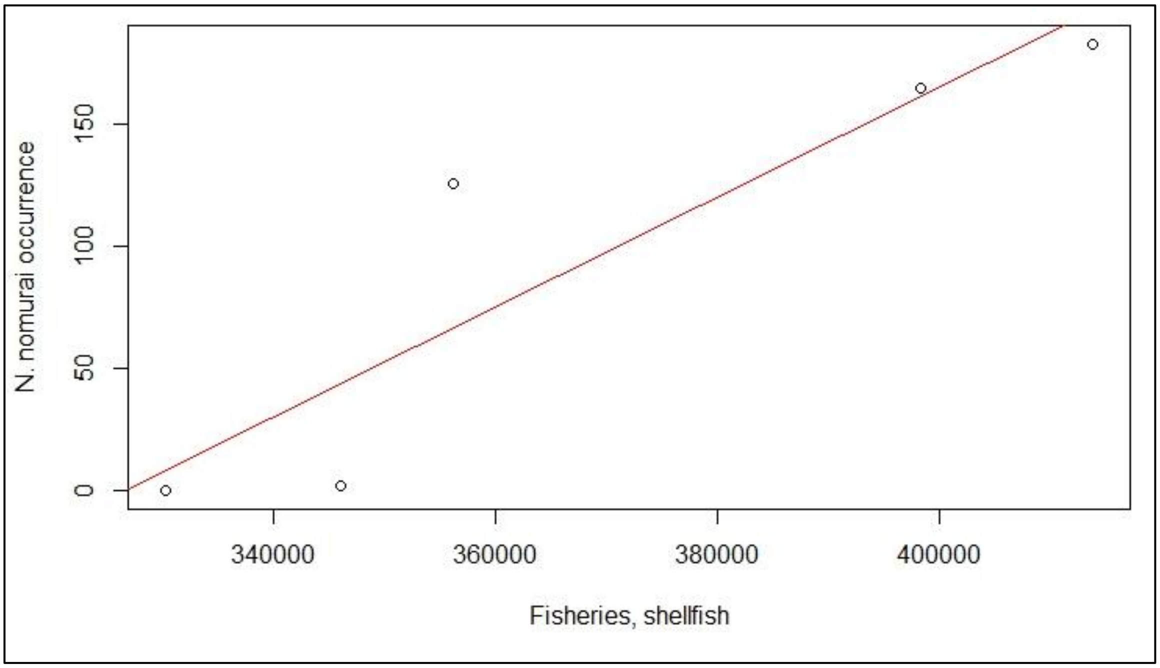


Figure A39. Fisheries, shellfish catch linear regression.

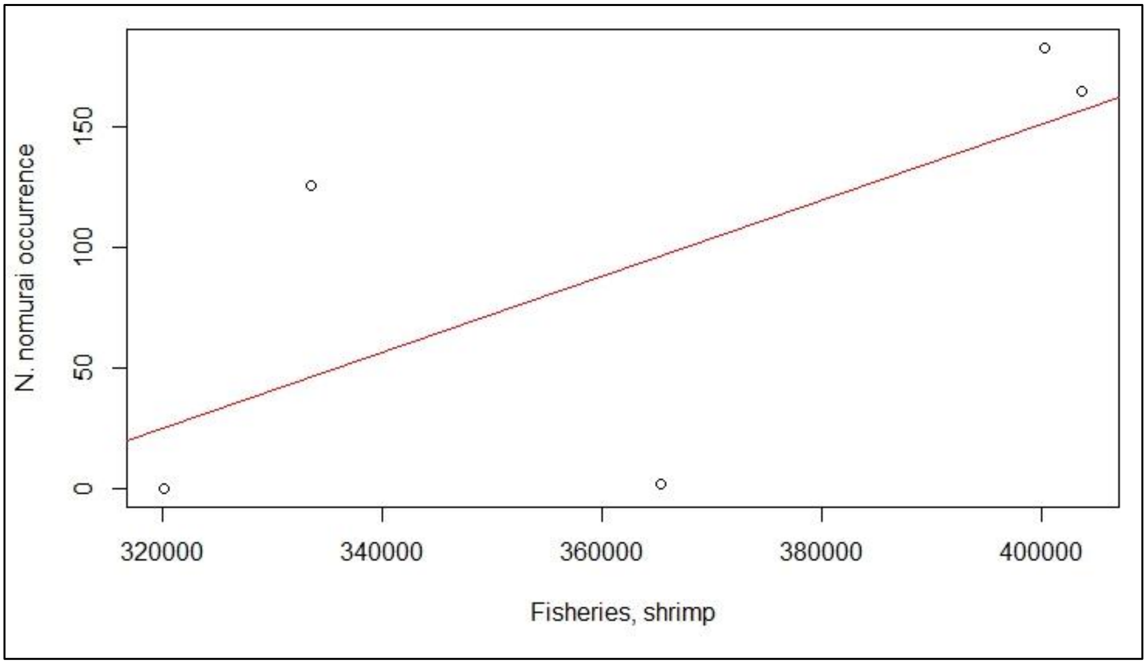


Figure A40. Fisheries, shrimp catch linear regression.

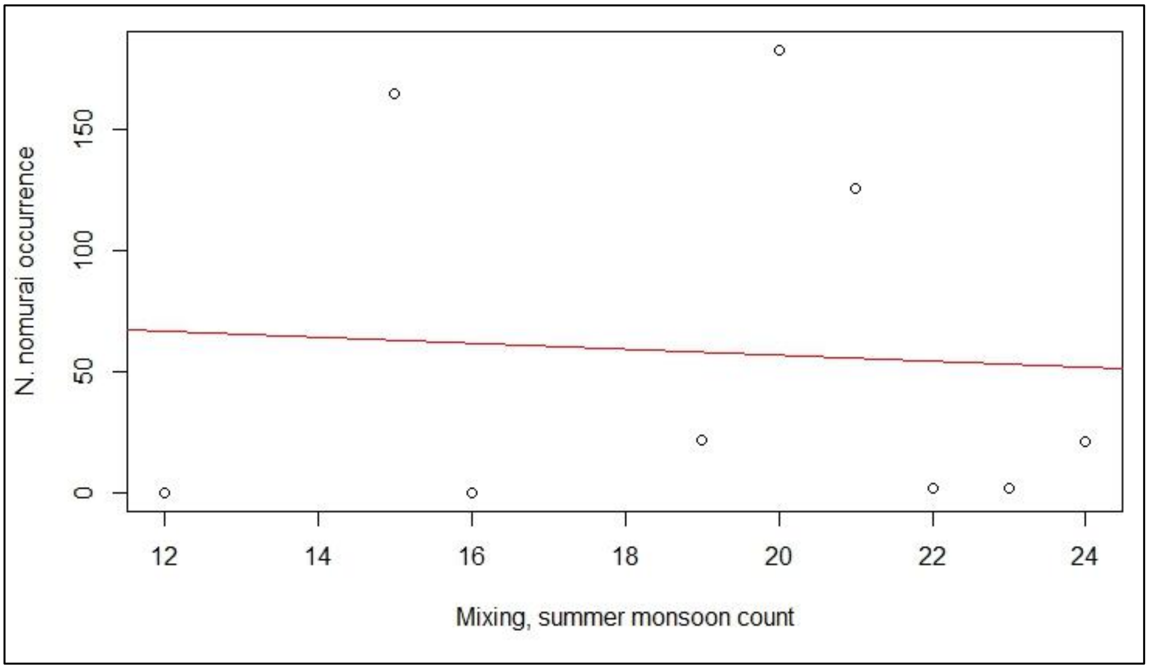


Figure A41. Hypoxia, mixing, storm count linear regression.

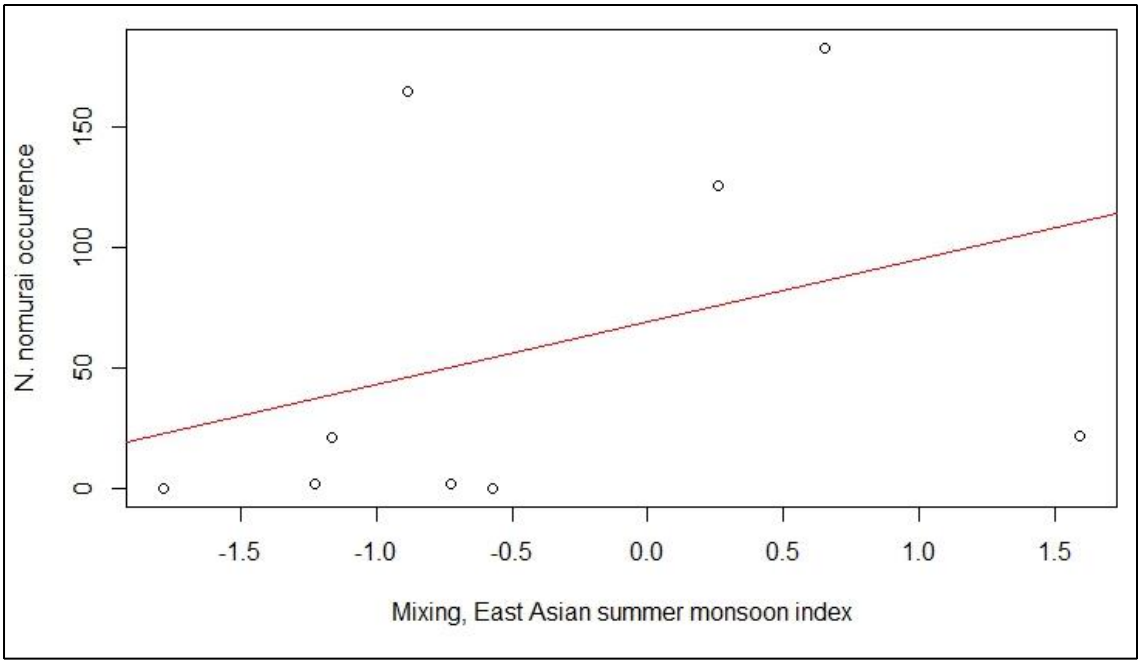


Figure A42. Hypoxia, mixing, storm intensity linear regression.

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