Are Jellyfish Populations Increasing Worldwide (and Why?)

By

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Dedication

To Matthew, Lance Arnold, and Linda Childress

For being their when I needed an ear,

introducing me to the ocean,

and for showing me that I can accomplish anything

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Abstract:

Fishing, nutrient pollution, climate variation, and temperature have significant impacts on marine ecosystems. Due to their life history strategies gelatinous zooplankton (or 'jellyfish') may benefit from all four factors, as they likely thrive in nutrient-rich warm waters with reduced fish predators and competitors. Hence jellyfish may serve as indicators of contemporary changes occurring within marine ecosystems. Global increases in jellyfish have been hypothesized by many authors, but not yet been consistently documented, nor have potentially important jellyfish predators been identified. Also there is little consensus as to what caused observed jellyfish blooms in places like the Black Sea, North Sea, Benguela upwelling, or the Bering Sea. Here I present the first global collation of jellyfish abundance records, along with measures of climatic and temperature variation, nutrient concentrations, and fish abundance, as compiled from literature sources. I also review our current knowledge of jellyfish predators which may be involved in trophic control of jellyfish populations. I use correlation analysis to identify patterns in the observed abundance trends among jellyfish, climate, temperature, nutrients, and fisheries. Results of a literature search documenting jellyfish predators found previously overlooked fish species to be important in controlling jellyfish population increase. Likewise, invertebrate and bird predators may be more common than previously thought. My time series analysis found consistent jellyfish population increases to occur in ten out of thirteen systems for which there were data. There was no evidence for any single factor explaining population increases across regions Nutrient supply was most strongly correlated to jellyfish population increase, the first time this relationship has been shown across ecosystems. Forage fish competing for food resources, predators, climate variability and temperature also correlated with jellyfish abundance, although not in a very consistent manner. I conclude that jellyfish increases appear to be common, although not universal, across a wide range of ecosystems. Although nutrient effects were particular strong, it is likely that synergistic effects among multiple environmental variables act to control jellyfish populations.

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Introduction

The term 'jellyfish' or more correctly 'gelatinous zooplankton' refers to a taxonomically diverse group of plankton with large, translucent bodies. So far, roughly 200 species of marine Scyphozoa, 700 species of Hydromedusae, 15 species Cubozoa, 12 genera of order Salpidae, and 150 species of ctenophores have been identified (Bouillon, 1999; Mianzan 1999; Mianzan and Cornelius, 1999). As these organisms are sometimes not easily sampled and identified, their importance in marine ecosystems has often been overlooked. Yet we know now that Hydrozoans, Scyphozoans, Cubozoans, and Ctenophores are important predators in marine food webs that are competing with forage fish species for resources, while salp populations are herbivores which through high rates of feeding play a dominant role in cycling phytoplankton carbon (Mills, 2001).

Though previously viewed as 'dead ends' in the marine food web, the importance of gelatinous zooplankton as prey species has begun to be investigated yielding surprising results (Harrison, 1984; Arai, 2005). In addition jellyfish are believed to serve as a refuge from predation for many juvenile fish species including the commercial important Walleye Pollock (*Theragra chalcogramma*), and may also serve as `survival food' for marine species when the abundance of other prey is low (Mainzan, 2001; Brodeur *et al.*, 2002)

Over the past three decades variation in population size of gelatinous zooplankton has gained increasing scientific interest. (Mills, 1995; Brodeur, *et al.,* 2002; Atrill, *et al.,* 2007). Though many studies have observed local increases in gelatinous zooplankton population abundance, few have attempted to quantify potential

causes of these increases, and predict effects of such changes on ecosystems in the future. The current literature focuses on four hypotheses that may explain gelatinous zooplankton increases including: climate fluctuation; temperature increase; nutrient pollution; and impacts of the fishing (Mills, 1995; Arai, 2001; Purcell, 2005). Local increases in gelatinous zooplankton population abundance occur in two forms (Mills, 2001). In the majority of ecosystems presented in the current study species have always been present in the ecosystem, but in recent times population sizes have dramatically increased ("population explosions"). In other ecosystems such as the Black Sea and Azov Sea, for example, jellyfish population increases have primarily occurred in non-indigenous species introduced to the ecosystem by human activity ("population invasions").

For the purpose of this thesis, the term jellyfish will be used to represent all marine gelatinous zooplankton groups including: the medusa forms of Hydrozoa, Cubozoa, and Scyphozoa of the phylum Cnidaria, *Salpa thompsoni* of the family Salpidae, and various members of the phylum Ctenophora. These functional groups can be considered under the collective name jellyfish as they all have similar life history strategies and bloom characteristics, and interact with their environment in similar ways quickly removing large amounts of food resources from the ecosystems in which they live (Loeb *et al.*, 1997; Mills, 2001; Purcell and Decker, 2005).

Life history of jellyfish

The majority of Hydrozoan and Scyphozoan and all Cubozoan species occur in two life stages. A polyp (sessile stage) reproduces via asexual budding to create a medusa (planktonic stage) which then undergoes sexual reproduction to produce polyps (Arai, 1997; Bouillon, 1999). The reproductive cycle of these groups is dependent on latitude with temperate species often reproducing annually during spring or fall, and tropical forms reproducing year round (Arai, 1997; Purcell, 2007).

The aforementioned life history characteristics allow Hydrozoa, Cubozoa, and Scyphozoa to reproduce and grow rapidly and to form large blooms (Purcell, 2007). In order to truly understand population abundance trends of most of these species it is crucial to consider both their sessile polyp and planktonic medusa life history phases (Mills, 2001). Due to near absence of information on the population dynamics of the polyp phases of all species considered here only the planktonic phases can be considered.

In contrast to the majority of Hydrozoa and Scyphozoa the Hydrozoan order Siphonophora and all members of the phylum Ctenophore do not possess a sessile life history stage (Purcell, 2007). Siphonophores reproduce through asexual and subsequent sexual reproduction of medusa while most Ctenophores are hermaphrodites reproducing via direct development at high rates of fecundity (Mianzan, 1999; Pugh, 1999). Because of these reproductive characteristics Siphonophores and Ctenophores are not constrained to a single generation per year. This allows them to rapidly increase in population size over short time spans (Purcell, 2007).

Members of the Order Salpidae reproduce through a complicated process (Esnal and Daponte, 1999). Solitary oozooids undergo asexual reproduction to form a chain of hermaphroditic blastozooids. These blastozooids separate and then reproduce through sexual reproduction to yield new oozooids. Several features of this reproductive cycle allow salps to increase rapidly in response to periodic food supply. The most notable are: the ability to create hundreds of decedents from a single asexual oozooid; high rates of growth (the highest among metazoans), and short generation times varying from 50 hours to 15 days between reproductive cycles (Esnal and Daponte, 1999).

While the life history characteristics of jellyfish allow them to bloom successfully under favourable environmental conditions the cues leading to reproduction remain to be determined for most species. Current research points to environmental factors including seasonal changes in: food supply, light, salinity, and temperature (Purcell, 2007). Therefore changes in these conditions both naturally and as a result of human influences could lead to changes in the seasonality of jellyfishes' reproductive cycle, increased reproductive capability, increased growth rates, or lengthening the jellyfishes' reproductively active period (Purcell, 2005).

Effects of climate variability

Many jellyfish appear to respond strongly to changes in climate (Lynam *et al.,* 2004; Molinero *et al.,* 2005). As a result of their short generation times (often ≤ 1 per year) jellyfish are believed to respond to climate forcing without a time lag, allowing

these species to adjust rapidly, and also to serve a potentially sensitive indicators of environmental change (Lynam e*t al.*, 2005).

Changes in climate are related to variety of oceanographic processes including: air pressure, wind, currents, air temperature, and ocean temperature, and therefore have a potentially significant influence the pelagic environment (Lynam, 2004; Purcell, 2007). Often these complex changes in climatic forcing are tracked using a synthetic index. For example, the North Atlantic Oscillation (NAO) index is a measure of the difference in pressure between the Icelandic low and Azores High (Hurell, 1995). Positive values for the NAO index correspond to the "high" phase, characterized by strong Westerlies leading to warmer than average winters and warm water in Northern Europe, while negative values correspond to the "low" phase characterized by the reverse pattern (Lynam *et al.*, 2004).

Lynam *et al.,* (2004) investigated ways the NAO could influence both fish and jellyfish abundances in the North Sea, however data were insufficient to determine the exact mechanisms through which climate effects jellyfish populations. Two scenarios are presented of how NAO related mechanisms could positively impact jellyfish populations. First NAO may directly impact species through altering dispersal of juvenile medusa aggregations through changes in ocean temperature, salinity, light availability, and current strength. Secondly the NAO could have indirect effects on jellyfish by altering the period of the spring phytoplankton bloom leading to increased secondary production, or by increasing the abundance of zooplankton and ichthyoplankton in the water column both factors which lead to increased food availability for jellyfish (Lynam *et al.,* 2004).

Another prominent climate index, the Pacific Decadal Oscillation (PDO) index is a fairly recently discovered phenomenon and is described as a long-lived El Niño-like pattern acting on time scales of 20-30 years (Mantua *et al.*, 1997). The PDO is primarily recognized for its impacts on temperature leading to alternating periods of warm and cold air over Alaska, the West Coast of Canada, and the North-western Contiguous United States. The PDO is also known to have significant impacts on coastal productivity in these regions, as well as contribute to variation in regional snow pack, sea ice, and stream flow (Mantua *et al.,* 1997).

The PDO further appears to impact atmospheric sea level pressure leading to lower or higher than average sea levels, as well as effecting wind intensity and oceanographic processes (Brodeur *et al.,* 1999). Variability in storm activity and changes in the timing and extent of regional sea ice appear to strongly impact jellyfish in the North Pacific through influencing the timing and size of phytoplankton blooms (Anderson and Piatt, 1999; Brodeur *et al.*, 1999).

Increases in primary productivity are indirectly related to jellyfish population size as increases the size and occurrence of phytoplankton blooms leads to larger zooplankton abundances and thus increased food availability. In addition as a primary food item for salps, impacts on phytoplankton abundance resulting from variation in sea ice and storm conditions would have a significant impact on salp populations (Loeb *et al.*, 1997). Due to the impacts of the PDO on temperature and primary productivity, and its potential impact on oceanographic processes, it is feasible that the PDO could impact continental shelf ecosystems on which it acts in similar ways to the NAO as observed by Lynam (2004).

Effects of temperature

The long-term trend in global temperature is slowly increasing, with mean air temperature showing a 0.74°C [0.56°C to 0.92°C] increase over the past 100 years (IPCC, 2007). An investigation by Levitus *et al.,* (2000) has also highlighted this trend in the world oceans showing a substantial increase in sea temperature (0-3000m depth) in all ocean basins. Temperature increases have profound effects on marine ecosystems. Species rely on consistent temperatures to maintain their physiology as changes in temperature directly affect metabolism, growth, and development rates of many species (Hughs, 2000). Temperature can also alter the seasonality and length of the reproductive active period for a number of species in addition to having strong impacts on the characteristics and timing of phytoplankton blooms (Hughs, 2000; Lynam *et al.*, 2004; Purcell 2005; Purcell, 2007).

Changes in temperature appear to be well tolerated by jellyfish and in many cases could lead to increases in their ability to thrive (Purcell, 2007). Increased temperature can lead to stratification and hence increased stability in the water column. This has been proposed as an explanation for increased jellyfish growth and survival in the Bering Sea, for example (Brodeur, 2002). Purcell (2005) examined effects of increased temperature and salinity on *Aurelia labiata*. Results showed increased production, and early initiation of production of ephyrae at warm temperatures. Increasing temperature has also been correlated to increased abundances of both ctenophores and jellyfish in the wild, to increased asexual reproduction in Scyphozoans and Hydrozoans and to increased rates of sexual reproduction in numerous species including *Mnemiopsis leidyi* (Purcell 2005).

Effects of nutrients

Nutrient pollution is of increasing concern in a large number of coastal and continental shelf habitats. Nutrient loading to coastal marine systems has strongly increased in recent decades through terrestrial inputs of sewage and human industry (e.g. fossil fuel combustion, forestry, and agriculture) (Arai, 2001). Although nutrient pollution of marine environments is detrimental to a majority of marine species, these changes could benefit some jellyfish species (Arai, 2001; Purcell, 2007).

Jellyfish may thrive in polluted environments for a variety of reasons. Phytoplankton communities can be positively affected by nutrient pollution (most notably phosphorous and nitrogen) leading to increased food resources for zooplankton and thus jellyfish (Arai, 2001). Jellyfish are also capable of rapid intake of food resources and are therefore able to respond rapidly to periodic pulses of production contrasting the relatively slow uptake rate of many forage fish species (Brodeur *et al.*, 2002). For this reason jellyfish can better utilize short term increases in productivity leading to increased growth and thus increased reproductive ability (Purcell, 2007).

Eutrophication of marine ecosystems resulting from nutrient pollution can lead to the formation of a hypoxic zone at depth, as exemplified by the hypoxic zone in the Northern Gulf of Mexico (Arai 2001). Such hypoxic conditions have strong impacts on marine ecosystems, decreasing diversity as many species that are unable to survive in low oxygen conditions (U.S. EPA, 2007). Research has shown some jellyfish species to persist under such conditions, with some species appearing to thrive under hypoxic conditions (Arai, 2001). Although the effects of nutrient pollution on jellyfish biomass and diversity remain unknown it is conceivable that such conditions could give hypoxia

tolerant jellyfish species an opportunity to increase and dominate in ecosystems where they would otherwise be unable.

Fishing impacts (loss of predators and competitors)

Increased fishing effort worldwide has strong effects on marine ecosystems leading to declines of commercially important and by-catch species, changes in food web structure, and shifts in species composition and diversity (Pauly, *et al.*, 1998). These changes might indirectly increase jellyfish population abundance via two mechanisms (Purcell, 2007). First the removal of predatory species could allow for population explosions of jellyfish species liberated from predator control. Second decreased competition with forage fishes for plankton resources could result in increased population growth rates for jellyfish.

With respect to predation, there is little documentation of the primary predators of dominant jellyfish species. Although predation by reptilian predators (Family Cheloniidae, Sea turtles) is well understood, there have been relatively few studies investigating the importance of fish, avian, and invertebrate species. Available information, primarily a result of a review by Arai (2005) shows this latter group to be of far greater importance in regulating jellyfish populations than previously realized, with multiple fish, invertebrate species capable to affecting jellyfish population growth.

With respect to a possible competition with fish for food resources, there is little information available at this time regarding the diet of many ecologically important jellyfish species. Jellyfish feed high in the marine food chain and therefore may

compete with many fish species (Purcell, 2007). It is conceivable that large removals of forage fish species by human harvest would lead to decreased resource competition and allow for increases in jellyfish population abundance as suggested for example by Brodeur *et al.* (2002). In addition increased jellyfish populations may impact forage fish stocks though consumption of icthyoplankton, and juvenile fish (Möller, 1984; Beucher, 1999; Lynam *et al.*, 2005; Purcell, 2007).

Importance of understanding jellyfish population change

In addition to their role as predators and their potential importance as indicators of change, jellyfish can also be detrimental to humans (Purcell 2005). Increased abundances of jellyfish can impact fisheries by clogging fishing gear and by fouling mariculture and aquaculture nets (Purcell, 2005). Furthermore, jellyfish could decrease fisheries catch if increased jellyfish populations are able to outcompete commercially important forage fish species, and by reducing population sizes of commercially important species through consumption of icthyoplankton and juvenile fish (Mills, 1995; Aria, 2001; Purcell, 2005).

One potentially positive impact of increased jellyfish abundance on commercially important fish species has recently been noted. Brodeur *et al.* (2002) remarks on the use of medusa by juvenile fish including walleye pollock as refugia from predation. In addition increasing numbers of jellyfish are used as a food resource, and total catches as reported to the United Nations Food and Agriculture Organization are increasing (Fig. 1).

Finally, many jellyfish species have long interfered with tourism presenting a health hazard to swimmers and forcing closures of popular beaches (Burnett, 2001, Purcell, 2007). Likewise jellyfish can be detrimental to industry, in particular to those which rely of saltwater input to cool machinery (Purcell 2007). There is a long standing record of Asian power plants being temporarily shut down as a result of clogged seawater intake screens (Purcell 2007).
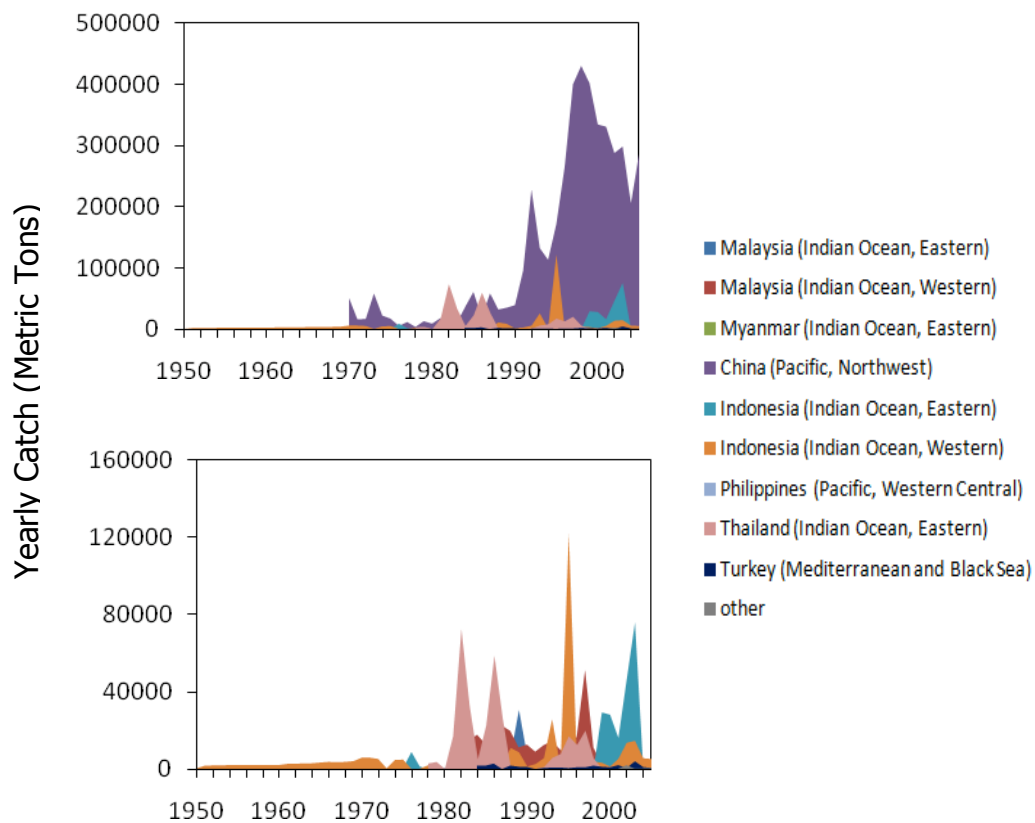
Figure 1. FAO capture fishery data of annual commercial catch of jellyfish by region.
Other includes catch from: Australia, Bahrain, Namibia, and the Russian Federation
Top panel: all regions. Bottom panel: China excluded.

Because of their potential use as environmental indicators, and their ability to impact both ecosystems and the economy, it is important to study the patterns in jellyfish abundance over time to allow scientists to understand the environmental factors that may cause further increases in jellyfish populations (Purcell and Decker, 2005, Purcell, 2005). The current investigation will present the first global collation of jellyfish population abundance records. I attempt to use this information to test four hypotheses of the possible causes of jellyfish population increase in continental shelf ecosystems, by exploring time-series correlations with leading climate indices, sea surface temperature, nutrient loading and fish abundance (both forage fish and predators). I am also collating data on the diets and predators of jellyfish to further elucidate their role in the ecosystem.

Methods

Creation of the database

Records of annual jellyfish population abundance were gathered from literature sources and university and government databases. Data were collected for any time period and any region where records of jellyfish abundance are currently available (Fig. 2). Datasets less than 5 years were excluded as they would not allow for a statistical evaluation of time trends. Time series for the variables of climatic variation, temperature variation, nutrients, and predatory and forage fish abundance were then complied for the same regions and years as jellyfish population records. All data were quality-checked, and compiled in a customized EXCEL spreadsheet database for future analysis. Forage fish and predatory fish abundance records were transformed using log + 1 transformation. Temperature data (average ºC) were standardized to

temperature anomaly by dividing by the all values by the mean temperature of the time series.

Jellyfish abundance records were standardized using a log+1 transformation for correlations of

the five proposed variables and jellyfish population abundance. For analysis of jellyfish

abundance through time jellyfish population abundance records were converted to a scaled

abundance index as explained below.
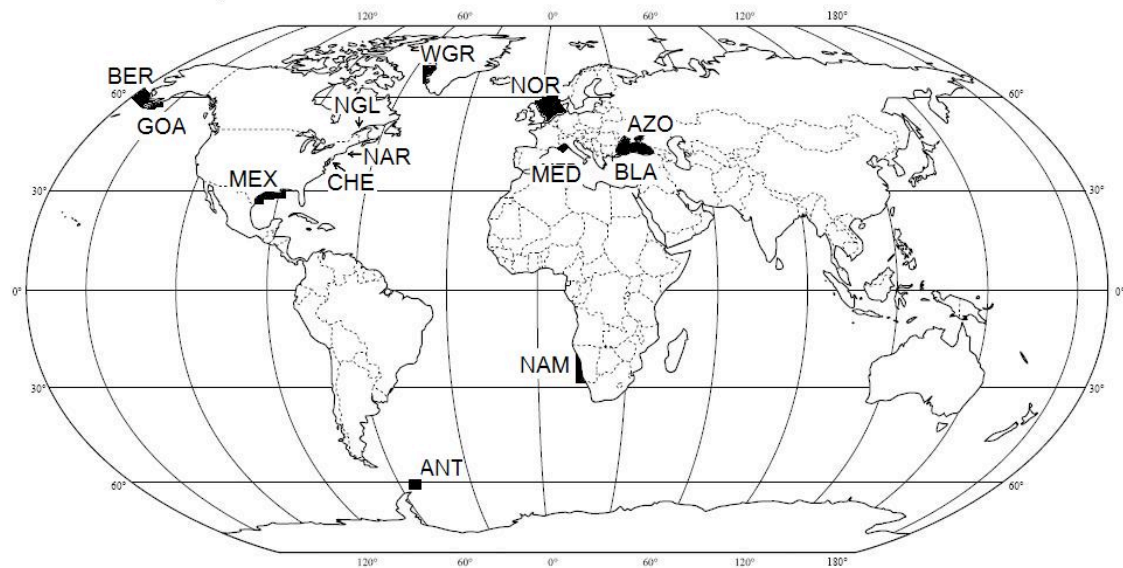
Figure 2. Systems used for analysis of jellyfish population trends and correlations between jellyfish abundance and variables of climate, temperature, nutrients, forage fish abundance, and predatory fish abundance. Black areas approximate size and dimensions of data series used in analysis: BER, Bering Sea; GOA, Gulf of Alaska; MEX, Gulf of Mexico; CHE, Chesapeake Bay; NAR, Narragansett Bay; NGL, Northwest Gulf of St. Lawrence; WGR, Western Greenland; NOR, North Sea; MED, Mediterranean; BLA, Black Sea; AZO, Sea of Azov; NAM, Namibia; ANT, Antarctica

Choice of specific variables

In all systems excluding the Gulf of Mexico and Namibia jellyfish population records are present only for single species or as total jellyfish abundance for multiple un-identified jellyfish species. In contrast distinct population abundance records were available both in the Gulf of Mexico (*Aurelia aurita* and *Chrysaora quinquecirrha*) and Namibia (*Aequorea aequorea and Chrysaora hysoscella*). For the Gulf of Mexico both species were combined in the analysis of population abundance verse time as preliminary analysis showed both species have positive trends in population abundance. For the analysis of factors causing observed increases (*A. aurita* and *C. quinquecirrha*) the species were treated independently as past study has shown them to respond differently to environmental variation (Graham, 2001). Preliminary analysis found (*A. aequorea and C. hysoscella*) from the Namibian system to show opposite trends in species abundance with time. Therefore these species were separated for the formal analysis of population increase verse time, and also for the analysis of factors causing variation in abundance.

The NAO and PDO were chosen as leading climate indices to be tested against trends in jellyfish. The NAO strongly affects eastern North American and Western European terrestrial ecosystems, as well as the North Atlantic Ocean, and North Sea while the PDO affects Northwest North America and the Bering Sea. For the analysis mean yearly indices of both the NAO and PDO were obtained by taking the average of monthly observations. Values for temperature are primarily measures of sea surface temperature (SST), when SST data was unavailable; either values of the cold intermediate layer (CIL) or water column temperature near the surface were used. Temperature data was matched as closely as possible to season in jellyfish were recorded. If seasonal temperature values were unavailable mean yearly temperature values were used.

Nutrient data used for the analysis are given as concentrations of nitrate or phosphorous as these are of primary importance for phytoplankton growth, leading to potential increased resources for jellyfish. Methods for nutrient data collection varied among sources; either nutrient loading from a point source or nutrient concentration in the water column was reported. Predator and forage fish species used were usually the principal groundfish (cod, pollock, for example) or small pelagics (herring, capelin, for example) in that particular ecosystem. These species may differ from those reported in the analysis of the predators of jellyfish.

Are jellyfish increasing with time?

I tested the hypothesis that jellyfish populations were increasing exponentially over time, following:

$$N_i(t) = N(0)\,e^{-r_i t} \qquad\qquad (0.1)$$

Where $N_i(t)$ is the abundance of jellyfish in ecosystem i at time t, $N(0)$ is the abundance in the first year and r_i is the rate of increase. To simplify, jellyfish abundance data were re-scaled into an index of relative abundance, where $N(0) = 1$. For time series containing zeroes (Bering Sea) data were converted to abundance + 1. The standardized values of abundance where then plotted against time, and an exponential trend fit to the data. Correlation coefficients and p-values (significant at $\alpha < 0.05$) for each system were determined after log transforming relative abundance data in each system (log + 4 for Bering Sea), plotting these values over time, and fitting a linear trend to the data. I report test statistics and values of r_i for each ecosystem.

Testing hypotheses for forcing factors

In order to test hypotheses about factors that may correlate with changes in jellyfish abundance over time, all abundance or biomass data (jellyfish abundance, predatory and forage fish biomass) were transformed using log (x+1), whereas climate indices, temperature and nutrient concentration were not transformed. Log-transformed jellyfish abundance was then plotted vs. each of the five variables (climate, temperature, nutrients, predators, forage fish) separately, where data permitted and a linear trend was fitted. Correlation coefficients and p-values were calculated using f-statistics for all plots with p-values < 0.05 considered significant.

Auto-correlation in the jellyfish time series was generally low, and therefore no attempts were made to correct for this. I also did not lag any of the time series, as I reasoned that changes in climate, temperature, nutrients or predation would likely affect jellyfish population immediately, due to short generation times. Not all variable were available in all ecosystems. A detailed description of all variables investigated and their sources can be found in Appendix 1.

Determination of jellyfish predators

Primary predators of jellyfish were determined by conducting a detailed literature search. Average percent consumption rates calculated by taking the mean of consumption rate of all species within each family group. Average percent occurrence were calculated by dividing occurrence rates of jellyfish prey in predator stomachs by the total number of stomachs investigated and multiplying by 100. Percent occurrence was then averaged for each family group by calculating the mean occurrence rate of all species in each family.

Quantitative estimates of occurrence rate were available for some avian predators and values were calculated following the same procedure as that used for fish predators though

average occurrence rates for family groups was not conducted. Consumption and occurrence rates from stomach contents were unavailable for invertebrate and reptilian predator groups and are reported as qualitative values of dietary importance as described in the source publications. Dietary importance of jellyfish species to representative families and species was subdivided as follows: Very high (greater than 50% stomach contents and for specialized jellyfish predators); high (between 20-50% stomach contents, and for generalist predators); Present (between 10-20% stomach contents for generalist predators); and unknown.

Results

Jellyfish vs. Time

Increases in jellyfish abundance were observed in 10 out of 13 systems (Bering Sea, Gulf of Alaska, North Sea, Black Sea, Gulf of Mexico, Gulf of St. Lawrence, Azov Sea, Mediterranean, Namibia [*C. hysoscella*], and Antarctica) (Figure 3). Rates of increase ranged from 0.01 to 0.81, with statistically significant increases in 5 of the 10 systems (Table 1, Fig. 4). Decreases in jellyfish abundance were observed in the remaining 3 systems as well as *A. aequorea* from the Namibian system. Only one system (Greenland), showed a significant decrease. Magnitudes of increase ranged from 2-35-fold (Table 1). The Black Sea and Bering Sea were found to have the greatest magnitudes of increase with 19- and 35-fold increases over time, respectively. The Gulf of Alaska, Gulf of Mexico, North Sea, and Gulf of St. Lawrence also had statistically significant increases, but the magnitude of increase in these systems was considerably lower (1.5-10).
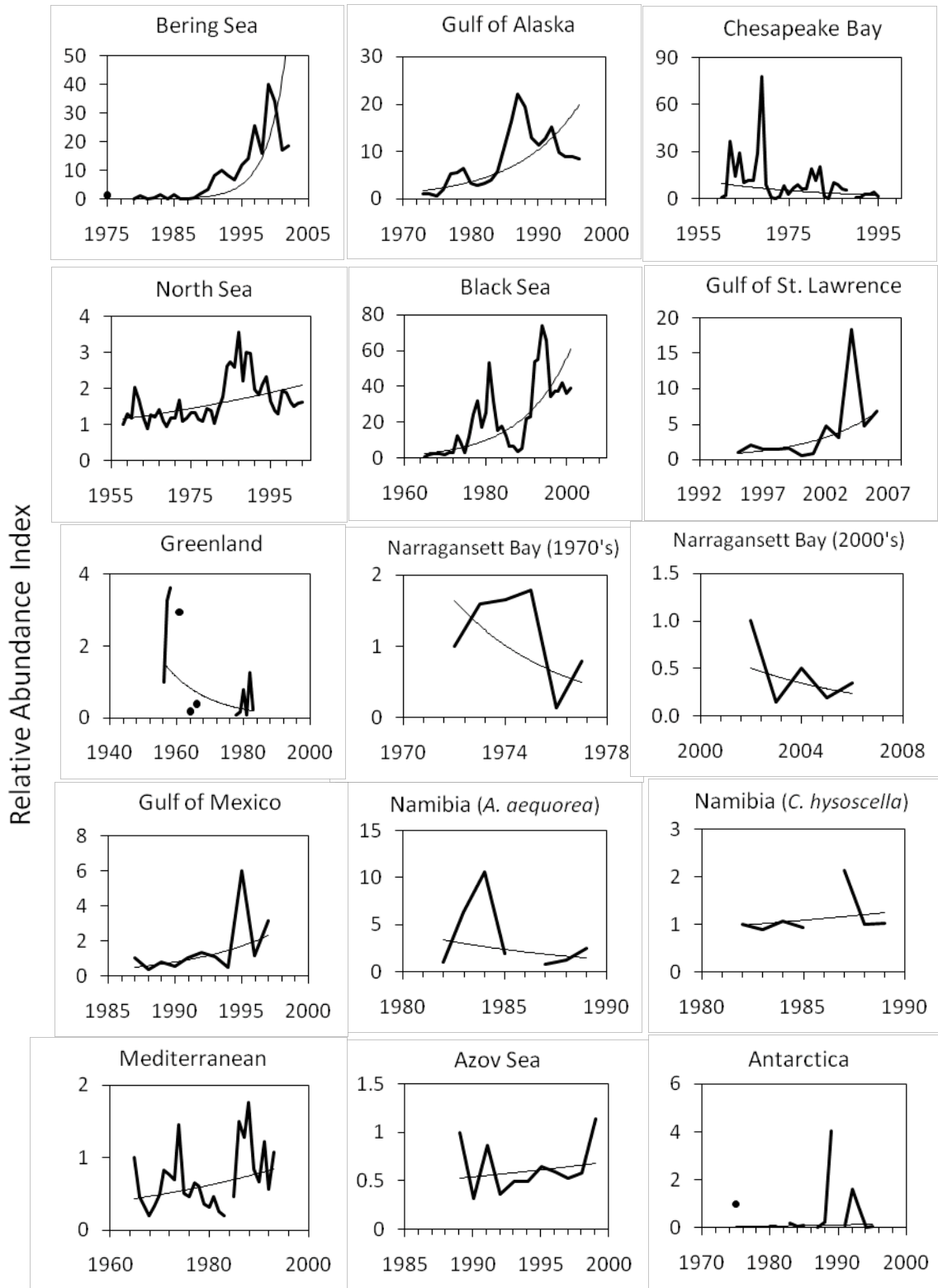
Figure 3. Interannual variation in relative jellyfish population abundance versus time for each of 13 systems. Abundance was scaled to the first year, such that N(0) = 1. Regression lines are fitted exponential trends. For statistics refer to Table 1.

Table 1. Summary statistics for analysis of standardized population abundance over time for 13 systems (see Fig. 3). The exponential yearly rate of increase is given, as well as the total magnitude of change in abundance, calculated as the mean of the last 3 years divided by the mean of the first three years of the time series.

System	Rate of Increase (r_i)	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value	Magnitude of Change
Bering Sea	0.093	0.7951	25	0.89	0.000	34.73
Gulf of Alaska	0.109	0.594	24	0.77	0.000	10.30
Chesapeake Bay	-0.039	0.083	35	- 0.29	0.093	0.21
North Sea	0.013	0.263	46	0.51	0.000	1.36
Black Sea	0.085	0.601	37	0.78	0.000	19.62
Gulf of St. Lawrence	0.188	0.471	12	0.69	0.014	6.55
Greenland	-0.08	0.339	13	-0.58	0.037	0.20
Narragansett (1970's)	-0.185	0.217	6	-0.47	0.352	0.64
Narragansett (2000's)	-0.242	0.149	5	-0.39	0.521	0.47
Gulf of Mexico	0.150	0.368	11	0.61	0.048	4.88
Mediterranean	0.024	0.118	28	0.34	0.074	1.58
Namibia (*A. aequorea*)	-0.125	0.109	7	-0.33	0.470	0.24
Namibia (*C.hysoscella*)	0.0345	0.0922	7	0.3	0.508	1.40
Azov Sea	0.026	0.049	11	0.22	0.513	1.04
Antarctica	0.062	0.03	15	0.17	0.537	0.85

Five out of 7 systems with sample sizes greater than 20 years showed significant trends in jellyfish abundance. The Mediterranean Sea had a non-significant increase in jellyfish and Greenland a significant decrease (p = 0.033). The Gulf of St. Lawrence was the only system below a sample size of 20 yielding significant results. Non-significant increases were also observed for the Azov Sea, Namibia (*C. Hysoscella*) and Antarctica, and decreases in Namibia (*A. Aequorea*), Narragansett Bay, and Chesapeake Bay. All these series excluding the Chesapeake Bay had sample sizes less than or equal to 15 years.
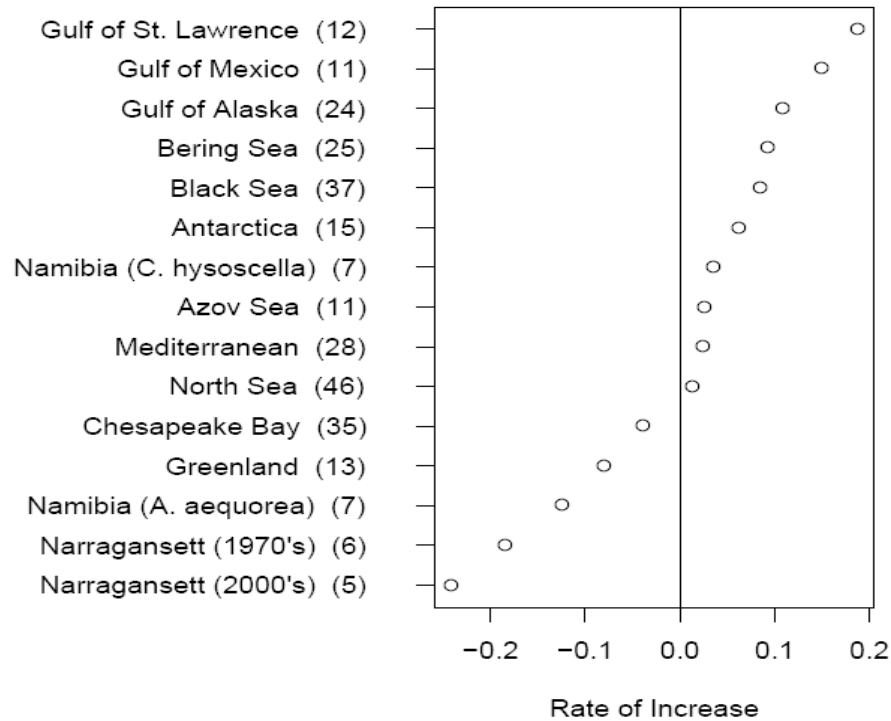
Figure 4. Rate of jellyfish population increase in each of 13 systems. Rate of increase determined from linear trend fit to log-transformed standardized abundance indices vs. time for each system.

Testing forcing factors

A significant negative correlation between jellyfish and forage fish abundance was observed (p = 0.019) in the Bering Sea. Climate, temperature, and predatory fish abundance were not correlated with jellyfish populations (Fig. 5, Table 2). In contrast, in the nearby Gulf of Alaska climate and temperature had a significant positive correlation to jellyfish (Table 3, Fig. 6). Predatory fish abundance was negatively correlated to jellyfish and one of only two systems (also North Sea) to show such a relationship. There was no correlation between forage fish and jellyfish in this system (p = 0.089).
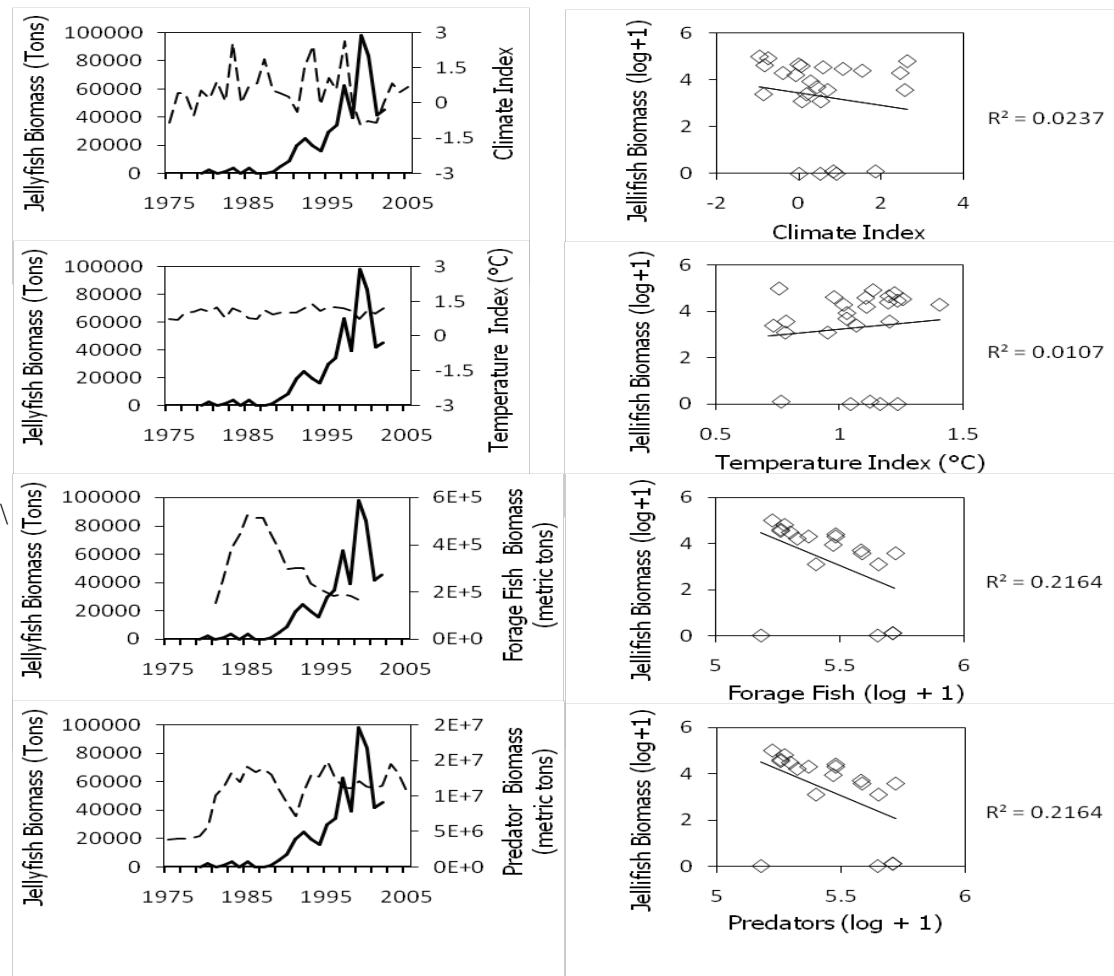
Figure 5. Bering Sea. Jellyfish trends in relation to other variables. Left panels: Time trends. Right panel: Correlation of log-transformed jellyfish population abundance (solid line) to each variables tested (dotted line). Lines indicate fitted linear regression trends. For statistics see Table 2.

Table 2. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Bering Sea.

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	0.024	25	- 0.15	0.463
Temperature	0.011	25	0.1	0.623
Nutrients	ND	ND	ND	ND
Forage Fish	0.216	25	- 0.47	0.019
Predatory Fish	0.021	25	- 0.14	0.494
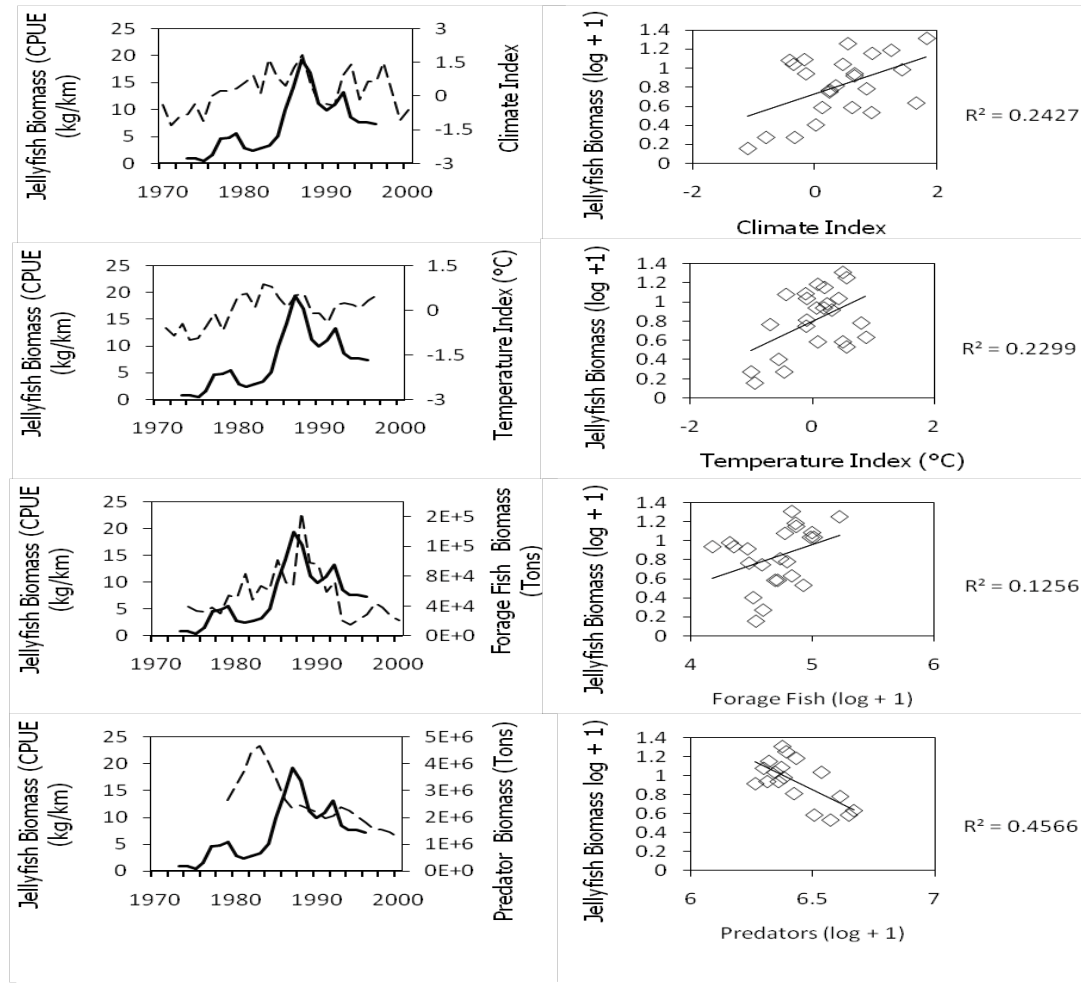
Figure 6. Gulf of Alaska. All symbols like Fig 5. See Table 3 for test statistics

Table 3. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Gulf of Alaska.

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	0.243	24	0.49	0.014
Temperature	0.230	24	0.48	0.018
Nutrients	ND	ND	ND	ND
Forage Fish	0.126	24	0.35	0.089
Predatory Fish	0.457	24	- 0.68	0.000

In Chesapeake Bay four of five variables tested were correlated to jellyfish abundance (Table 4, Fig. 7). A negative correlation was observed between jellyfish abundance and both temperature and the NAO index (p = 0.016 and p = 0.014 respectively). A positive correlation was observed between forage fish and jellyfish population size, while predatory fish abundance was not correlated to jellyfish population change.

Figure 7. Chesapeake Bay. All symbols like Fig. 5. See Table 4 for test statistics.

Table 4. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Chesapeake Bay.

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	0.1713	35	- 0.41	0.013451
Temperature	0.1649	35	- 0.41	0.015501
Nutrients	ND	ND	ND	ND
Forage Fish	0.1418	35	0.38	0.02577
Predatory Fish	0.0012	35	- 0.03	0.843393

The North Sea had the greatest sample size of all systems (n = 46) and was the only system for which measures of all five variables were available. Here, correlation of jellyfish abundance and nutrient concentration was particularly strong (r=0.77, p < 0.0001) (Table 5, Fig. 8). Forage fish abundance was also showed a positive correlation with jellyfish abundance. Climate was not significantly correlated to jellyfish, but did show a non-significant trend towards positive relationship (p=0.079). Temperature and predatory fish abundance were not correlated with jellyfish in this system.

Like in the North Sea, nutrients and forage fish abundance both correlated positively with jellyfish abundance in the Black Sea (Table 6, Fig. 9). Predatory fish abundance, in contrast was negatively correlated to jellyfish nor was temperature correlated to jellyfish abundance in this system (p = 0.337)

Figure 8. North Sea. All symbols like Fig. 5. See Table 5 for test statistics.

Table 5. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the North Sea.

| Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	0.090	46	0.3	0.079
Temperature	0.047	46	0.22	0.211
Nutrients	0.595	46	0.77	0.000
Forage Fish	0.139	46	0.37	0.027
Predatory Fish	0.069	46	- 0.26	0.127

Figure 9. Black Sea. All symbols like Fig. 5. See Table 6 for test statistics.

Table 6. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Black Sea.

Variable	r^2	Sample Size (n)	Correlation Coefficient(r)	p-value
Climate	ND	ND	ND	ND
Temperature	0.026	37	0.16	0.337
Nutrients	0.379	37	0.62	0.000
Forage Fish	0.119	37	0.35	0.036
Predatory Fish	0.211	37	0.35	0.036

In the Gulf of St. Lawrence climate and temperature were not correlated to jellyfish abundance (Table 7, Fig. 10). Forage fish abundance was negatively correlated to jellyfish (correlation coefficient 0.62, p = 0.0301) while no relationship was observed between predators and jellyfish in this system. Narragansett Bay had two short times series available that could not be merged due to different methods employed. In the 1970's series neither climate nor temperature explained any of the variation in jellyfish abundance (Table 8, Fig. 11). In the 2000's nutrients were positively correlated to jellyfish (Table 9, Fig. 12). As in the earlier series, temperature was not correlated to jellyfish abundance.

In the Gulf of Mexico results for the two dominant species (*A. aurita* and *Chrysaora quinquecirrha*) were similar. Neither climate nor nutrients explained a significant portion of variation in either species while temperature was found to be positively correlated to both (Table 10, Fig. 13 and Table 11, Fig. 14). Greenland, the Mediterranean, Antarctica, Azov Sea, and both *A. aequorea* and *C. hysoscella* in Namibia showed no correlation between any tested variables (climate, temperature, forage fish, and predatory fish) and jellyfish abundance(Tables 12 – 17 and Fig. 15 - 20 respectively).
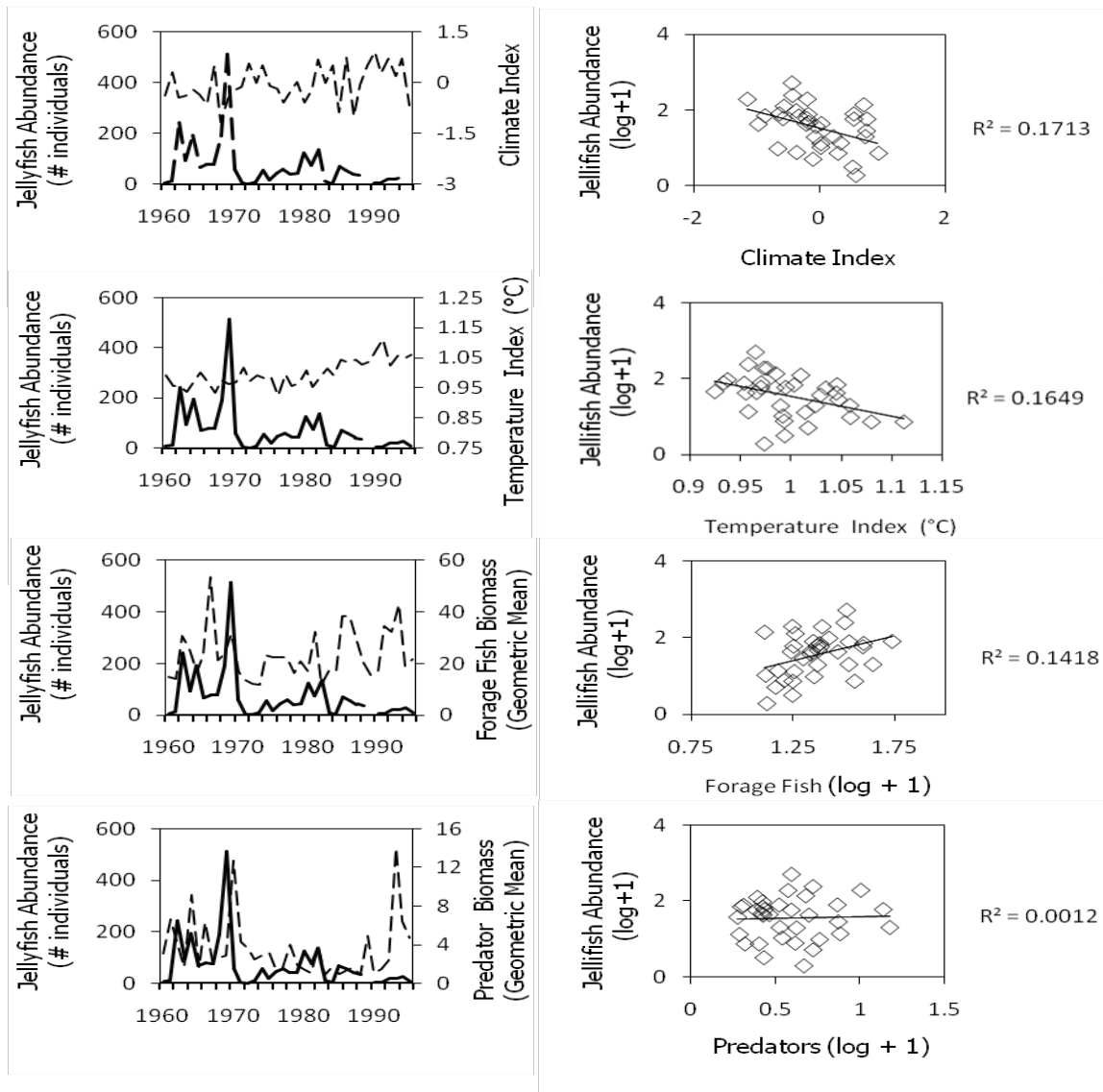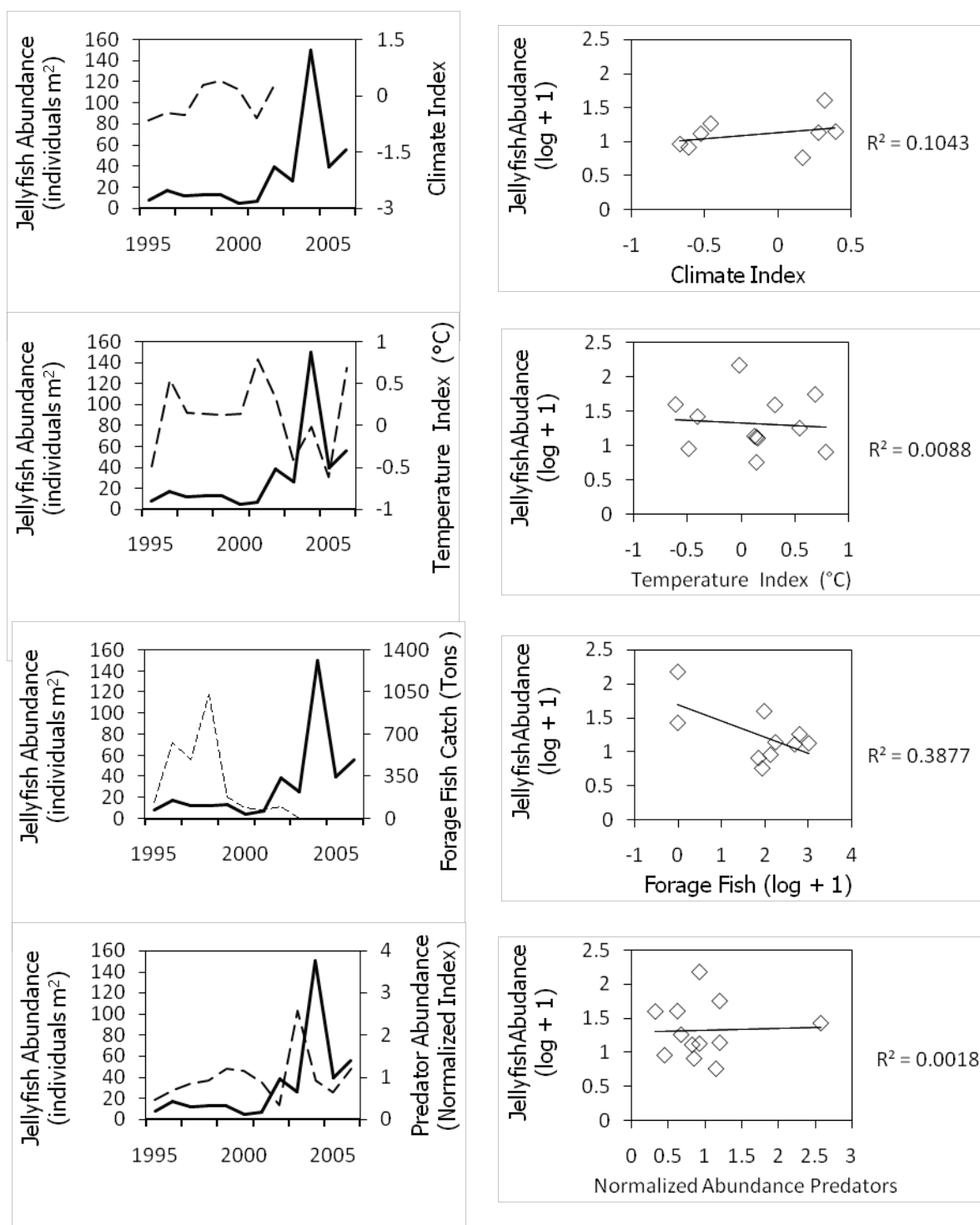
Figure 10. Northern Gulf of St. Lawrence. All symbols like Fig. 5. See Table 7 for test statistics.

Table 7. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Gulf of St. Lawrence.

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	0.104	12	0.32	0.306
Temperature	0.009	12	0.09	0.772
Nutrients	ND	ND	ND	ND
Forage Fish	0.388	12	- 0.62	0.031
Predatory Fish	0.002	12	0.04	0.896

Figure 11 Narragansett Bay 1970s. All symbols like Fig. 5. See Table 8 for test statistics.

Table 8. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Narragansett Bay (1970's).

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	0.137	6	0.37	0.471
Temperature	0.006	6	0.08	0.886
Nutrients	ND	ND	ND	ND
Forage Fish	ND	ND	ND	ND
Predatory Fish	ND	ND	ND	ND

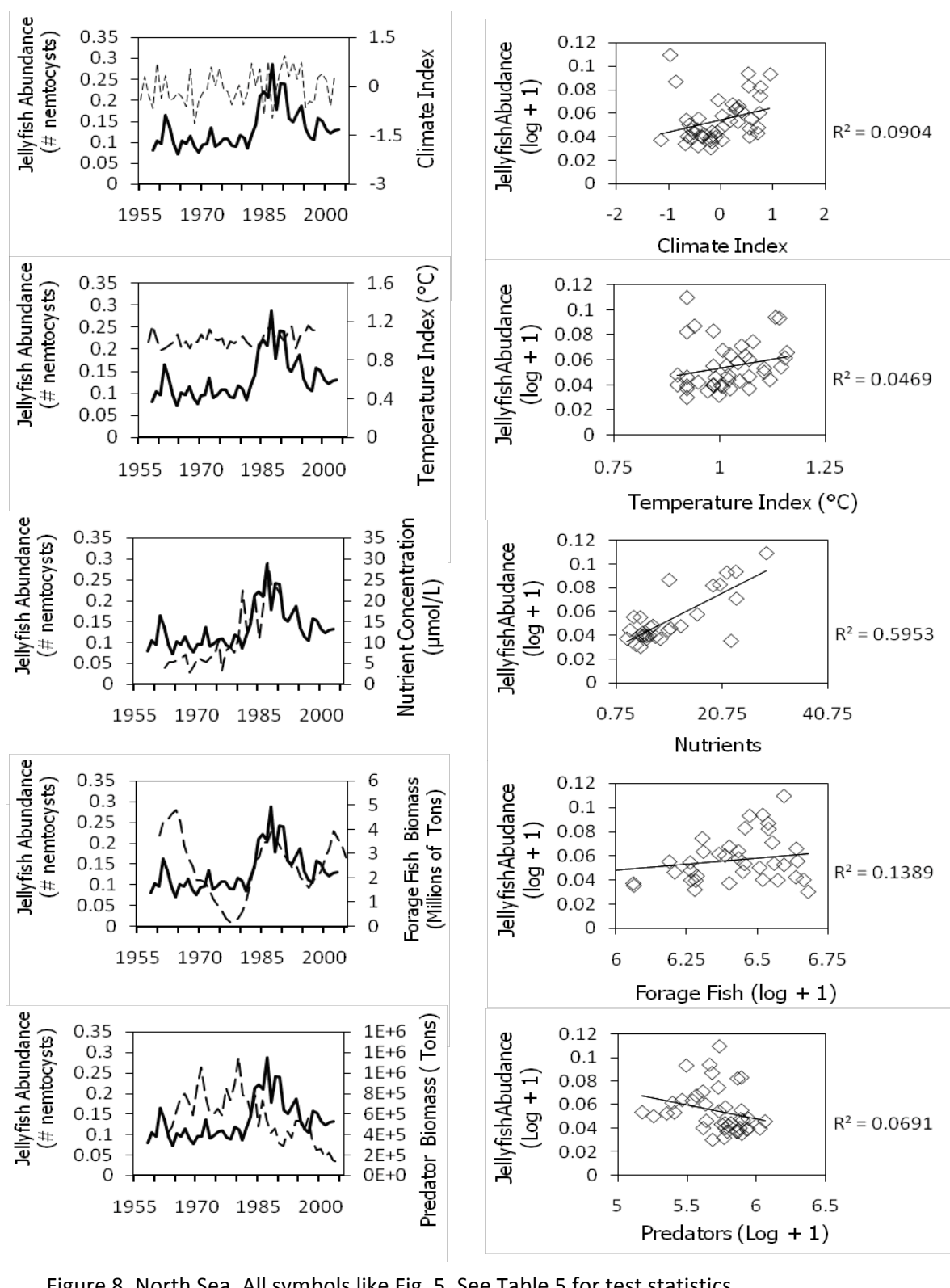Figure 12 Narragansett Bay 2000s. All symbols like Fig. 5. See Table 9 for test statistics.

Table 9. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Narragansett Bay (2000's).

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	ND	ND	ND	ND
Temperature	0.043	5	- 0.21	0.738
Nutrients	0.824	5	- 0.91	0.033
Forage Fish	ND	ND	ND	ND
Predatory Fish	ND	ND	ND	ND

In the Gulf of Mexico results for the two dominant species (*A. aurita* and *Chrysaora quinquecirrha*) were similar. Neither climate nor nutrients explained a significant portion of variation in either species while temperature was found to be positively correlated to both (Table 10, Fig. 13 and Table 11, Fig. 14). The Azov Sea, both *C. hysoscella* and *A. aequorea* in Namibia, the Mediterranean, Antarctica, and Greenland showed no correlation between any tested variables (climate, temperature, forage fish, and predatory fish) and jellyfish abundance (Tables 12 – 17 and Fig. 15 - 20 respectively).
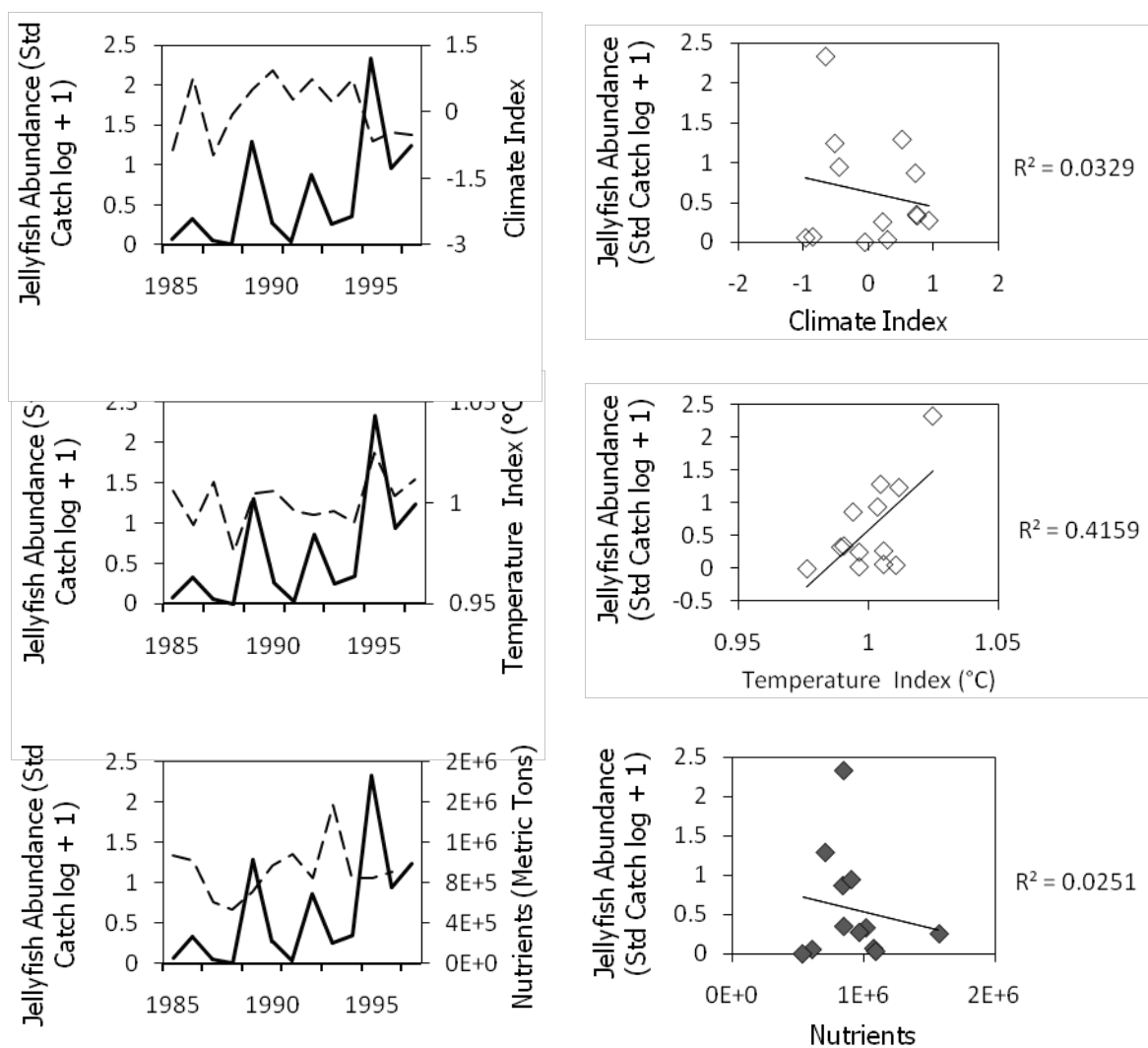
Figure 13. Gulf of Mexico (*Aurelia aurita*). All symbols like Fig. 5. See Table 10 for test statistics.
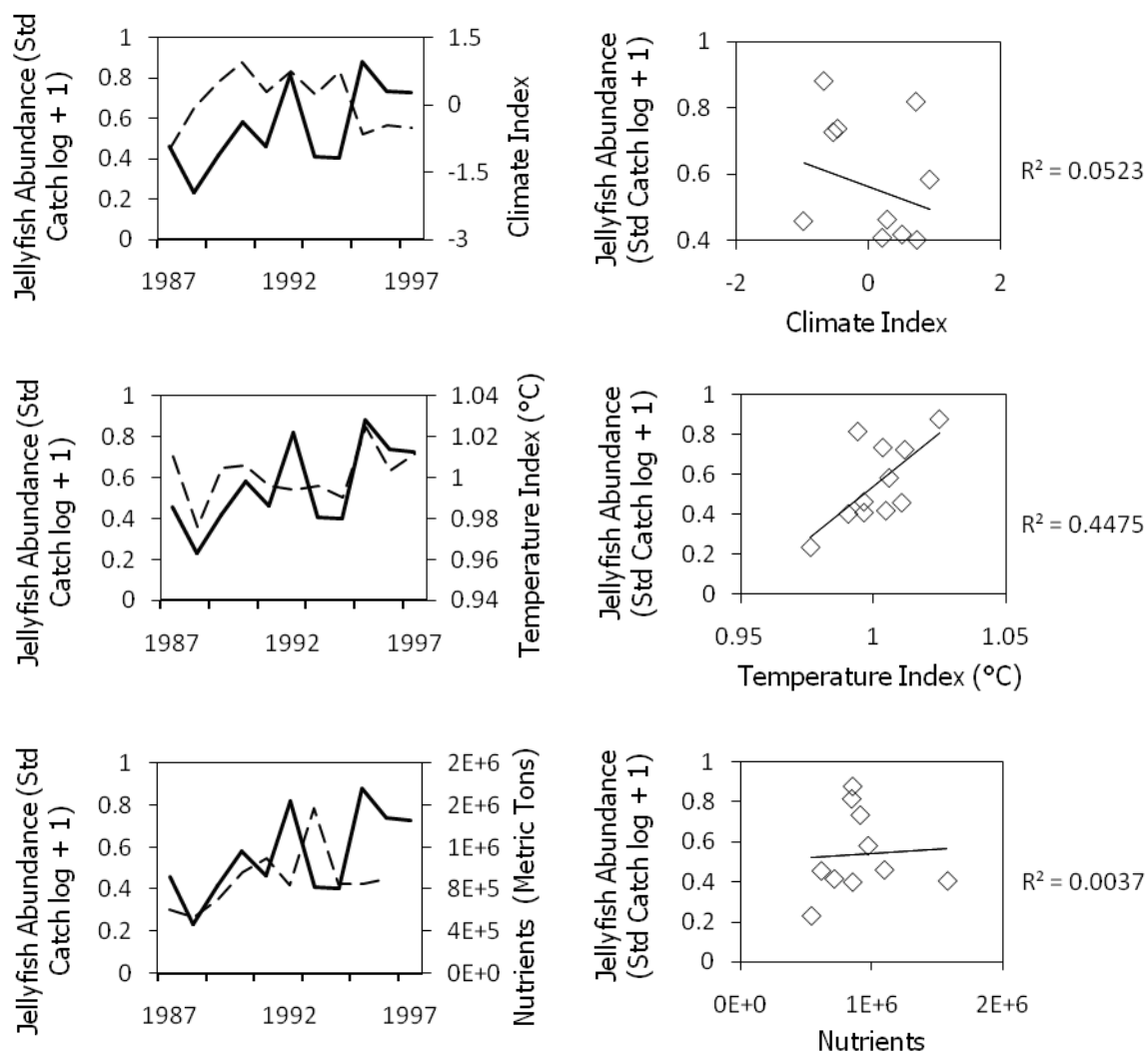
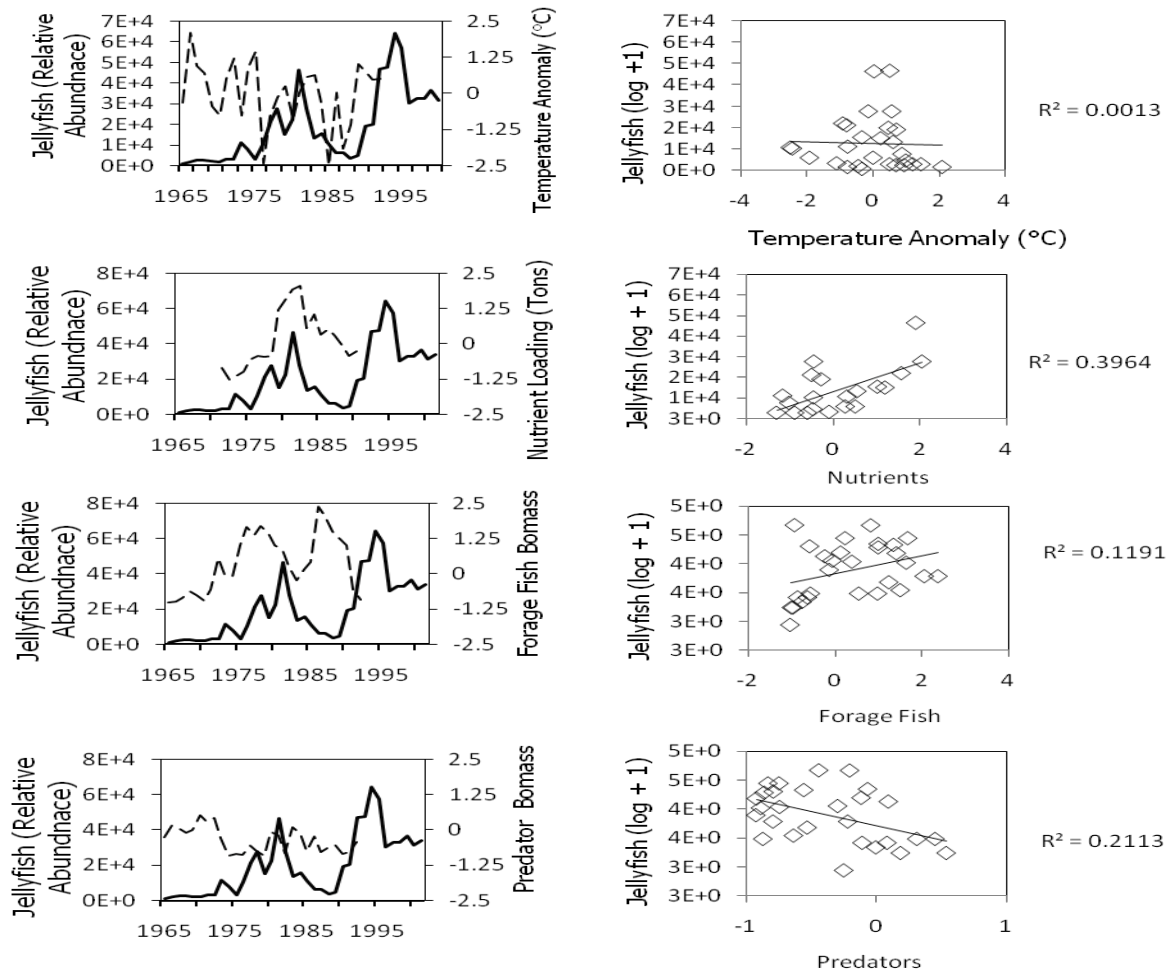Figure 14. Gulf of Mexico (*Chrysaora quinquecirrha*). All symbols like Fig. 5. See Table 11 for test statistics.

Table 10. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Gulf of Mexico (*Aurelia aurita*).

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	0.033	13	0.18	0.55
Temperature	0.416	11	0.64	0.032
Nutrients	0.025	13	- 0.16	0.61
Forage Fish	ND	ND	ND	ND
Predatory Fish	ND	ND	ND	ND

Table 11. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Gulf of Mexico (*Chrysaora quinquecirrha*).

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	0.052	11	- 0.23	0.499
Temperature	0.448	11	0.67	0.024
Nutrients	0.004	11	0.06	0.859
Forage Fish	ND	ND	ND	ND
Predatory Fish	ND	ND	ND	ND
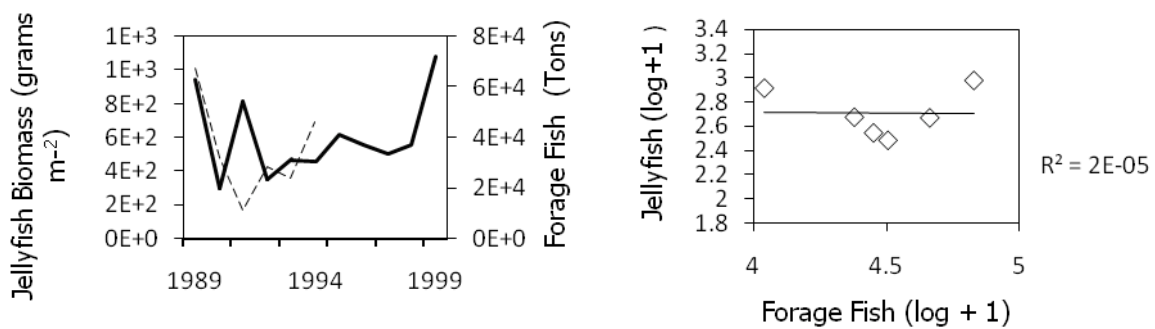
Figure 15.Azov Sea. All symbols like Fig. 5. See Table 12 for test statistics.

Table 12. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in Azov Sea

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	ND	ND	ND	ND
Temperature	ND	ND	ND	ND
Nutrients	ND	ND	ND	ND
Forage Fish	2E-05	11	0	0.990
Predatory Fish	ND	ND	ND	ND
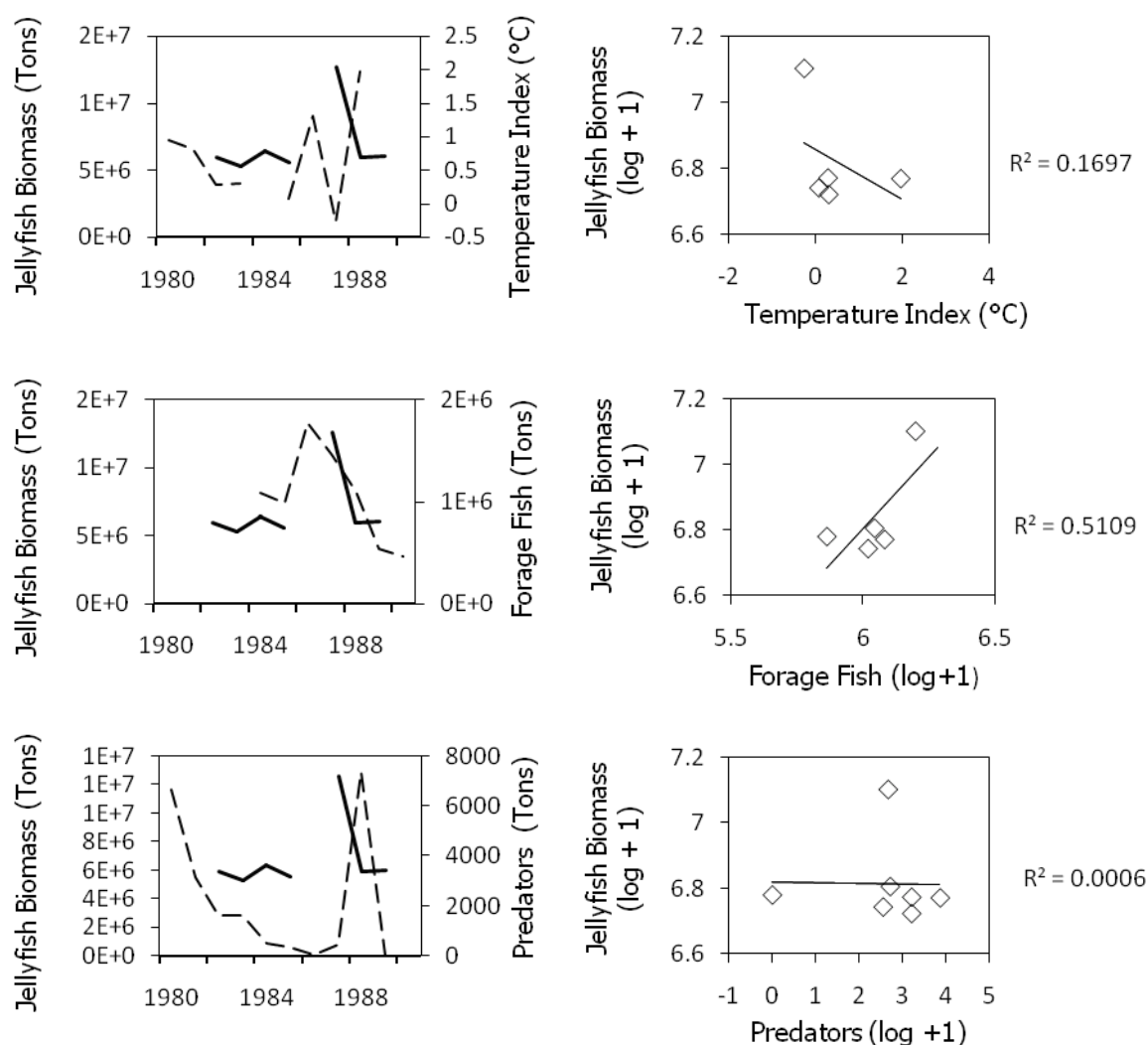
Figure 16. Namibia (*Chrysaora hysoscella*). All symbols like Fig. 5. See Table 13 for test statistics.

Table 13. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Namibia (*Chrysaora hysoscella*).

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	ND	ND	ND	ND
Temperature	0.170	7	- 0.41	0.358
Nutrients	ND	ND	ND	ND
Forage Fish	0.511	7	0.71	0.071
Predatory Fish	0.001	7	- 0.02	0.958
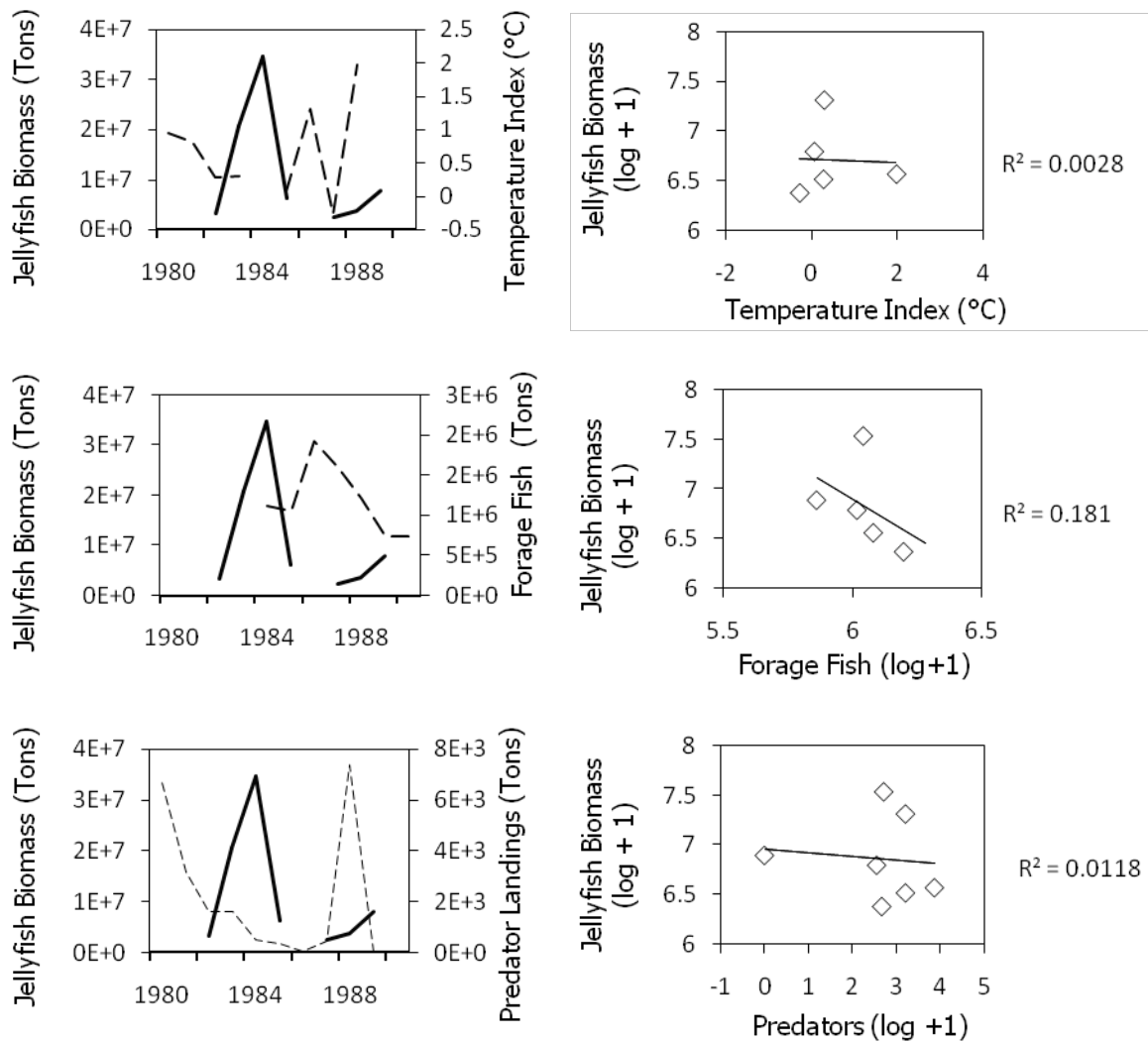
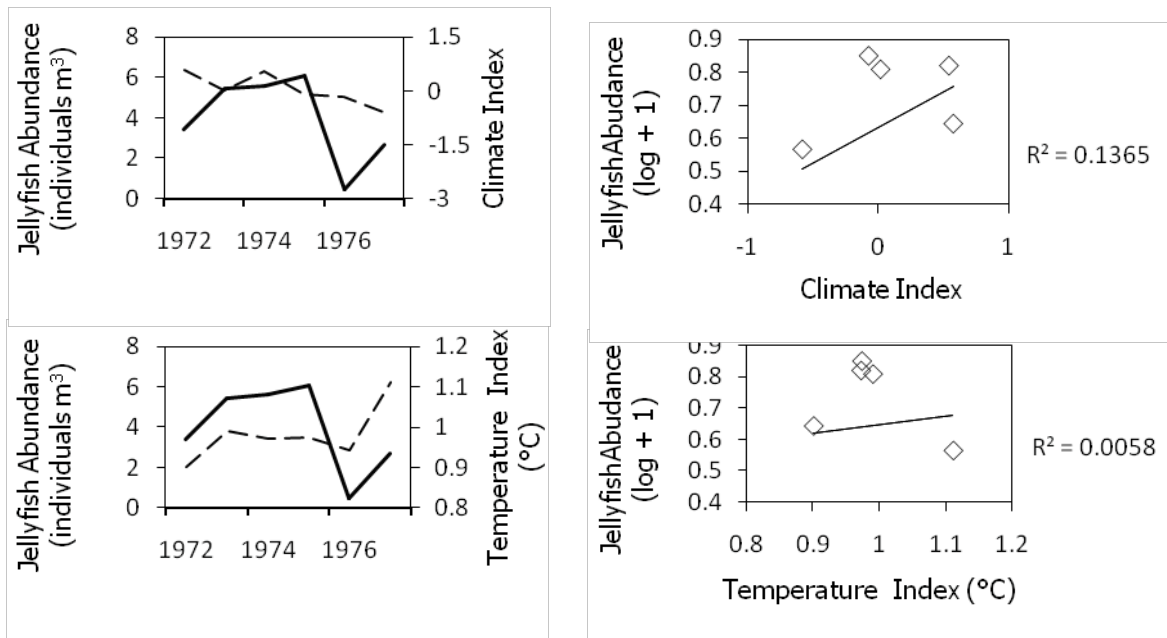Figure 17. Namibia (*Aequorea aequorea*). All symbols like Fig. 5. See Table 14 for test statistics.

Table 14. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Namibia (*Aequorea* aequorea).

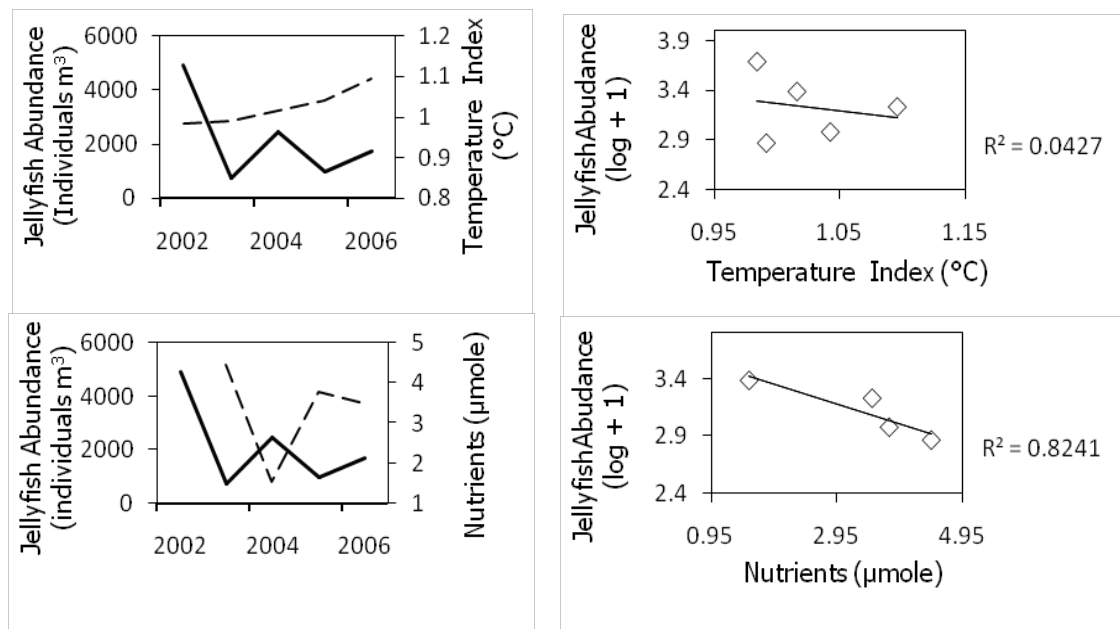| Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	ND	ND	ND	ND
Temperature	0.028	7	- 0.05	0.910
Nutrients	ND	ND	ND	ND
Forage Fish	0.181	7	- 0.43	0.341
Predatory Fish	0.002	7	- 0.04	0.928
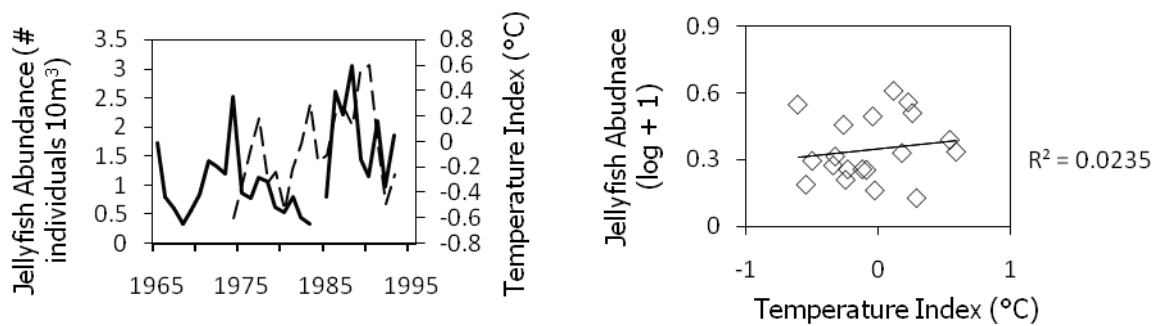
Figure 18. Mediterranean. All symbols like Fig. 5. See Table 15 for test statistics.

Table 15. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Mediterranean Sea

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	ND	ND	ND	ND
Temperature	0.024	28	0.15	0.436
Nutrients	ND	ND	ND	ND
Forage Fish	ND	ND	ND	ND
Predatory Fish	ND	ND	ND	ND
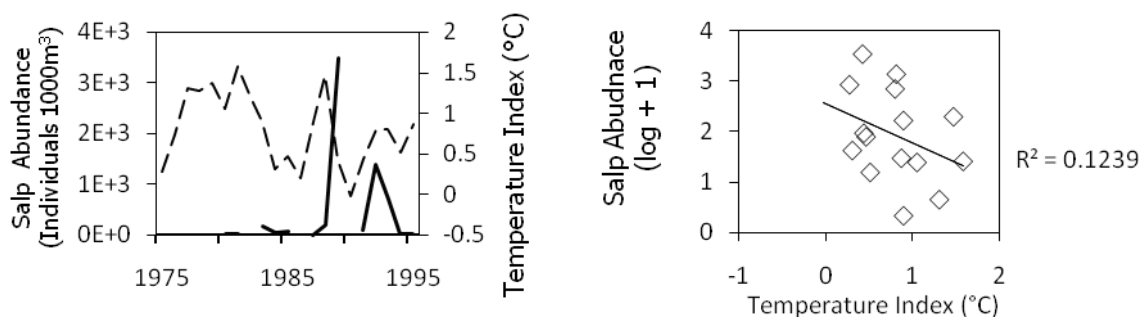
Figure 19.Antarctica. All symbols like Fig. 5. See Table 16 for test statistics.

Table 16. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in Antarctica

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	ND	ND	ND	ND
Temperature	0.124	15	- 0.35	0.198
Nutrients	ND	ND	ND	ND
Forage Fish	ND	ND	ND	ND
Predatory Fish	ND	ND	ND	ND

Table 17. Summary statistics for correlation analysis of jellyfish population abundance and potential variables leading to observed jellyfish abundance trends in the Greenland.

Variable	r^2	Sample Size (n)	Correlation Coefficient (r)	p-value
Climate	0.003	13	- 0.05	0.859
Temperature	0.164	13	0.4	0.170
Nutrients	ND	ND	ND	ND
Forage Fish	0.141	13	0.38	0.205
Predatory Fish	0.000	13.00	- 0.01	0.980
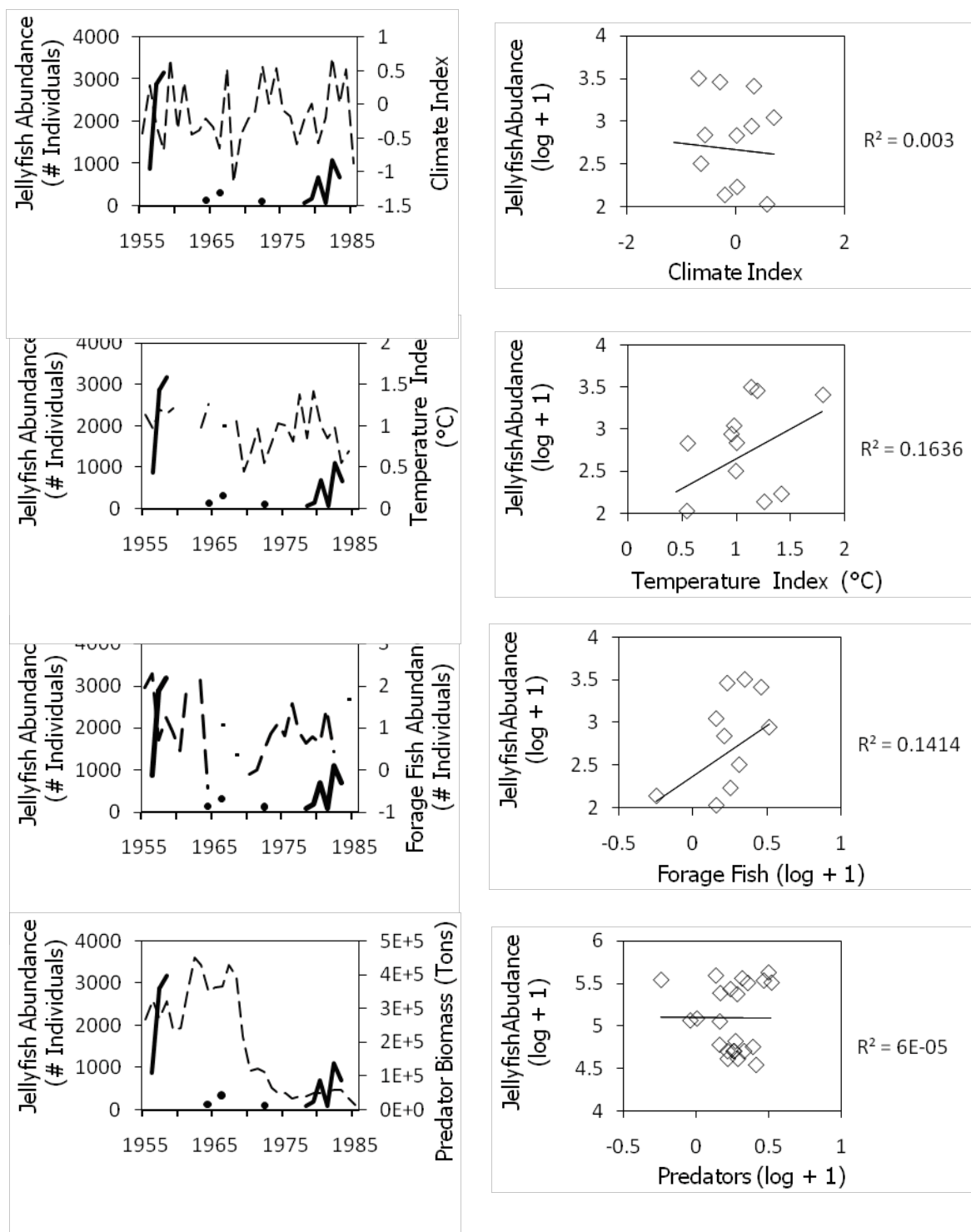
Figure 20. Western Greenland. All symbols like Fig. 5. See Table 17 for test statistics.

Jellyfish predators

A detailed compilation of jellyfish prey in the diets of fish, invertebrates, birds, and reptiles can be found in appendix 2 and 3. Literature searches confirm that the leatherback turtle (*Dermochelys coriacea*) consumes jellyfish as a primary prey item (Table 18) (Ates 1991, Arai, 2001). The Loggerhead turtle (*Caretta caretta*) and Hawksbill Turtle (*Eretmochelys imbricata*) also feed extensively on jellyfish, and the green turtle (*Chelonia mydas*) whose diet is primary herbivorous has also been observed to prey upon jellyfish occasionally (Arai, 2001). The importance of jellyfish to the diet of other sea turtle species remains unknown at this time.

Butterfish (Family Stromateidae), Ocean Sunfish (*Mola mola*), and Spiny Dogfish (*Squalus acanthias*) are well established in the literature as important jellyfish predators. The Spiny Dogfish has been shown to consume jellyfish at high rates, yielding up to 94% of stomach contents (Arai, 2001). Diet studies of the Butterfish (*Stromateus brasiliensis*) found ctenophores in 74.6% of 285 stomachs investigated (Arai, 2001). In total 13 families of fish were found to consume high to very high levels of jellyfish ($\geq$ 20% stomach contents) (Table 18). Jellyfish were also observed as prey in an additional 10 families including commercially important species of the families Salmonidae and Gadidae and others including Rajidae, Argentinidae, Myctophidae, Anoplopomatidae (10-20% stomach contents).

The role of invertebrate jellyfish predators is poorly known. Most information available shows predation among different jellyfish species to be important in affecting population sizes (Aria, 2001). For example, *C. quinquecirrha* feeds primarily on *M. leidyi* in Chesapeake Bay regulating the annual population size of this species (Purcell and Decker, 2005). Scyphozoans prey on other scyphozoans as well as on ctenophores and hydromedusae. Siphonophores such as *Apolemia uvaria* consume primarily hydromedusae and ctenophores (Arai, 2001).

Table 18. Example of gelatinous zooplankton predators. Dietary importance subdivided as follows: Very high, greater than 50% stomach contents, and specialized predators; high between 20-50% stomach contents, and generalist predators. Present, between 10-20% stomach contents, generalist predators; Unknown. Complete species list and sources available in appendix 1 and 2.

Group	Subgroup	Importance to diet
Coelenterates	Hydromedusae , Scyphozoa, Ctenophora	High
Molluscs	Nudibranchs	High
	Gastropoda, Cephlopoda	Unknown
Fish	Families: Gadidae, Rajidae, Argentinidae, Myctophidae, Anoplopomatidae, Hexagrammidae, Sciaenidae, Zoarcidae	Present
	Families: Scorpaenidae, Salmonidae	Present - High
	Families: Carcharhinidae , Clupeidae, Alepocephalidae, Teraponidae, Centrolophidae, Balistidae	High
	Families: Bathylagidae, Nototheniidae	High - Very High
	Families: Squalidae, Kyphosidae, Stromateidae, Scromberesocidae, Molidae	Very High
Marine Turtles		High - Very High
Birds	Order procellariiforms, Order Charadriformes	Unknown - Present

Nudibranchs are also known to feed primarily on the benthic stages of jellyfish and may be capable of controlling the population sizes of some jellyfish species (Arai, 2001). Many incorporate Cnidarian nematocysts into their tissue for protection and thus depend on jellyfish prey not just for food but also for defence (Arai, 2001). Knowledge of other invertebrate predators is minimal. Arthropods of the classes Malacostraca, Copepoda, Ostracoda, Cirripedia,

and Poycnogonida all interact with jellyfish at some point in their life history (Arai, 2001). The importance of these species as potential predators has not been quantified.

Bird species of the Orders Procellariiformis and Charadriiformes may feed on large numbers of jellyfish. Eleven of 17 bird species of the Order Procellariiformis and Charadriiformes investigated by Harrison (1984) were found to consume jellyfish prey. Occurrence rates of jellyfish in the stomach contents of *Fulmarus glacialis* were found to exceed 42%, while *Oceanodroma furcata* showed substantially lower occurrence of jellyfish in 15/55 stomachs (Table 18). Rooks (*Corvus* spp.) have been regularly observed consuming *Aurelia aquinas* in the Black Sea and 12 of 32 stomachs of *Rissa tridactyla* contained scyphozoan tissue (Ates, 1991).

Discussion

In this thesis I asked the question whether jellyfish are increasing worldwide and what may be explaining such changes. The available data show mixed patterns, with jellyfish populations increasing in 10 out of 13 cases, but decreasing in Narragansett Bay, Chesapeake Bay, and Greenland. Namibia showed both positive and negative trend for the species *C. hysoscella* and *A. aequorea* respectively. Most significant correlations were found between jellyfish population abundance and nutrients and forage fish abundance (2 and 5 systems) respectively. Fewer significant correlations were observed between jellyfish abundance and predatory fish abundance (2 systems) and climate indices (2 systems), while three systems (Gulf of Alaska, Chesapeake Bay, and Gulf of Mexico) showed significant relationships between temperature and jellyfish.

Effects of nutrients

Correlations between jellyfish and nutrients were particularly strong where data is available. The North Sea and Black Sea showed the highest correlation of any variable to jellyfish population abundance ($0.62 \leq r \leq 0.77$). Lack of data made it impossible to test the impacts of nutrients in the remaining systems, but it would be expected that nutrients would have positive impacts on jellyfish in most situations, particularly where populations are food limited.

Increased nutrients can have a positive impact on jellyfish populations for two reasons, increased food availability, and by providing an opportunity for jellyfish to bloom in conditions not tolerated by some other species (reduced competition for food), for example in hypoxic zones (U.S. EPA, 2007).   Increased nutrient input into marine environments leads to increased primary production, as most phytoplankton become nutrient limited impeding further growth (Falkowski, *et al.,* 1998). Increases in primary production indirectly impact jellyfish through subsequent increases in prey species including zooplankton and icthyoplankton and juvenile fish which aggregate to feed on zooplankton (Arai, 2001). Although no jellyfish species are known to feed directly on phytoplankton many species are known to have symbiotic relationships with species that are able to utilize dissolve organic matter (DOM) resulting from phytoplankton blooms (Arai, 2001). Therefore in addition to increases in zooplankton, as well as increases in icthyoplankton and juvenile fish species which serve as prey the potential of uptake of dissolved organic material (DOM) by jellyfish could prove important to jellyfish in nutrient rich ecosystems (Aria, 2001).

Increased nutrients can also shift production in favour of particular phytoplankton species. For example diatoms which require silica and coccolithophores which require calcium carbonate could still become nutrient limited in ecosystems with high concentrations of nitrogen and phosphorus. As a nitrogen or phosphorus input can shift phytoplankton communities can to

high abundances of flagellates or bacteria for example (Falkowski, *et al.,* 1998; Arai, 2001). The precise effects of such changes on secondary production and thus on jellyfish and forage fish remain poorly known at this time (Aria, 2001).

Excessive nutrient pollution can result in eutrophication and in some cases causes hypoxic anoxic conditions at depth. Though hypoxia is known to have negative impacts on the majority of marine species many jellyfish species have been found to persist and even thrive in hypoxic conditions. As hypoxia most often only affects water at depth many jellyfish species that live in surface layers are able to avoid hypoxic conditions, examples of such species include *A. digitale, A. aurita, L. tetraphylla*, as well as a variety of ctenophores (Arai, 2001). Other species such as *M. leidyi, Rathkea lizzioides,* and *C. quinquecirrha* are known to have life stages capable of surviving in hypoxic and even temporarily in anoxic conditions (Arai, 1997; Arai, 2001; Graham, 2001).

The correlation between jellyfish population abundance and nitrogen concentration in the North Sea was among the strongest of all variables tested here. The importance of nutrients in controlling jellyfish population sizes in this ecosystem has not been previously demonstrated. Due to the prominence of currents moving water through the North Sea west from the United Kingdom to the Baltic Sea increased nutrients were not believed to be retained in the ecosystem at high enough levels to impact jellyfish populations (Aria, 2001). Eutrophication of the German Bight has been observed and thought to have increased demersal fish catch, but changes in jellyfish abundance were not considered (Caddy, 1993). Jellyfish population change in this ecosystem are thought to result primarily from fluctuations in the NAO index as shown by the studies of Attrill, *et al*., (2007), Lynam *et al*., (2004), and Roff *et al*., (1988). My results suggest that nitrate concentrations in the North Sea may also be important in leading to population increase of jellyfish species. Correlation of the NAO to jellyfish abundance in the current study showed a statistically non-significant trend ($p= 0.007$) which will be discussed below.

The Black Sea also showed a significant correlation between jellyfish abundance and nutrient loading. The Black Sea is currently the largest body of eutrophic water in the world (Aria, 2001). Inputs of nutrients have greatly increased in recent years from a drainage basin covering 9 counties and areas of intense agriculture (Kolavov and Piontkovski, 1998). At present 90% of the water below the halocline is anoxic (Arai, 2001).

Such conditions have lead to a drastic shift in both species diversity and population sizes in this ecosystem. (Kolavov and Piontkovski, 1998). Such substantial environmental degradation in conjunction with increased fishing has contributed to stock collapse of many fish species and shifted the ecosystem to one dominated by small pelagics and jellyfish. Increased food availability resulting from large phytoplankton blooms and the ability of many jellyfish species including the introduced *M. leidyi* to persist in oxygen poor waters are recognized as the key factors leading to jellyfish population increases (Aria, 2001; Shiganova, 2001). However, it is difficult to separate the impacts of nutrients in the Black Sea from other anthropogenic impacts such as fishing and species introductions (i.e. *M. leidyi* and *Beroe* spp.). Further research is needed to quantify the relative effects and potential interactions among these variables on observed population trends.

The correlation of nutrient concentration to the abundance of *M. leidyi* in Narragansett Bay (2000's) was negative, but only based on four data points, therefore difficult to interpret. Nutrients and jellyfish abundance showed a negative correlation and the general trend in jellyfish population abundance was a decrease (rate of increase -0.185 for 1970's and -0.242 for 2000's). NAO mediated oceanographic impacts including variability in temperature and salinity are thought to have impacts on multiple north-western Atlantic jellyfish populations (Gulf of Mexico, Chesapeake Bay, and possibly Narragansett Bay. Although *M. leidyi* has been shown to be strongly correlated to zooplankton abundance in Narragansett Bay, it is possible that NAO

driven oceanographic impacts are the primary factor controlling population size of this species as will be discussed below.

The Gulf of Mexico did not show a significant relationship between either jellyfish species *C. quinquecirrha* or *A. aurita* and nutrient loading, however a positive correlation was observed between both species and temperature. Nutrient loading into the Gulf of Mexico is of great concern due to the scale of nutrients entering the ecosystem. The source of nutrient data for this system nutrient loading from the Mississippi-Atchafalaya River system is responsible for approximately 90% of the Gulf's freshwater input. The Mississippi water-shed covers 41% of the continental United States, 50% of which is farmland (Arai, 2001). As a result this river carries large amounts of nutrients (primarily in the form of runoff fertilizer) to the Gulf of Mexico (Arai, 2001). Nutrients entering the ecosystem follow the westward flow of water toward the Texas coast which has led to the formation of a 'Dead Zone' of hypoxic water covering up to 18000 km^2 of the Northwest Gulf (Aria, 2001).

Rates of nutrient flux into the Gulf of Mexico has been linked to high production rates of phytoplankton as well as to increased zooplankton grazing and secondary production and has also been coupled to tropic transfer of energy to fish in this region (Graham, 2001). Jellyfish as zooplankton predators create an alternative pathway for primary and secondary production, leading to potential increased competition between fish and jellyfish species, and to increased abundance of jellyfish in the Gulf (Graham, 2001). While a general increase in both jellyfish populations coincides with increasing nutrient input, the large year-to year variation in these variables may be obscuring a positive relationship (also note that available time series are relatively short).

In conclude that nutrient pollution leading to eutrophication has been observed to have impacts on a variety of ecosystems included some of those analysed here. Nutrient pollution has

also greatly impacted many ecosystems in Asia, though documentation of such change rarely

exists. Tokyo Bay, for example, has been affected by nutrient pollution resulting in the

extermination of most fish species and leading to multiple blooms of jellyfish including *A.*

aurita aggregations (Aria, 2001).

Effects of climate variability

Previous studies have shown climate indices specifically the NAO, PDO, and North

Pacific Index (NPI) to be of significant importance in the structuring of marine ecosystems. I

did not find climate to be generally correlated to jellyfish abundance in this study with

significant correlations in only 2/8 systems for which this variable was tested. The majority of

time series analyzed here were relatively short, between10-25 years. This may not be sufficient

to test changes due to long term variability in climate (~20-30 years for the PDO and ~10 for

the NAO). In the North Atlantic the NAO has been long established as a factor having

significant effects on both physical and biological processes of marine ecosystems. The role of

the NAO has been studied in far greater detail than the PDO and NPI of the North Pacific as

measures of NAO fluctuation have been back-calculated to the 1880's (Hurrell, 1995).

Although I did not find a statistically significant correlation between the NAO and

jellyfish population abundance in the North Sea, other studies have established its importance.

The North Sea is thought to have undergone a regime shift since the 1980's causing changes in

the abundance, distribution, and production of the pelagic environment. This regime shift is

considered to have caused a large increase in jellyfish abundance as a result of increased water

inflow to the northern North Sea, which increased primary productivity leading to increases in

prey abundance (Attrill *et al*., 2007). Atrill and colleagues report a significant positive

correlation between jellyfish abundance and the NAO in the northern North Sea (p < 0.001) but

did not find significant correlation between jellyfish and the NAO for entire North Sea (p= 0.07). Using Attrill's data for this study, I found the same non-significant trend (p = 0.07). Attrill's work and that of the current study contradict two earlier studies by Lynam *et al.,* (2004, 2005) which reported negative NAO effects on jellyfish abundance. Variation in the results between studies may come from differences in the length and temporal coverage as well as the removal of an outlier in the analysis of Lynam (2004)

A negative correlation was observed between the abundance of jellyfish and the NAO index in Chesapeake Bay. The jellyfish *C. quinquecirrha* and *M. leidyi* are the dominant jellyfish species in this system. They are becoming widespread in spring and summer and disappearing from the water column in the fall. Oceanographic conditions are known to determine the occurrence and distribution of both species (Cargo and King, 1990, Purcell and Decker, 2005). Occurrence of *C. quinquecirrha* has been correlated to low precipitation leading to increased salinity while *M. leidyi* has been correlated to increased spring water temperature.

The NAO, through impacts on such conditions may be a primary factor influencing the population abundance of both species. This relationship is exemplified by the high abundance of jellyfish in Chesapeake Bay from the 1960s to the mid 1980's when the NAO was strongly negative with decreased abundance of both species both before and toward the tail end of the negative cycle, continuing to decrease as the NAO shifted from a negative to positive phase (see figure 7). The large drop in population abundance occurring in the early 1970's is thought to be a direct result of Hurricane Agnes in 1972 (Purcell and Decker 2005). The hurricane led to low salinity which may have reduced polyp populations leading to reduced reproductive potential for scyphozoan jellyfish species. The impact of the hurricane on the eurohaline ctenophore *M. leidyi* is not known.

The NAO was not correlated to jellyfish population increase in the Gulf of Mexico though the NAO is hypothesized as a factor influencing jellyfish population size in that region (Graham, 2001). Both the NAO and El Niño Southern Oscillation (ENSO) cause variation

freshwater input and nutrient flux into the Gulf factors which lead to increased primary

production and thus increased resources for jellyfish (Graham, 2001). Hurricane activity in the

Gulf of Mexico could also have large indirect effects on jellyfish by increasing fresh water input

and thus decreasing salinity which will impact both rates of primary and secondary production

(Graham, 2001).

In the North Pacific the Pacific Decadal Oscillation (PDO) is thought to significantly

impact ocean temperature, the timing and extent of sea ice, storm activity, and the transport of

nutrients onto the continental shelf (Brodeur *et al.,* 1999). While numerous studies have

investigated climate effects on commercially important fish species, forage fish species, marine

mammals, production of phytoplankton and zooplankton, but few have investigated the impacts

of climate on jellyfish (Brodeur *et al.*, 1999). It appears that the oceanographic variation caused

by changes in the PDO could influence both the size and timing of phytoplankton blooms and

hence lead to variation in jellyfish abundance (Brodeur, 1999). However, I did not observe a

correlation between jellyfish population abundance and the PDO. Due to the long time scale at

which the PDO varies (~30 years) it is possible that the current studies time frame was too short

to investigate this fully.

A climate regime shift in 1977 is also thought to have strongly impacted species in the

Gulf of Alaska potentially leading to the observed increases in jellyfish abundance (Anderson

and Piatt, 2000). This hypothesis is supported by the current study, which documented a

positive correlation between jellyfish and climate in this system. The mechanisms for observed

increases in abundance following the regime shift remain unknown. Leading hypotheses point

to wind forcing promoting increases in both phytoplankton and zooplankton which could lead to

enhanced fish recruitment and jellyfish abundance (Anderson and Piatt, 2000).

Effects of temperature

Temperature was found to be significantly correlated to jellyfish abundance in Gulf of Alaska, Chesapeake Bay, and Gulf of Mexico. Previous research has shown water temperature to play a crucial role in determining yearly zooplankton production in the Northeast Pacific (Brodeur *et al.*, 2002). Warm temperatures are associated with higher production while low production in cold years leads to increased resource competition between zooplankton predators. Increased temperature resulting in increased zooplankton production would yield increased resources for jellyfish relieving resource competition between species and ultimately causing increased abundance of jellyfish. It is also thought that jellyfish eventually grow to sizes that allow them to escape predation. Therefore increased food availability resulting indirectly from increased water temperature could allow jellyfish to reach large size faster (Brodeur *et al.*, 2002). These potential mechanisms may explain positive correlation observed between jellyfish and temperature in the Gulf of Alaska.

Temperature was positively correlated to both *A. aurita* and *C. quinquecirrha* in the Gulf of Mexico. This effect has not been previously discussed in this ecosystem. I propose that the positive trend results from processes similar to those explained in for the Gulf of Alaska above (Increased water temperature leading to stratification, increased production and food availability for jellyfish in addition to allowing jellyfish to have increased growth rates decreasing predation risk (Brodeur *et al.*, 2002).

In contrast to the Gulf of Alaska and Gulf of Mexico, temperature was negatively correlated with jellyfish abundance in Chesapeake Bay. *C. quinquecirrha* are primary predators of *M. leidyi* in the Chesapeake Bay ecosystem. As *M. leidyi* occurs and reproduces when water temperature is higher, increased water temperature may allow *M. leidyi* to grow beyond the vulnerable early life stages and avoid predation by *C. quinquecirrha* (Purcell and Decker, 2005). Such change could shift *C. quinquecirrha*'s diet from jellyfish to zooplankton and

ichthyoplankton, and increase the overall abundance of *M. leidyi.* This hypothesis is not supported here, however, and the mechanism explaining a negative correlation between jellyfish and temperature is not known.

Salp species such as *S. thompsoni* which feed directly on phytoplankton could also benefit from increased temperature indirectly through decreased sea ice leading to larger phytoplankton blooms (Loeb *et al.*, 1997). Temperate increase in Antarctica has been observed since the 1940's and due to the strong correlation between air temperature and the extent of sea ice it is surprising that a correlation between salp population size and air temperature was not observed in the current study.

Impacts of forage fish abundance

In this study forage fish were found to be both positively and negatively correlated to jellyfish population abundance. Decreases in forage fish abundance are thought to have significant positive impacts on jellyfish through decreasing resource competition for zooplankton prey (Lynam, *et al.,* 2005). The diets of most jellyfish species overlap with forage fish as both prey on copepods, cladocerans, larvaceans, fish eggs, icthyoplankton, and meroplanktonic invertebrate larvae (Purcell, 2001). Decreasing forage fish abundance as a result of fishing, larval predation by jellyfish or other causes would increase the above food resources and could account for increases in jellyfish abundance observed in the Bering Sea and Gulf of St. Lawrence (Purcell, 2001; Lynam *et al.,* 2005).

Decreased competition for food resources between *A. aurita* and forage fish species has been noted as an important factor leading to large population increase in this species prior to the introduction of *M. leidyi* in the mid 1980's (Shiganova, 2001; Dansolv, 2003). *A. aurita* were found at highest recorded abundances in the early 1980s a time corresponding to catch of 1

million tons for anchovy, sprat and horse mackerel*)* (Dansolov, 2003). Likewise, decreased abundance of forage fish species has been hypothesized to cause an observed population explosion of jellyfish off Namibia (Lynam *et al.*, 2006). I could not confirm these trends in the current study, probably in part due to low sample sizes in the Namibian data.

Though there has been much speculation about competition between forage fish and jellyfish in many ecosystems including those presented above, there has been few direct comparisons of the diets of these groups. Purcell and Sturdevant (2001), attempted to quantify diets of four jellyfish and four forage fish species in the Gulf of Alaska. This study found percent similarity indices (PSI) comparing diets of these species to average 50% and reach as high as 78%. Further studies of its kind are needed before any quantitative estimates of competition between jellyfish and forage fish can be conclusively made (Purcell, 2001).

In contrast to the hypothesized competition between jellyfish and forage fish I observed positive correlations between in Chesapeake Bay, North Sea, and Black Sea. I suggest that in these systems, there is an underlying driver (e.g. food abundance, temperature, and/or climate) that affects these species groups in a similar way, causing some degree of synchrony over time. For further research it will be important to understand the mechanisms of resource overlap and potential competition between forage fish and jellyfish, so that more definitive conclusions on the importance of these interactions in marine ecosystems can be made.

Removal of predators by fishing

Increased fishing effort resulting in large removals of predatory fish species is of great concern in most ecosystems (Pauly *et al*., 1998; Myers and Worm 2003). As the predators of jellyfish are poorly understood it becomes very difficult to correlate changes in predatory fish

abundance to observed changes in jellyfish populations. Also as stock assessments and abundance estimates for many known jellyfish predators are not available the analysis of predatory species verse jellyfish had to be carried out using representative predator species (i.e. species of known predatory importance in representative ecosystems but whose impact on jellyfish abundance is unknown). This results in a large potential for error, as these species may not represent actual predation impacts on jellyfish.

Negative correlations were found between jellyfish species and predatory fish in two of six systems analysed (Black Sea and Bering Sea), which are both intensely fished. Increase in *A*. *aurita* in the Black Sea prior to the introduction of M. *leidyi* has been hypothesised to be the result of both decreases in forage fish competitors and predatory mackerel species supporting the findings of the current study (Purcell, 2001; Daskalov, 2003). A similar correlation between predatory fish and jellyfish has also observed in the Adriatic Sea (Purcell, 2001).

Jellyfish predators

The importance of jellyfish as prey species has often been overlooked for several reasons. First it is very difficult to identify jellyfish tissue using standard methods of diet analysis (Harison, 1984; Arai, 2005). Second jellyfish have long been labelled as 'dead ends' in marine food webs, such that they would not be consumed in the pelagic ecosystems but instead simply sink to the bottom (Mainzan, *et al.,* 2001; Arai, 2005). Third as jellyfish contain a high ratio of water to tissue it has been assumed that such species have little nutritional value (Arai, 2005).

Most preservation methods of predator species such as freezing or fixation in formalin and alcohol lead to a loss of soft tissues (Arai, 2005). As jellyfish lack hard skeletons, estimation of jellyfish abundance in preserved stomachs is often impossible. Even if

preservation is not done prior to analysis of stomach contents the rapid degradation of the soft tissue comprising jellyfish often makes them indistinguishable among other stomach contents (Harrison, 1984).Better preservation techniques, and better methods of identifying broken down tissue are hence needed.

Though often considered 'dead ends' in marine food web, jellyfish are often a good prey choice for marine predators. Although jellyfish are relatively low in utilizable energy (calorimetric values less than 20% that of arthropods (Davis *et al.,* 1998)) the speed at which jellyfish tissue can be broken down and assimilated into the biomass of the predator far exceeds rates of other prey items (Arai, 2005). For example, Arai (2003) found digestion rates of jellyfish by chum salmon (*Oncorhynchus keta*) to be more than 20 times faster than for shrimp. For this reason if jellyfish is present in high abundances it may prove more effective for a predator to feed on jellyfish than other available prey.

In addition jellyfish are often hosts to a variety of parasitic organisms including amphipods, barnacles, and helminths (Arai, 2005). This diversity of associated organisms, in addition to the relatively low mobility of jellyfish presents a unique opportunity to easily capture prey (Harrison, 1984). From this finding Harrison (1984) hypothesized jellyfish to be an important prey species in the Bering Sea food web.

As for our current knowledge of jellyfish predators the leatherback, loggerhead, hawksbill, and green sea turtles stand out. These species are well established predators of jellyfish, while the importance of the remaining species of marine turtle as jellyfish predators remains unknown (Arai, 2005; Benson *et al.,* 2007). With all species of marine turtle are currently listed on the IUCN Redlist, it is not currently understood what impacts past or future decreases in the population size of marine turtles have on jellyfish population abundance (IUCN, 2007).

Though only few fish species are known to feed selectively on jellyfish prey (ocean sunfish, spiny dogfish, and butterfish) many others are generalists which consume jellyfish occasionally. Throughout my literature search I find this group of generalist jellyfish predators to be larger and more diverse than previously believed. Thirteen families of fish were found to consume high to very high levels of jellyfish ($\geq$ 20% stomach contents), and jellyfish was observed as prey in an additional 10 families (10-20% stomach contents). As global fishing effort continues to increase and jellyfish appear to be increasing as well in many ecosystems it is important in an for ecosystem management context to determine how further fishing will affect abundances of prominent jellyfish species.

Invertebrate predators, primarily other jellyfish species were found to be capable of controlling population size of many jellyfish species. The jellyfish *C. quinquecirrha* can remove *M. leidyi* from Chesapeake Bay while other species including the siphonophore *Apolemia uvaria* feeds almost exclusively on hydromedusae and ctenophores (Arai 2005; Purcell and Decker 2005). Nudibranchs are the primary molluscan predators of jellyfish and are known to feed on both benthic polyp and planktonic medusa forms (Arai, 2001). The nudibranch *Coryphella verrucosa* has been observed controlling the population size of *A. aurita*, while other species including *Glaucilla marginata* and *Fiona pinnata* feed almost exclusively on jellyfish (Arai, 2005). Though no quantitative and little qualitative evidence of mollusc predation outside nudibranchs has been recorded, the cephalopods *Loligo opalescens* and *Argonauta argo* have been observed feeding on jellyfish species (Arai, 2001). While many arthropods are known to interact with jellyfish both through parasitic and commensal relationships the importance of these species as potential predators is not understood.

Very few studies have investigated the role of jellyfish prey in the diet of marine birds. Harrison's (1984) pioneering work found jellyfish prey in the stomachs of 11 out of 17 species investigated in the Bering Sea. Harrison found jellyfish to be more prominent in bird diets

summer, when jellyfish are more abundant. It is therefore possible that factors leading to increases in jellyfish abundance could result in increased predation rates by such bird species. The results presented are an underestimate of the importance and prevalence of jellyfish as prey to birds. As birds must be killed to determine stomach contents, sample sizes are generally small providing only limited insights into patterns of bird predation in marine systems.

While many species do utilize jellyfish as a food source on a regular basis, there is also evidence that others rely on jellyfish as 'survival food' when their primary prey are in low abundance. Mianzan *et al.* (2001) showed this trend in anchovy off the coast of South America. Anchovy feed primarily on crustacean zooplankton but were found to consume large quantities of salps when crustacean plankton abundance was low, a trend that appears to hold true for a number of fish species (Mianzan *et al*., 2001). This trend is also seen in many marine birds. Bird species have been shown to change feeding strategies to jellyfish as other prey's abundances changed throughout the year (Harrison, 1984). Though the extent of `survival` feeding on jellyfish is not known, it points to a further importance of jellyfish as prey in marine communities.

Caveats of the current study

The major factor biasing the results of the current study is the lack of available data. Due to a historic lack of recognition as an important part of the food web, and also due to sampling problems, long term records of jellyfish abundances do rarely exist. The shortness and of available time series, however, is making it difficult to determine factors leading to jellyfish population change. In addition all data compiled here originated in the western hemisphere. This is surprising considering the known problems resulting from increasing jellyfish populations in regions such as Australia and Asia (Burnett 2001; Purcell 2007). Also it would

be expected that more data would be available from Asia due to the large jellyfish fisheries in countries such as China and Japan (FAO, 2007).

Data records were also difficult to obtain for potentially important jellyfish predators. For this reason the analysis of relationships between jellyfish and predatory fish abundance was based on population records for well understood predator species, not all of which may prey on jellyfish. This of course makes the observed correlations hard to interpret. Values of nutrient pollution were also difficult to obtain for most regions with information only available for the eastern coast of North America, Black Sea and North Sea. This is surprising as nutrients are the basis of trophic interactions and the functioning of marine ecosystems. Lack of available data makes it difficult to resolve multiple causations and thus the potential for synergistic effects could not be determined.

Finally, the use of simple correlation analysis is fraught with uncertainty, as correlation does not prove causation. Mechanistic studies, experiments, and meta-analytic comparisons may allow for further insight into some of the factors that influence jellyfish populations worldwide. However, based on the preliminary results from this study I would caution that no single factor seems to be decisive, and multiple causalities and potential interactions among climate, nutrients, and predation are possibly important in affecting jellyfish population trends in different marine ecosystems.

Conclusions

The current study expands upon previous knowledge of factors impacting jellyfish population abundance. Although jellyfish were not found to be strongly correlated to either temperature or climate, these factors have been established to have significant impacts on marine communities and have potential to influence jellyfish population abundance as exemplified in the Gulf of

Mexico, Chesapeake Bay, and North Sea. Nutrient pollution and forage fish abundance were found to be more important than previously thought, and point to the potential for further jellyfish population increase as a result of increased nutrient pollution and high levels of fishing effort. It still remains unknown how predatory fish abundance affects jellyfish. The compilation of jellyfish predators presented here shows many previously underrepresented groups to be important in affecting jellyfish populations through predation.

With a better understanding of the population dynamics of such predatory species it will become apparent how they may affect jellyfish population size. Though one factor alone cannot be said to cause jellyfish population change, synergistic factors that appear to have the greatest influence on jellyfish population size are all linked. Climate variability directly affects temperature and often nutrient supply, both of which impact jellyfish and potential jellyfish prey. As longer more complete records of jellyfish population abundance become available it will become possible to further separate the independent effects of factors leading to jellyfish population change and therefore lead to a better understanding of how climatic, anthropogenic, and biological variation interact in structuring marine ecosystems.

Appendix 1. System specific description and source information for Jellyfish population abundance records, and all variables analysed in the current study

System	Time Series Variable	Description	Units	Source
Bering sea	Jellyfish	Jellyfish	Tons	Overland *et al.* (2005)
	Climate Index	PDO	°C	Mantua (ND.b)
	Temperature	SST	°C	Mantua (ND.b)
	Forage Fish	Herring, landings	Metric tons	Witherell, *et al.* (2000)
	Predators	Pacific Cod & Walleye Pollock, biomass	Metric tons	AFSC (2006)
Gulf of Alaska	Jellyfish	Jellyfish, CUPE	Kg Km^{-1}	Anderson and Piatt (1999)
	Climate Index	PDO	°C	Mantua (ND.b)
	Temperature	Normalized water column temperature	°C	Anderson (2000)
	Forage Fish	Herring, trawl survey	Tons	Boldt, e*t al.* (2005)
	Predators	Pacific Cod & Walleye Pollock, trawl survey	Tons	Cod: Boldt, *et al.* (2005); Walleye Pollock: Guttormsen (2007)
Chesapeake Bay	Jellyfish	Jellyfish	Average daily counts (1000m^{-2})	Cargo and King (1990) series continued by Denise Breitburg at the Smithsonian Estuarine Research Center (Unpublished)
	Climate Index	NAO	Noramlized sea level air pressure anomaly	Hurrell (2005)
	Temperature	SST	°C	Cargo and King (1990) series continued by Denise Breitburg at the Smithsonian Estuarine Research Center (Unpublished)
	Forage Fish	Alewife, Silverside, Bay Anchovy, Blueback Herring, Menhaden, Mummichog & Spotttail Shiner, Seine survey	Geometric mean	Durell and Weedon (2007)
	Predators	Stripped Bass & Bluefish, seine survey	Geometric mean	Durell and Weedon (2007)

Appendix 1 (*continued.*)

North Sea	Jellyfish	Jellyfish, abundance	Percent frequency of nematocysts (presence/absence)	Atrill, *et al.* (2007)
	Climate Index	NAO	Noramlized sea level air pressure anomaly	Hurrell (2005)
	Temperature	SST	°C	Wiltshire and Manly (2004)
	Nutrients	Nitrate concentration, yearly median values	µmol L^{-1}	Hickel, *et al*. (1992)
	Forage Fish	Atlantic Herring, Biomass	Tons	ICES, 2007
	Predators	Atlantic Cod, biomass	Tons	ICES, 2008
Black Sea	Jellyfish	Jellyfish	Relative abundance index	B mstedt U (2005)
	Temperature	SST	°C	
	Nutrients	Inorganic phosphorous loading	Tons	Daskalov (2003)
	Forage Fish	Anchovy, Sprat & Horse Mackerel, biomass	Relative abundance, carbon weight (g C m^{-2} yr^{-1})	Daskalov (2003)
	Predators	Mackerel, Bonito, & Bluefish , biomass	Relative abundance, carbon weight (g C m^{-2} yr^{-1})	Daskalov (2003)
Gulf of St. Lawrence	Jellyfish	Jellyfish, Abundance	Individuals (m^{-2})	Harvey, *et al.* (2004)
	Climate Index	NAO	Noramlized sea level air pressure anomaly	Hurrell (2005)
	Temperature	Average temperature 0-30m Depth	°C	Galbraith, *et al.* (2007)
	Forage Fish	Capelin, landings	Tons	DFO (2006)
	Predators	Atlantic Cod, trawl survey	Normalized abundance index	DFO (2007)

Appendix 1 (*continued.*)

Greenland	Jellyfish	*Agiantha digitale (average red and white forms),* biological survey	Survey study, abundance indicies	Pederson and Smidt (2000)
	Climate Index	NAO	Noramlized sea level air pressure anomaly	Hurrell (2005)
	Temperature	Average temperature 10-50m Depth	°C	Pederson and Smidt (2000)
	Forage Fish	Sandeel Larvae (average of 3 transects), biological Survey	Abundance indicies	Pederson and Smidt (2000)
	Predators	Atlantic Cod, landings	Tons	Buch, *et al*. 2004.
Narragansett	Jellyfish	*Mnemiopsis leidyi*, Biomass	Number (m^3)	
	Climate Index	NAO	Noramlized sea level air pressure anomaly	Hurrell (2005)
	Temperature	SST	°C	Univeristy of Rhode Island The Graduate School of Oceanography Bottom Trawl Survey
	Nutrients	Nitrate & disolved inorganic phosphrous	µmol	Univerity of Rhode Island Plankton Database
Namibia	Jellyfish	*Aequorea aequorea and Chrysaora hysoscella ,* Biomass	Tons	Fearson, *et al*. (1992)
	Temperature	SST	°C	Jury and Courtney (1995)
	Forage Fish	Round Sardinella & European Anchovy, acoustic biomass estimates	Tons	Hutchings, *et al*. (1998)
	Predators	Snoek, handline landings	Tons	Hutchings, *et al*. (1998)

Appendix 1 (*continued.*)

Mediterranean	Jellyfish	*Liriope tetraphylla,* biomass, verticle plankton tow	number individuals per $10m^3$	Buecher, *et al*. (1997)
	Temperature	Average temperature 0-75m depth	°C	Licandro, *et al*. (2006)
Gulf of Mexico	Jellyfish	*Chrysaora quinquecirrha* & *Aurelia aurita, Biomass use in analysis jellyfish increase with time (combined abundance) factors increasing (seperate)*	standard catch	Graham (2001)
	Climate Index	NAO	Noramlized sea level air pressure anomaly	Hurrell (2005)
	Temperature	SST	°C	Earth System Research Laboratoy (ND)
	Nutrients	Nitrate + nitrate, Nutrient loading	Metric tons	Goolsby *et al*. (2001)
Azov Sea	Jellyfish	*Mnemiopsis leidyi, biomass*	grams m^{-2}	Shiganova (2001)
	Forage Fish	European Anchovy, biomass	grams m^{-2}	Shiganova (1998)
Antarctica	Jellyfish	*Salpa thompsoni,* abundance	number of individuals (Mean $1000m^3$)	Loeb *et al*. (1997)
	Temperature	Air temperature	°C	Loeb *et al*. (1997)

APPENDIX 2. Fish predators. Data gathered from Aria 2005. Occurence rate converted to percent by dividing values of prey occurenec by total number of stomachs investigating and mutiplying the value by 100.

Family	Species	prey	% Consumption rate	% occurence	N	source
Carcharhinidae	Galeorhinus galeus	Velella	24.8		no./ 14 st.	Brodeur *et al.*, 1987
Squalidae	Squalus acanthias	Velella, Siphonophore, cnidaria, Ctenophora	52.3		no./ ≥ 343 st.	Brodeur *et al*., 1987; Brodeur & Pearcy, 1992; Laptikhovsky, *et al.* 2001.
		Ctenophora		19.91	obs/ 221 st. (winter)	Mianzan, *et al.* 1996
Rajidae	Bathyraja macloviana	Ctenophora		17.74	obs/ 64 st. (spring)	Mianzan et al. 1996
Clupeidae	Alosa aestivalis	Ctenophora	43		wt./ 11 st.	Bowman et al., 2000
Argentinidae	Argentina silus	Ctenophora	9.2		wt./ 24 st.	Bowman et al., 2000
Bathyergidae	Bathylagus antarcticus	siphonophores		50.00	obs/ 28 st.	Lancraft et al., 1991
	Bathylagus pacificus, Leuroglossus schmidti, Lipolagus ochotensis Pseudobathylagus milleri (medusae consumption	medusae	32.7		wt./ ≥ 5473 st.	Balanov *et al*., 1995; Sobolevskii & Senchenko, 1996; Gorbatenko & Il'inskii, 1992; Il'inskii & Gorbatenko, 1994; Balanov *et al.,* 1994;

Appendix 2 (*continued.*)

Family	Species	Prey	Value 1	Value 2	Measure	Reference
Alepocephalidae	Alepocephalus rostratus	Pelagic coelenterates, Siphonophores	31.9		no./≥ 128 st.	Carrasson & Matallanas, 1990
Salmonidae	Oncorhynchus keta, O. Kisutch, O. Clarki clark	Ctenophore, Velella, Hydromedusae		13.78	obs./ ≥ 667 st.	Healey, 1991; Brodeur *et al.*, 1987
	Oncorhynchus keta	Beroe, Jellyfish	18.2		wt./ ≥ 314 st.	Sobolevskii & Senchenko, 1996; Tadokoro et al., 1996
Myctophidae	Stenobrachius leucopsarus, S. nannochir	Medusae	9.32		wt./ 1394 st.	Gorbatenko & Il'inskii, 1992; Balanov et al., 1994; Il'inskii & Gorbatenko, 1994; Sobolevskii & Senchenko, 1996
Gadidae	*Pollachius virens*	Medusae		17.29	obs./ 133 st.	Hall et al., 1990
Scombersesociadae	*Scomberesox saurus*	Siphonophora	54.4		wt./ 30 st.	Bowman et al., 2000
Scomberesocidae	*Sebastes melanops*	Pleurobrachia; Beroe	13.3		wt./ 50 st.	Brodeur et al., 1987; Brodeur & Pearcy, 1992
	Helicolenus dactylopterus, Sebastes mystinus	Velella, Stephanomia, Pleurobrachia, Scyphozoa, Muggiaea, Beroe, Ctenophora, Cnidaria		28.13	obs./ ≥ 372 st.	Brodeur, *et al.* 1987; Hobson & Chess, 1988; Brodeur & Pearcy, 1992; Hobsen *et al.*, 1996
Anoplopomatidae	*Anoplopoma fimbria*	Velella, Cnidaria, Scyphomedusae	13.01		wt./ 907 st.	Brodeur et al., 1987; Brodeur & Pearcy, 1992

Appendix 2 (*continued.*)

Family	Species	Prey			Method/stations	Reference
Hexagrammidae	*Pleurogrammus monopterygius*	Scyphomedusae	19		wt./ 42 st.	Yang & Nelson, 2000
Teraponidae	*Terapon theraps*	Siphonophora		38.60	obs./57 st.	Senta et al., 1993
Carangidae	*Trachurus murphyi*	Siphonophora	27.7		wt./ 57 st.	Nevin, 2004
Sciaenidae	*Micropogonias furnieri*	Ctenophora		10.57	obs./350 (spring)	Mianzan et al., 1996
Kyphosidae	*Kyphosus cinerascens, K. vaigiensis*	Siphonophora		61.07	obs./ ≥ 54 st.	Senta et al., 1993
Ephippidae	*Chaetodipterus faber*	Chiropsalmus	9.4		vol./ 177 st.	Hayse, 1990
Zoarcidae	*Bothrocarina microcephala, Lycogrammoides schmidti*	Medusae	8.68		wt./ ≥ 190 st.	Il'inskii & Gorbatenko, 1994
Nototheniidae	*Lepidonotothen squamifrons*	Ctenophora, Medusae	29		wt./ 50-2231 st. (depending on month)	Pakhomov, 1993
	Patagonotothen ramsayi	Ctenophora		18.52	obs./ 81 st. (spring)	Mianzan et al., 1996
		Mnemopsis		65.31	no./ 81 st. (summer)	Laptikhovsky & Arkhipkin, 2003

Appendix 2 (*continued.*)

Centrolophidae	*Seriolella porosa*	Ctenophora		46.62	obs./133 st. (spring/summer)	Mianzan et al., 1996
Stromateidae	*Peprilus triacanthus*	Cnidaria	8.7		wt./327 st.	Bowman et al., 2000
	Stromateus brasiliensis	Ctenophora		75.79	obs./ 285 st. (spring/summer)	Mianzan et al., 1996
Balistidae	*Canthidermis maculata*	Siphonophora		27.27	obs./ 66 st.	Senta et al., 1993

st. stomachs examined; obs., stomachs in which jellyfish were observed no., number; wt., weight

Appendix 3. Non fish predators. Dietary importance subdivided as follows: Very high, greater than 50% stomach contents, and specialized predators; high between 20-50% stomach contents, and generalist predators. Present, between 10-20% stomach contents, generalist predators; and unknown

Predator Group	Subgroup	Known Species	Percent Occurrence	Importance to diet	Source
Reptiles	Marine turtles	*Chelonia mydas* (Green Turtle)		Unknown	Arai (2005)
		Caretta caretta (Loggerhead Turtle)		Present	Arai (2005)
		Dermochelys coriacea (Leatherback Turtle)		Very High	Ates (1991); Arai (2005); Benson, *et al. (*2007)
		Eretmochelys imbricate (Hawksbill Turtle)		Present - High	Ates (1991)
Birds	Family Procellariiformis	*Fulmaris glacialis* (Northern Fulmar)	45 obs. /136 st.	Unknown	Harrison (1984)
		Puffinus griseus (Sooty Shearwater)	50 obs. / 2 st.	Unknown	Harrison (1984)
		Puffinus tenuirostris (Short-tailed Shearwater)	23 obs. /36 st.	Unknown	Harrison (1984)
		Oceanodroma furcata (Fork-tailed Storm-Petrel)	37.5 obs. /55 st.	Unknown	Harrison (1984)
	Family Laridae	*Rissa tridactyla* (Black-legged Kittiwake)	43 obs. /32 st.	Unknown	Harrison (1984)
		Larus hyperboreus (Glaucous Gull)	50 obs. / 2 st.	Unknown	Harrison (1984)
	Family Alcidae	*Aethia cristatella* (Crested Auklet)	50 obs. / 2 st.	Unknown	Harrison (1984)

		Uria aalga (Common Murre)	20 obs. / 20 st.	Unknown	Harrison (1984)

Appendix 3. (*continued.***)**

		Uria lomvia (Thick-billed Murre)	20 obs ./ 10 st.	Unknown	Harrison (1984)
	Family Diomedeidae	*Diomedea* spp. (albatross)		unknown	Catry et al (2004)
Jellyfish	Hydromedusae			High - Very High	Arai (2005)
	Scyphozoa			High - Very High	Purcell and Decker (2001); Arai (2005)
	Ctenophores			High - Very High	Kovalov (1998); Arai (2005)
Molluscs	Nudibranchs	*Glaucid nudibranchs*		High	Thompson and Bennett (1970)
	Cephlopods	Market Squid		Unknown	Brodeur and Pearcy, 1992)
Arthropods	Classes Malacostraca, Copepoda, Ostracoda, Cirripedia, and Poycnogonida			Unknown	Arai (2005)

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