

Exploring intraspecific life history patterns in sharks

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Marine ecosystems compose the major source (85%) of world fisheries production (Garcia and Newton, 1997). Although only a few fish species tend to dominate fishery catches (Jennings et al., 2001), a large diversity of fishes representing varied taxonomic levels, ecological guilds, and life histories is commonly taken. Recently, 66% of global marine resources were determined to be either fully, heavily, or over-exploited (Botsford et al., 1997). Considering the current state of many fisheries, the large diversity of species taken globally, and the general lack of resources to adequately assess many stocks, it has become important to develop shortcuts that may provide methods fisheries scientists can use to determine which stocks are in danger of overexploitation and which recovery plans are appropriate when biological data are limited (Stobutzki et al., 2001).

Applications of life history theory have proven a potentially useful means to accomplish such tasks (Stearns, 1992; Reynolds et al., 2001). Life history traits such as maximum size and age, maturity, mortality, and growth are correlated among teleost fishes (Adams, 1980; Wine-miller and Rose, 1992; Gunderson, 1997; Cortés, 2000) and the relationships among such traits can be used to infer some general life history patterns. These general patterns reveal that teleost fishes with higher maximum ages tend to be larger, mature later, grow more slowly, and have lower natural mortality rates (K-selected species, Adams, 1980), whereas teleost fishes with lower maximum ages tend to show the opposite relationships (r-selected species, Adams, 1980). Correlations among traits may also allow one to approximate dif-

ficult to measure life history traits from traits that are easier to measure and possibly anticipate response to exploitation rates where life history data are limited (Jennings et al., 1999).

Applying these patterns to fisheries trends reveals some consistent and useful explanations. Jennings et al. (1998) found that teleost fishes from the northeast Atlantic that have decreased in abundance are generally K-selected species. Jennings et al. (1999) demonstrated that tropical teleost fishes of greatest maximum sizes were most vulnerable to exploitation. And Rochet (2000) illustrated the limitations of life history plasticity to compensate for heavy fishing pressure among four orders of teleosts.

Elasmobranchs, and particularly sharks, have also shown life history patterns similar to those of teleosts (Cortés, 2000; Frisk et al., 2001). Cortés (2000) offered three general life history patterns for sharks: 1) large litters, moderate to high longevity, large size, small offspring, slow growth, 2) small litters, high longevity, large size, large offspring, slow growth and 3) small litters, low longevity, small size, small offspring, fast growth. Simplified applications of the life history patterns have also been applied to elasmobranch fisheries. Smith et al. (1998) demonstrated that larger, later-to-mature Pacific shark species have lower rebound potentials (i.e., abilities to recover from fishing pressure), whereas Frisk et al. (2001) showed a similar pattern in sharks and rays in the north Atlantic. These relationships have been recommended as particularly useful when managing data-poor elasmobranch species (Musick et al., 2000).

As indicated by the above studies, variation in life history traits and patterns among shark species is well established (Cortés, 2000) and such relationships may be useful for the management of these fishes, but it is not known how these relationships may change within a species. Specifically, if and how do intraspecific life history traits of cosmopolitan species vary in different areas of the world? The spiny dogfish (*Squalus acanthias*) provides an alluring preamble to the topic: northeast Pacific spiny dogfish have been aged to 80+ years, and females mature at around 35 years (Jones and Geen, 1977; Saunders and McFarlane, 1993), whereas spiny dogfish in the north Atlantic obtain a maximum age of about 40 years, maturing at 12 years (Rago et al., 1998).

In the present study, I used generalized linear models (GLMs) to investigate whether spatial differences in life history traits, such as those seen in the spiny dogfish, reveal consistent patterns when compared with other spatially resolved life history information from other shark species. I then, as demonstration of potential utility, applied these models to predict life history trait values for areas lacking information for two species of shark, spiny dogfish (*S. acanthias*) and blue shark (*Prionace glauca*).

Materials and methods

Information for five life history traits (age at maturity, longevity (maximum age), mean fecundity, maximum size, and size at maturity) from 17 shark species in six families (Appendix, Table 1) for seven general areas (North Pacific (NP); North Atlantic (NoA); Gulf of Mexico (GM); Indian Ocean (I); Central Pacific (CP); South Pacific (SP); South Atlantic (SA)) was extracted from three primary literature sources (Smith et al., 1998; Cortés, 2000, 2002). Area distinctions were based on those by Cortés

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Table 1

List of shark species used in the analyses. Species abbreviations are used in tables and figures to simplify presentation.

Scientific name	Common name	Abbreviation
Carcharhinidae		
<i>Carcharinus acronotus</i>	Blacknose shark	Cac
<i>Carcharinus amblyrhynchos</i>	Grey reef shark	Cal
<i>Carcharinus falciformis</i>	Silky shark	Cfa
<i>Carcharinus leucas</i>	Bull shark	Cle
<i>Carcharinus limbatus</i>	Blacktip shark	Cli
<i>Carcharinus longimanus</i>	Oceanic whitetip shark	Clo
<i>Carcharinus obscurus</i>	Dusky shark	Cob
<i>Carcharinus plumbeus</i>	Sandbar shark	Cpl
<i>Galeocerdo cuvier</i>	Tiger shark	Gcu
<i>Prionace glauca</i>	Blue shark	Pgl
<i>Rhizoprionodon taylori</i>	Australian sharpnose shark	Rta
Sphyrnidae		
<i>Sphyrna lewini</i>	Scalloped hammerhead shark	Sle
Triakidae		
<i>Galeorhinus galeus</i>	Soupsfin shark	Gga
Lamnidae		
<i>Isurus oxyrinchus</i>	Mako shark	Iox
Alopiidae		
<i>Alopias superciliosus</i>	Bigeye thresher shark	Asu
Squatinae		
<i>Squalus acanthias</i>	Spiny dogfish	Sac
<i>Squalus mitsukurii</i>	Shortspine spurdog	Smi

(2000). Spatial resolution to the particular ocean basins in this study was defined by the information I was able to obtain, as were the choice of species and life history traits to analyze. Although other information for these and other species may be currently available, I limited my data to those found in primary peer-reviewed literature. When mean fecundity values were unavailable, the mean was assumed to be the middle value of the fecundity range given. Phylogenetic variance was controlled because I strictly evaluated intraspecific comparisons.

Initial data exploration was performed by visualizing intraspecific gender-based pairwise comparisons by area with dot plots (Fig. 1). Within each species and gender, the outcome of each comparison (i.e., the value for a particular trait in one area greater than, less than, or equal to that of another area) was evaluated. An overall relationship among areas for each life history trait was then constructed as a composite of each pairwise result. The purpose of this exercise was to visually explore the data and assess whether any intraspecific life history patterns by area were apparent.

A GLM framework was then used to construct simple models that quantitatively relate the effect of certain factors (e.g., area, gender, or taxonomic level) to a response variable—in this case to a particular life history trait. The flexibility of the GLM framework also allows one to consider non-normal response distributions

while maintaining the advantages of linear regression (Venables and Ripley, 2002) by means of a link function relating the response variable mean to the linear predictors. I had no *a priori* knowledge of the variance structure for each life history trait (some of which will not have variance, given that they are maximum recorded values), so both lognormal (with an identity link) and gamma (with a log link) distributions were considered because of their appropriateness to continuous and nonzero data. Akaike's information criterion (AIC; Burnham and Anderson, 2002) was used to select among models, with the lowest AIC value indicative of the most appropriate model among all considered. Models explored included all combinations of the following factors: area, gender, and the taxonomic levels of species, genus, or family. Models that included the interaction between gender and area and gender and taxonomic level were also considered. Area effects and predictions of life history values among models with the use of the lognormal and gamma distributions were similar, but models with gamma error structure resulted in the lowest standard errors for area effects; thus a gamma error structure was ultimately chosen for each model.

Resultant model effects were used to compare area effects and to predict species- and gender-specific life history trait values for each area. The predicting models were then applied to two species (*S. acanth-*

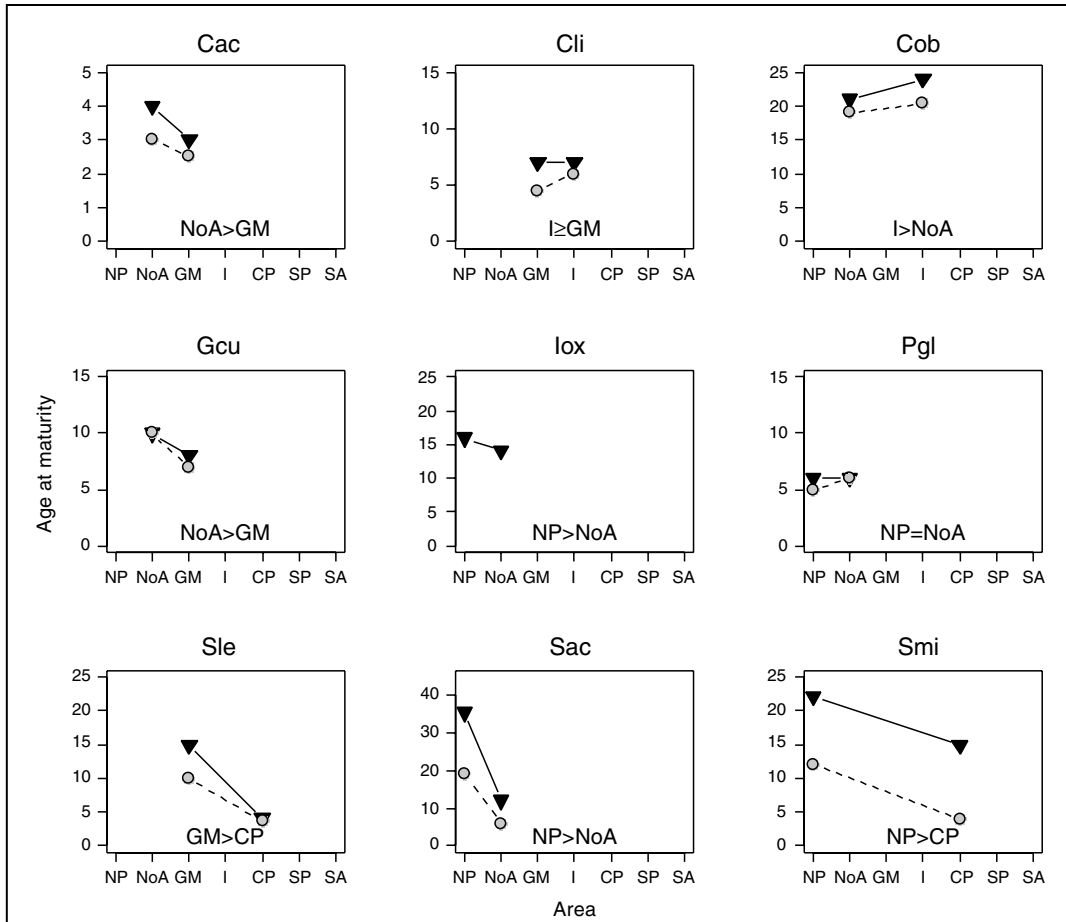


Figure 1

Example of plots used to evaluate the pairwise life history trait (y-axis) comparisons among areas (x-axis) by species (indicated by the abbreviation at the top of each panel). Gender-specific age at maturity (solid triangles=females; solid circles=males) is illustrated in this example, and the qualitative outcome of the pairwise comparisons is provided within each panel. A key to the species abbreviated names is found in Table 1. Areas: NP=North Pacific; NoA=North Atlantic; GM=Gulf of Mexico; I=Indian Ocean; CP=Central Pacific; SP=South Pacific; SA=South Atlantic.

ias and *P. glauca*) to demonstrate the calculation of life history trait values for areas with missing values. These species were chosen as examples because they are taxonomically different, are found in most of the area designations, and are represented by at least one pairwise comparison for each life history trait. Further investigation of the predictive capacity of these models to fecundity, size at maturity, and maximum size for the two species was performed by cross-validation: for each life history trait, *S. acanthias* or *P. glauca* data for one area were removed, the models were re-estimated, and predicted values for the newly missing area were calculated. Model fits to age at maturity, longevity, and male *P. glauca* size at maturity were not explored with cross validation because these data lacked the sufficient sample size needed to calculate the species effect once one area was removed (at least two remaining areas were needed).

Results

Model structure

For each life history trait that contained gender as a factor, the following final GLM model with a gamma distribution and a log link was selected (i.e., had the lowest AIC value):

$$\ln y_{A+sp \times g} = \ln \beta_A + \ln \beta_g + \ln \beta_{sp} + \ln \beta_{g \times sp}, \tag{1}$$

where β_A = area effect;
 β_g = gender effect;
 β_{sp} = species effect;
 $\beta_{g \times sp}$ = gender and species interaction effect.
 $y_{A+g \times sp}$ = value of the response variable (age, litter size, or length) for each area, species, and gender, accounting for the gender-species interaction.

This model is also biologically realistic because it includes the possibility that males in one species may be smaller than females and vice versa. For fecundity, the following model was chosen:

$$\ln y_{A+sp} = \ln \beta_A + \ln \beta_{sp}. \quad (2)$$

An assessment of Cook's statistic for all models revealed no evidence of any highly influential data points. A subsequent analysis of residuals by species indicated, in one case, a potential departure from the assumption that both genders of all species in all areas have the same variance. Highest residuals were reported for age at maturity in *S. acanthias*. Whether these high residual values are truly reflective of the species or an artifact of low sample size is unknown, so I carried forth with the analysis using the above models.

Area effects

Despite the low and unbalanced numbers of comparisons among coarse area designations, inter-regional variation and bias in sampling each life history trait, and the concomitant lack of power to resolve statistically significant relationships across all areas, a general and consistent trend emerged among the five life history traits. Intraspecifically, populations progressed from larger, longer-lived, later-to-mature populations in the northern-most latitudes to smaller, shorter-lived, and earlier-to-mature populations in the mid and southern latitudes (Fig. 2).

Predicting missing life history information by area

In addition to providing a comparison of the area effects on the response variables, the resultant predicting model offers a way to estimate missing life history values by area for each species and gender:

$$y = e^{(\beta_A + \beta_g + \beta_{sp} + \ln \beta_{sp \times g})}. \quad (3)$$

The factors β_g and $\beta_{sp \times g}$ in the above equation are not present in the fecundity predictions.

For both *S. acanthias* and *P. glauca* (Fig. 3), the predicted values mimicked the area trends of the reported values within two standard errors in all but one case (North Pacific *P. glauca* size at maturity was overestimated for both genders), and provided a means to estimate values for each life history by species and gender for areas not yet reported. The outlying cases may indicate an area (the North Pacific) where sampling is not representative of the true population (in this case, of *P. glauca*) and is in need of further investigation.

Cross validating models produced response variables similar to those of the full models in all but two cases (Fig. 4). In both cases (*S. acanthias* fecundity minus the South Atlantic, and *P. glauca* size at female maturity minus the North Pacific), the observed values were in opposite magnitude to that predicted. This difference could reflect either true relationships or possibly indi-

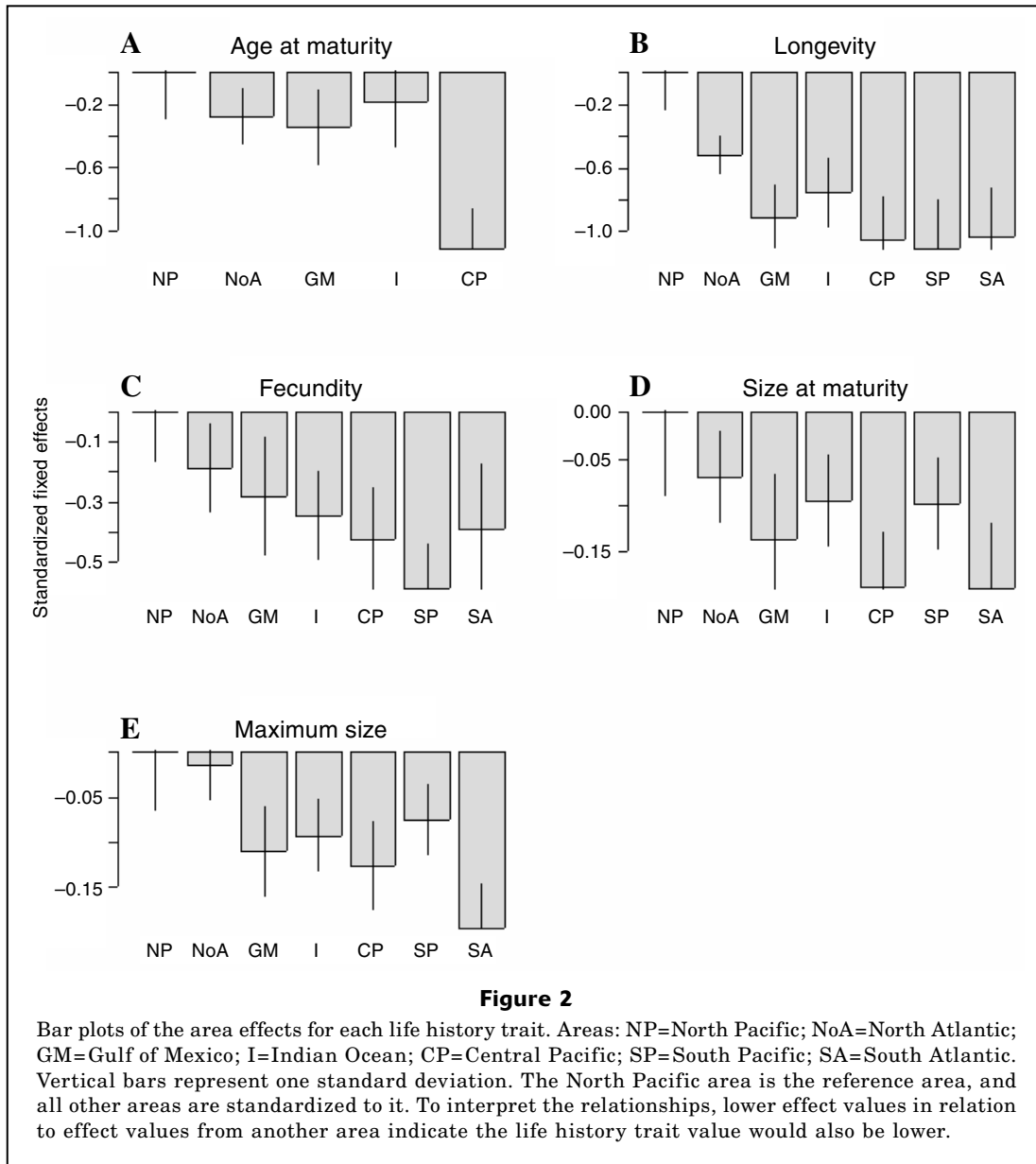
cate areas that are undersampled (i.e., North Pacific for the size at maturity for female *P. glauca*).

Discussion

Knowledge of large-scale intraspecific spatial patterning in life history traits may be important when considering the population dynamics of a species, but such large-scale patterning has seldom been formally explored. Winemiller and Rose (1992) included median and range latitude correlations in their consideration of several life history variables of North American fishes, but comparisons were only interspecific. Vila-Gispert et al. (2002) demonstrated that fishes from higher latitudes north of the equator matured latest and had the highest fecundity, whereas fishes from South America had the lowest fecundity and earliest maturation, although these comparisons were again made interspecifically. Myers et al. (2001) described the relationship between maximum reproductive rate and carrying capacity among 21 stocks of Atlantic cod (*Gadus morhua*) in the North Atlantic using mixed effects models, but their analysis was done for only one species in a limited region. Helser and Lai (2004) also performed a similar analysis for individual growth rates in North American largemouth bass (*Micropterus salmoides*) populations and found latitudinal changes in growth rate.

Regarding elasmobranchs, Cortés (2000) considered trends in intraspecific reproductive traits for sharks but did not explicitly investigate the spatial patterning of those trends. Frisk et al. (2001) found regional differences across five areas for the spiny dogfish using three life history measures (maximum size, and size and age at maturity), but did not specify regional patterns. The authors also performed a similar analysis with several skate species, finding no difference among areas, but they considered only interspecific patterns. Cortés and Parsons (1996) compared the demography of two Floridian populations of the bonnethead shark (*Sphyrna tiburo*), which included several life history measures in the life table analyses, but the small spatial resolution was inadequate to indicate large-scale spatial life history correlations within this species. Lombardi-Carlson et al. (2003) extended the bonnethead shark investigation to a larger portion of the eastern Gulf of Mexico and found latitudinal variation in maturity and size, but again the scale of this study was relatively small. Additional small scale studies on intraspecific geographic variation in reproductive parameters of sharks have been presented by Horie and Tanaka (2002), Taniuchi et al. (1993), and Yamaguchi et al. (2000).

The results of the present study, specifically aimed at sharks as an example, indicate an emerging pattern for intraspecific life history variation, not unlike previously recognized interspecific patterns. Generally, there is a distinct difference in life history traits among areas—a pattern potentially useful when considering region-specific population dynamics. Across taxonomic designations, populations in the northern latitudes tended to be



larger, to mature later in life, to have longer life spans, and to have greater fecundity compared to conspecifics in the central and southern latitudes. Populations in the North Pacific, in particular, seem to demonstrate dramatic departures in life history measures compared to conspecifics in other areas. Therefore, instead of assuming life history information from one region should be applied to another region, the trends and predictive methods offered in the present study provide a means to extrapolate life history traits of cosmopolitan species in specific areas when only information from other areas is available; this method may prove useful for developing informative priors for Bayesian analyses (Punt and Hilborn, 1997). Caveats to these results include area-specific biases (i.e., certain-size individuals susceptible

to capture) and errors in sampling programs and migratory patterns of specific species (e.g., individuals may be found in multiple areas during different parts of their life history). Thus a proper knowledge of the biology of the species is recommended before interpreting the interpolated life history values.

Other factors, such as fishing pressure, may influence regional differences in life history traits, challenging the interpretation of such patterns. Truncation of size and age classes, and reduction in age at maturity are recognized byproducts of heavy fishing (Longhurst, 1998a; Rochet, 2000). Although all the populations used in this study are and have been fished—some more intensely than others—this study assumes there is no consistent pattern to such exploitation in shark

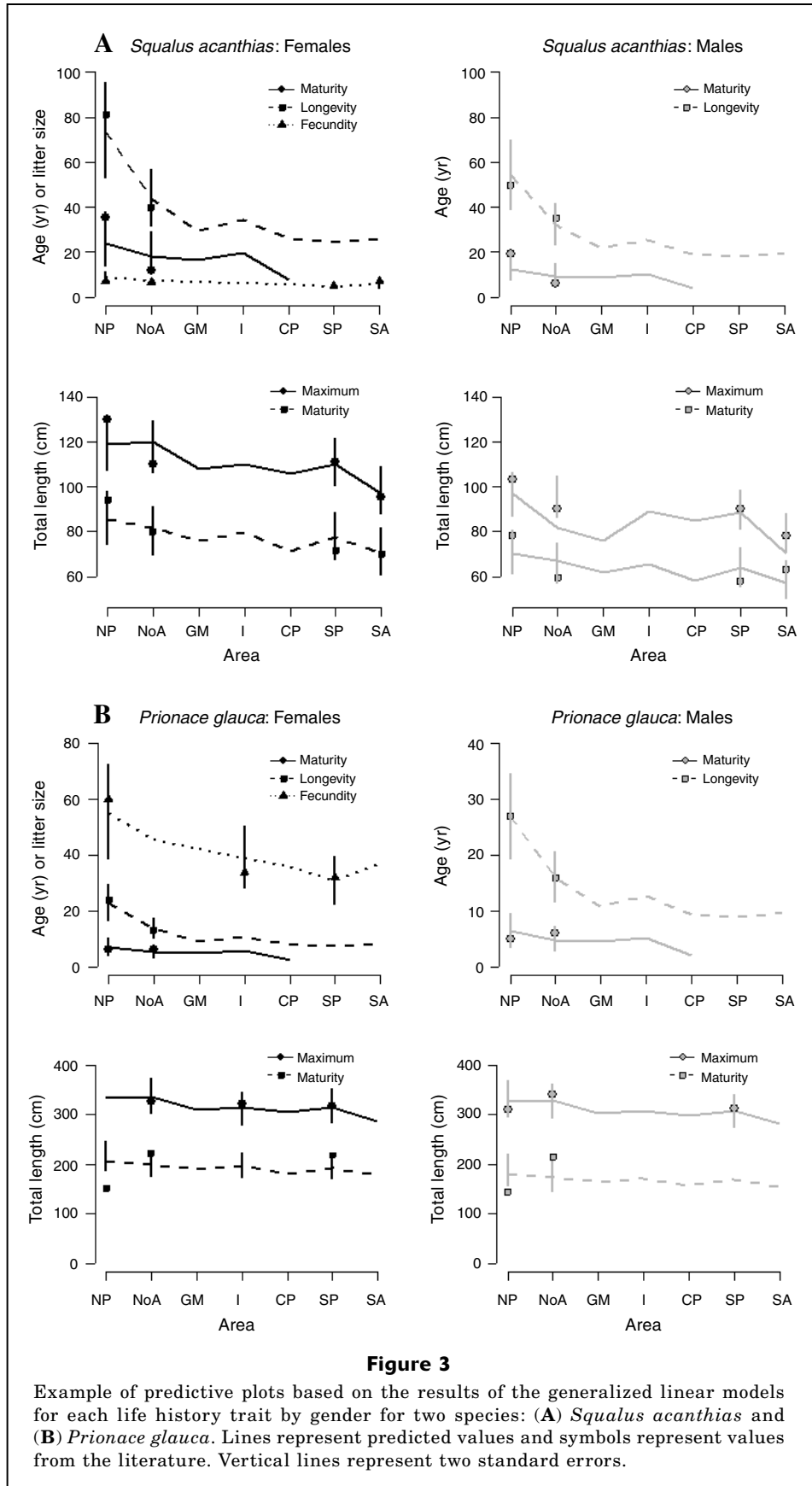


Figure 3

Example of predictive plots based on the results of the generalized linear models for each life history trait by gender for two species: (A) *Squalus acanthias* and (B) *Prionace glauca*. Lines represent predicted values and symbols represent values from the literature. Vertical lines represent two standard errors.

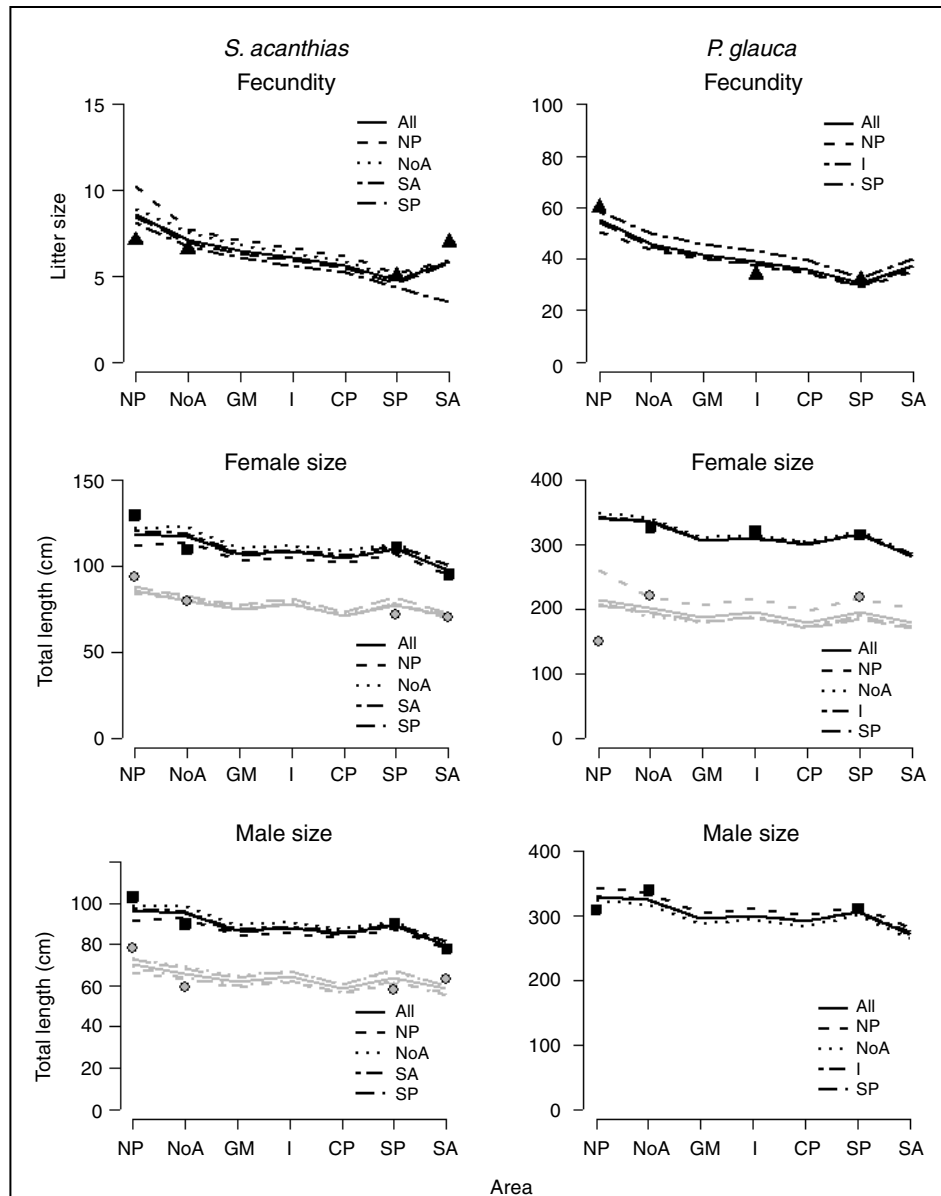


Figure 4

Plots of model predictions derived by cross validation for *S. acanthias* and *P. glauca*. Lines representing predicted value are distinguished as follows: "All"—all areas are included in the prediction; Lines denoted by area are predictions made without that area. Literature values are indicated as follows: triangles—fecundity, circles—size at maturity, squares—maximum size. Size at maturity for male *P. glauca* was not included because of insufficient data. Areas: NP=North Pacific; NoA=North Atlantic; GM=Gulf of Mexico; I=Indian Ocean; CP=Central Pacific; SP=South Pacific; SA=South Atlantic.

populations that would explain the results. Specifically, there is no reason to believe that species in the southern hemisphere have been more heavily fished than conspecifics in the northern hemisphere.

The results offered in the present study are based on small sample sizes in most areas, but hopefully they will bring attention to the usefulness of collecting spa-

tially varying intraspecific information with the idea of constructing more robust models. Most investigations describing the patterns of shark life history traits suffer from insufficient biological resolution (either temporally or spatially) of the very parameters and subsequent relationships they attempt to explain (Smith et al., 1998; Cortés, 2000). Limited biological knowledge and

subsequent high uncertainty in the estimation of vital rates of many marine species, including elasmobranchs, is testimony to the fact that the accumulation of life history information should be a priority to biologists, fisheries scientists, and resource managers. Results from the models presented here could be used to hypothesize life history values in areas currently lacking information and thus be tested with further sampling in those areas. It is also hoped that the approach offered here may indicate areas where sampling may not be sufficient, as denoted by departures from the general model trend. Targeted sampling in that area would help resolve whether the departure is from a true area effect or species effect. As more data is gathered, it will be possible to explore other factors—such as temperature and guilds (e.g., coastal versus oceanic)—in the model structure.

Once steps are made to further resolve the species and area effects, one may start to ask questions regarding the cause of particular area effects. Potential mechanisms of true coarse-scale gradation of life history traits may be contained within the generalized characteristics of oceanic zoogeographic realms (Longhurst, 1998b), although a slightly less abstract mechanism could be found in the physical forcing events that characterize regions in the northern and southern hemisphere. Although both hemispheres demonstrate similar large-scale current and wind patterns, physical forcing events tend to be stronger in the northern hemisphere (Trenberth et al., 1998). Because this study offers coarse area designations to intraspecific life history variation, it is most likely a product of some macro-scale characteristics of each region. Attention should therefore be directed towards large-scale characteristics of each region to explain these patterns, although small-scale dynamics are important for understanding each population's specific response to local environmental conditions (i.e., countergradient variation in growth rates [Conover, 1990; Conover and Present, 1990]).

It is becoming increasingly important to be able to assess fish stocks with minimal data. By combining genetic data revealing differing levels of intraspecific population substructure with the increasing number of studies demonstrating localized adaptations and plasticity in population parameters, it is apparent that intraspecific spatial differences must be considered in species management (Avisé, 2000; Roff, 2002). Although the predictive power of this study may currently be weak because of low sample sizes, it offers a method to quantify potential spatial patterning in intraspecific life history traits that may allow responsible management of regionally data-poor species, and it may help frame future sampling protocols and studies of spatial patterns in life history traits.

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Appendix

Life history traits and area assignments for species used in the analyses. Sizes are total length (cm). Areas: NP=North Pacific; NoA=North Atlantic; GM=Gulf of Mexico; I=Indian Ocean; CP=Central Pacific; SP=South Pacific; SA=South Atlantic.

Species	Area	Maximum size		Size at maturity		Age at maturity		Mean fecundity	Longevity	
		F	M	F	M	F	M		F	M
<i>Carcharinus acronotus</i>	GM	130	122	110	103	3	2.5	5		
<i>Carcharinus acronotus</i>	NoA	154	164	120	110	4	3	5		
<i>Carcharinus amblyrhynchos</i>	CP	190	185	137	132.5			5		
<i>Carcharinus amblyrhynchos</i>	I	178	168	135	130			3		
<i>Carcharinus falciformis</i>	GM	308	314	235	217.5			11		
<i>Carcharinus falciformis</i>	NoA	330		234	218			10		
<i>Carcharinus falciformis</i>	I	283	244	248				11		
<i>Carcharinus falciformis</i>	SP	250	225	200	212.5			7		
<i>Carcharinus leucas</i>	GM	285		225	215			8		
<i>Carcharinus leucas</i>	I	300		239.5	239.5			9		
<i>Carcharinus limbatus</i>	GM	191	175	156	133	7	4.5	4.9	10	9
<i>Carcharinus limbatus</i>	NoA	202	189	156	143.5			4		
<i>Carcharinus limbatus</i>	I	247	246	208.5	201.5	7	6	6	11	10
<i>Carcharinus longimanus</i>	NoA	260		175				12.5		
<i>Carcharinus longimanus</i>	SA	250	235	185	185				17	14
<i>Carcharinus longimanus</i>	I	270	245	185	198					
<i>Carcharinus longimanus</i>	SP	270	251	200				6		
<i>Carcharinus longimanus</i>	CP	272	240	182	182			7	11	11
<i>Carcharinus obscurus</i>	NoA	371	360	284	279	21	19	11	39	39
<i>Carcharinus obscurus</i>	I	389	324	300	280	24	20.5	9.9	34	
<i>Carcharinus plumbeus</i>	CP	190	172	144	131			5.5		
<i>Carcharinus plumbeus</i>	NoA	234	226	183	180	15	15	9	32	40
<i>Carcharinus plumbeus</i>	I	199	190.5	169	167			8		
<i>Galeocerdo cuvier</i>	NoA	450		317.5	310	10	10	55	16	15
<i>Galeocerdo cuvier</i>	GM	450				8	7		11	9
<i>Galeocerdo cuvier</i>	I	410	370	340	290			35		
<i>Galeocerdo cuvier</i>	SP	428	350	287				31		
<i>Prionace glauca</i>	NP		310	150	145	6	5	60	24	27
<i>Prionace glauca</i>	NoA	327	340	221	215	6	6		13	16
<i>Prionace glauca</i>	SP	316	312	218				32		
<i>Prionace glauca</i>	I	321.5		214				34		
<i>Rhizoprionodon taylori</i>	SP	78	69	54	56			4.5		
<i>Rhizoprionodon taylori</i>	I	66	55	45	43			5		
<i>Sphyrna lewini</i>	GM	310	300	250	180	15	10		17	12
<i>Sphyrna lewini</i>	NP	324	305	210	198	4.1	3.8	26	14	11
<i>Sphyrna lewini</i>	I	346	301	200	150			16.5		
<i>Galeorhinus galeus</i>	NP	195	185	180	175					
<i>Galeorhinus galeus</i>	SP	174	175	140	135	15	17	28.4	53	41
<i>Galeorhinus galeus</i>	SA	155	148	128	117	17.5	13	23	36	36
<i>Isurus oxyrinchus</i>	NP	351		280		16			34	
<i>Isurus oxyrinchus</i>	SP	340	270	280	195			9		
<i>Isurus oxyrinchus</i>	NoA	375	298	280		14		13.5	23	9
<i>Isurus oxyrinchus</i>	I	333	271	266	199.5			11.5		
<i>Alopias superciliosus</i>	NoA	444	410	341	276			2		
<i>Alopias superciliosus</i>	NP	422	357	341	288	13	10	2	20	19
<i>Squalus acanthias</i>	NP	130	103	94	78.5	35.5	19	7.1	81	50
<i>Squalus acanthias</i>	NA	110	90	80	59.5	12.1	6	6.6	40	35
<i>Squalus acanthias</i>	SA	95.5	78	70	63			7		
<i>Squalus acanthias</i>	SP	111	90	71.5	58			5		
<i>Squalus mitsukurii</i>	NP	114	94	97.5	70	22	12	8.8		
<i>Squalus mitsukurii</i>	I	95	81	69	60			6.4		
<i>Squalus mitsukurii</i>	CP	91	82	69	48	15	4	3.6	27	18
<i>Squalus mitsukurii</i>	SP	104	102	85				3.5	16	14