

Final Report

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Signature of Principal Investigator **Date**

Recruitment Dynamics of Northern Shrimp (Pandalus borealis)

The objectives of this project were to investigate environmental and ecological mechanisms influencing recruitment of Gulf of Maine northern shrimp and consider the implications of these for fishery management. The specific goals of the project were to (1) investigate the influence of physical factors on recruitment, (2) investigate the match-mismatch hypothesis (Cushing 1971) as a potential explanation for a previously demonstrated temperature effect on shrimp recruitment, (3) evaluate the effects of changes in predator community composition on shrimp recruitment, and (4) develop a stock-recruitment model which incorporates effects of significant environmental and ecological variables. A fifth objective, to evaluate overfishing definitions, was not completed.

The Role of Physical Factors in Recruitment of Northern Shrimp and Stock-Recruitment Model with Environmental Inputs

We examined the influence of sea surface temperature, sea bottom temperature, freshwater inputs, and the NAO winter index on recruitment of northern shrimp. This work is an extension of earlier analyses which examined the influence of ocean temperatures on recruitment of northern shrimp (Richards et al. 1996).

Ocean temperature data were derived from hydrographic observations made on routine bottom trawl surveys conducted by NEFSC during spring and autumn, 1968-2002. On average 40 stations were sampled in the western GoM each season. Bottom temperature measurements were made using a mechanical bathythermograph from 1968-1970 and an expendable bathythermograph (XBT) from 1971-1990. Surface temperatures during this period were measured by a surface bucket and thermometer. Since 1991 the surface and bottom temperatures were measured by an electronic profiling conductivity/temperature/depth (CTD) instrument.

For each station, surface and bottom temperature anomalies were calculated using the method described by Holwarth and Mountain (1990). The method uses a set of reference annual cycles for temperature at fixed locations to estimate a reference surface or bottom temperature value for the location and day of the year the survey observation was made. The anomaly is the difference between the observed value and the reference value. This method compensates for changes in the timing of surveys from year to year to provide a consistent estimate of interannual temperature variability. Regional average values for the surface and bottom temperature and temperature anomalies in the western GoM were calculated for each survey using the method described by Holwarth and Mountain (1990).

We examined three temperature anomaly series (Figure 1) appropriate to hypothesized biological mechanisms:

- 1) fall bottom temperatures (potential influence on rates of embryonic development and egg parasitism).
- 2) spring bottom temperatures (potential influence on rates of embryonic development, egg parasitism, timing of hatching)
- 3) spring surface temperatures (potential influence on planktonic larval development and survival)

Stream flow data for the Penobscot, Androscoggin, Saco and Kennebec Rivers were obtained from United States Geological Survey gaging stations (stations 01034500, 01046500,

01059000, 01066000; <http://waterdata.usgs.gov>) (Figure 2). Freshwater discharge affects circulation patterns within the Gulf of Maine (Lynch 1996) and we reasoned that effects on shrimp might be mediated through larval retention in nearshore nursery areas or through effects on bloom timing and duration. Therefore we included estimates of mean flow during March and April and estimates of timing of the peak flow during March-May. The timing of the peak flow was estimated as the first week with discharge greater than the 75th percentile of discharge levels for weeks 5-22 of each year. We examined discharge for the Penobscot River only (PEN), for the Androscoggin, Saco and Kennebec Rivers combined (ASK), and for all four rivers combined (PASK).

The NAO winter index measures sea level pressure differences between Lisbon, Portugal and Reykjavik, Iceland during Dec-Mar of each year and was obtained from <http://www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html#winter> (Climate Analysis Section, NCAR, Boulder, USA, Hurrell (1995)) (Figure 3).

We used the Box-Jenkins approach to time series analysis (Box and Jenkins 1976) to identify significant crosscorrelations between the recruitment time series and the input series (spawning stock indices, environmental variables). Parameters that were significant at the $\alpha=0.10$ level and that were not correlated with other independent variables were included in the stock-recruitment models. To examine the influence of the identified environmental factors on recruitment of northern shrimp, we fit a stock-recruitment model with environmental inputs (Cushing 1971).

Results

Spawning capacity (lag 2), spring sea surface temperature anomaly (SSTA) (lag 1), spring sea bottom temperature anomaly (SBTA) (lag 4), and the NAO winter index (lag 1) were significantly crosscorrelated with recruitment in the bivariate Box-Jenkins transfer function models (Figure 4). River flow variables were not significant and were dropped from further consideration. The crosscorrelation between recruitment and spawning capacity at lag 2 was positive whereas the crosscorrelations with the NAO index and temperature variables were negative. When the anomalous 2002 recruitment index was included in the time series analysis, there was an additional significant crosscorrelation between recruitment and spawning capacity at lag 1 (negative). This effect was not significant unless 2002 was included, and we did not retain it for the stock-recruitment model.

The NAO winter index was positively correlated with spring SSTA in the same year ($r=0.38$, $P<0.05$). We retained spring SSTA for the stock-recruitment model because it resulted in a slightly better fit in the transfer function models and because temperature is the more proximate influence. Thus the initial stock-recruitment model included spawning capacity (lag 2), spring SSTA (lag 1), and spring SBTA (lag 4) as independent variables.

Spawning capacity ($P<0.01$), spring SSTA ($P<0.10$), and spring SBTA ($P<0.05$) were significant in the stock-recruitment model for 1968-2001. The model explained 46% of the variance in the data (Figure 5). No significant autocorrelation was evident in the residuals. Recruitment was negatively related to spring SBTA and SSTA and positively related to reproductive capacity. When the 2002 point was included, only spawning capacity ($P<0.05$) and

spring SSTA ($P < 0.05$) remained significant, and the model r^2 was reduced to 0.29.

Evaluation of the Match-Mismatch Hypothesis

To test the match-mismatch hypothesis for northern shrimp we attempted to develop time series of estimates of timing of the spring phytoplankton bloom and the northern shrimp hatch in the western Gulf of Maine. The timing of the bloom was estimated using the methods of Townsend and Spinrad (1986) and Townsend and Cammen (1988), who have shown that the onset of the bloom in shallow coastal waters of the Gulf of Maine is determined primarily by the amount of solar radiation reaching phytoplankton, which can be estimated as:

$$E^* = 1/z \int E_0 e^{-Kz} dz$$

where: E^* = the depth-averaged, vertically integrated irradiance, z = average depth, E_0 = solar irradiance reaching the surface, and K = the diffuse attenuation coefficient. Townsend and Cammen (1988) estimated initiation dates for the bloom in Sheepscot Bay, Maine for 1971-1980; we attempted to extend their time series to 1968-1997 using irradiance data from collectors in nearby Wiscasset (Maine Yankee Atomic Power Plant) and assuming the average diffuse attenuation coefficient reported for this region by Townsend and Spinrad (1986).

Estimation of Bloom Timing Using Solar Insolation

We obtained pyrheliometer charts recording daily solar insolation from Maine Yankee Nuclear Power Plant. The pyrheliometer is an analog device that measures the net amount of radiant energy reaching a horizontal surface. Charts were available for 1982-1999; these were photocopied, scanned and read using an image analysis system (Optimus software). We digitized the daily insolation traces from the charts for mid-January through mid-March of each year and calculated the area under the curve. Figure 6 shows an example of the resulting daily solar insolation record. We used these data to estimate the timing of the bloom using the methods of Townsend and Spinrad (1986) and Townsend and Cammen (1988).

Results

Estimates of bloom timing derived from the pyreheliometer charts were not reasonable, and this portion of the project was abandoned. We consulted with climatologists familiar with this now-antiquated instrument, but were not able to resolve the issues. Instead, we adopted an alternative approach to testing the match-mismatch hypothesis, in which we developed estimates of timing of the shrimp hatch based on temperature data, so that we could compare these with Townsend and Cammen's bloom timing estimates (described below).

Direct Estimation of Shrimp Hatch Dates

We obtained biological data from fishery-dependent sampling conducted by Maine Department of Marine Resources (ME DMR) during 1980-1983 and 1988-2002. Sampling

extends back to 1973, but during 1973-1979 presence/absence of eggs was not recorded. Data collected during 1984-1987 could not be located. The northern shrimp fishery occurs during the winter and spans the period of hatching. Samples are collected from shrimp dealers according to a proportional sampling scheme, thus dealers handling the greatest volume of shrimp are the most heavily sampled. The reproductive and life history stage composition of each sample is determined, and we used changes in the proportion of egg-bearing females to estimate hatch timing for each year. We used probit analysis of the percent of sampled females whose eggs had hatched to estimate the date of 50% hatch, and the duration of the hatch period (defined as the time from 10% hatch through 90% hatch). Figure 7 shows the hatch date curves fit using probit analysis, and Figure 8 and Table 1 summarize percentiles of the hatch date distributions.

Indirect Estimation of Hatch Dates

Since we needed hatch dates for the same years for which we had estimates of the timing of the phytoplankton bloom, we investigated the possibility of developing indirect estimates of hatch dates based on the relationship of developmental rates with temperature. The effects of temperature on shrimp developmental rates are well known from laboratory studies (Stickney and Perkins 1977, 1979; Nunes 1984). We used daily sea surface temperature records from the Boothbay Harbor environmental monitoring database (<http://www.state.me.us/dmr/rm/environmentaldata.html>) to calculate the number of degree days (cumulative temperature) during oogenesis and embryonic development (which we took as May 1 through February 10) for each year. We then examined the relationship between our estimated hatch dates for 1980-1983 and 1988-1993 and cumulative degree days during those years (Figure 9). The relationship ($r^2=0.54$) indicated that the hatch occurred earlier in warmer years. A weaker relationship was found for hatch duration vs. temperature ($r^2=0.18$); however, it appears that the length of the hatching period is longer in colder years.

We used the relationship between 50% hatch and degree days (Figure 9) to predict hatch dates for 1971-1980 from observed cumulative degree days during 1971-1980. The resulting estimates allowed us to compare bloom and hatch dates for 1971-1980 (Figure 10). During this time period, there was a wide variation in the degree of mismatch, with the bloom starting from 1 day before the midpoint of the hatch to 25 days after the midpoint of the hatch.

Shrimp Early-Life Survival Rates

Survival rates of northern shrimp up to age 1.5 yr were estimated from the spawner and recruit abundance indices developed for the stock-recruitment model with environmental inputs (described above), as:

$$S_i = R_i/P_{i-2}$$

where i = year

S = survival index

R = recruitment index

P = spawner abundance index 2 years previous

Spawner indices were lagged two years because recruitment is not observed until age 1.5 (the spawners measured two years earlier result in a given years' recruitment index). Survival indices are shown in Figure 11.

Effects of Bloom and Hatch Timing on Survival

The survival index vs. the degree of mismatch in bloom and hatch timing for each year is shown in Figure 12. There appears to be an effect of mismatch on the survival of early life stage shrimp ($r^2=0.35$), with greater mismatch leading to higher survival. This appears the opposite of what might be expected; however a plausible explanation lies in the development of species composition during the bloom. The estimates we have are for the onset of the phytoplankton bloom. As the bloom starts, it consists primarily of small phytoplankton and chain-forming diatoms, later of larger diatoms and after about a month, significant densities of zooplankton appear (Stickney and Perkins 1979, 1980; Townsend 1984). The diet of shrimp reflects this progression (Stickney and Perkins 1979, 1980) (Figure 13), with larger proportions of zooplankton in the diet later in the season. It is possible that shrimp larvae grow and survive better on a diet that contains significant amounts of zooplankton than on a diet composed entirely of phytoplankton. Based on a series of feeding experiments with larval shrimp Stickney and Perkins (1979) tentatively concluded that large diatoms (e.g. *Coscinodiscus*) are excellent food, smaller diatoms are satisfactory, though perhaps not sufficient for long term survival, and copepods (and probably other crustacea) are excellent food.

Predation on Northern Shrimp

We investigated predation on northern shrimp but did not include this factor in the stock-recruitment models.

Predators of Pandalid shrimp in the Gulf of Maine were identified from NEFSC food habits data collected during 1973-1999 as part of annual trawl surveys. From 1973 to 1980, individual stomach samples were preserved at sea and examined in the lab for prey identification, weight, number, percent composition, total stomach weight, and length (Overholtz et al 2000). During 1980-1985, most stomach content data were collected at sea, and after 1985 all stomach contents were identified at sea.

Shrimp are infrequently identified to species in the food habits database, therefore we included predators which consumed any Pandalids as well as predators with confirmed *Pandalus borealis* in their stomachs. We then examined predator size distributions to determine which sizes of each predator actually consume shrimp. We examined seasonal, interannual, and spatial variation in predation pressure on shrimp.

Results

The list of fish species in the western Gulf of Maine that had Pandalids in their stomachs is shown in Table 2. Of predators with large sample sizes, Atlantic cod, little skate, red hake, smooth skate, and white hake had the highest frequency of occurrence of Pandalids in their stomachs; an additional 7 species consumed sufficient shrimp to be included in our analyses (goosefish, longhorn sculpin, pollock, sea raven, silver hake, spiny dogfish, thorny skate, and winter skate). The percent frequency of occurrence of shrimp in stomachs by predator size suggests changing selectivity for shrimp with predator size (Figure 14). The size ranges at which some of the primary predators appear to select shrimp are: Atlantic cod: 25-65 cm; red hake 25-50 cm; silver hake 10-35 cm; white hake 25-65 cm; and spiny dogfish 55-85 cm. For each predator, we are included only the size ranges that appear to select shrimp in developing our indices of predation pressure.

Seasonal variation in occurrence of shrimp in predator stomachs is shown in Figure 15 (successive 5-year time blocks). The figures include all predators that were found with shrimp in their stomachs during each time block. Some species (e.g. Atlantic cod) show little seasonal variation in percent frequency of occurrence of shrimp, while others show greater seasonal and interannual variation (e.g. smooth skate). The variation for some species is due to low sample sizes while for others it probably reflects seasonal changes in spatial overlap between predator and prey.

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Table 1. Julian Day corresponding to progression of hatch from probit analysis of proportion of egg-bearing females in commercial fishery samples.

	10% hatch	25% hatch	50% hatch	75% hatch	90% hatch
1980	52	56	61	65	69
1981	53	59	66	72	78
1982	27	37	49	60	71
1983	42	49	57	65	73
1989	56	60	64	68	71
1990	32	43	54	66	77
1991	38	46	55	64	73
1992	36	44	53	63	71
1993	46	54	62	71	78
1994	40	49	60	70	79
1995	25	37	50	63	75
1996	39	47	57	67	75
1997	15	27	39	52	64
1998	42	54	67	80	92
1999	15	31	48	66	82
2000	39	49	60	71	82
2001	29	39	50	62	72
2002	32	40	49	58	66

Table 2. List of predators with Pandalid shrimp found in their stomachs in the western Gulf of Maine, NEFSC trawl surveys, 1973-1999.

Predator	# of Stomachs Examined	# of Stomachs with Pandalids	% of Stomachs with Pandalids
Acadian Redfish	488	3	0.61
American Plaice	832	1	0.12
Atlantic Cod	3790	457	12.06
Atlantic Halibut	62	4	6.45
Atlantic Wolffish	28	1	3.57
Fourspot Flounder	167	5	2.99
Goosefish	1182	25	2.12
Haddock	702	4	0.57
Little Skate	397	41	10.33
Longhorn Sculpin	1090	89	8.17
Pollock	1213	54	4.45
Red Hake	3558	436	12.25
Sea Raven	966	41	4.24
Silver Hake	10347	681	6.58
Smooth Skate	156	23	14.74
Spiny Dogfish	3582	117	3.27
Thorny Skate	1403	95	6.77
White Hake	5323	777	14.60
Windowpane	67	1	1.49
Winter Skate	228	10	4.39
Wrymouth	3	2	66.67
Total	35584	2867	8.06

Table 3. Percent frequency of occurrence of Pandalids in stomach for each predator by season and 5-year time blocks (n = number of stomachs with shrimp).

Predator	5-Year Block	Spring % freq (n)	Summer % freq (n)	Fall % freq (n)
Acadian Redfish	1973-1977			0.77 (1)
	1983-1987	2.22 (2)		
American Plaice	1973-1977	0.34 (1)		
Atlantic Cod	1973-1977	9.62 (10)		7.73 (17)
	1978-1982	8.47 (16)	7.27 (8)	
	1983-1987	3.66 (9)		5.44 (16)
	1988-1992	12.53 (62)	13.94 (29)	7.97 (55)
	1993-1997	20.67 (87)	23.41 (48)	21.03 (77)
Atlantic Halibut	1978-1982	8.33 (1)	12.50 (1)	
	1988-1992	20.00 (1)		7.69 (1)
Atlantic Wolfish	1978-1982		5.88 (1)	
Fourspot Flounder	1993-1997	5.88 (3)		5.00 (1)
Goosefish	1973-1977	3.13 (1)		
	1983-1987			3.64 (2)
	1988-1992	1.98 (2)	2.60 (2)	1.49 (2)
	1993-1997	1.44 (2)	5.11 (9)	2.86 (5)
Haddock	1973-1977			1.59 (1)
	1978-1982	0.51 (1)	0.58 (1)	0.96 (1)
Little Skate	1988-1992	2.38 (2)	34.78 (8)	
	1993-1997	18.18 (12)	12.50 (5)	9.90 (10)
Longhorn sculpin	1983-1987	7.84 (4)		
	1988-1992	2.61 (6)	10.00 (1)	8.54 (10)
	1993-1997	8.88 (23)	18.28 (17)	12.56 (27)
Pollock	1973-1977	3.80 (3)		7.97 (11)
	1978-1982			1.92 (1)
	1983-1987	1.77 (2)		2.00 (2)
	1988-1992	1.89 (2)	3.51 (2)	3.76 (7)
	1993-1997	5.36 (6)	4.41 (3)	11.34 (11)
Red Hake	1973-1977	1.18 (1)		
	1978-1982	3.00 (6)	2.16 (3)	7.84 (12)
	1983-1987	2.30 (5)		5.47 (17)
	1988-1992	4.80 (13)	24.53 (65)	18.01 (96)
	1993-1997	7.21 (22)	20.85 (64)	19.67 (120)
Sea Raven	1978-1982		25.00 (1)	
	1983-1987	5.00 (4)		
	1988-1992	3.62 (8)	1.18 (1)	3.72 (7)
	1993-1997	7.43 (11)	6.35 (4)	4.00 (3)

Table 3, continued.

Predator	5-Year Block	Spring % freq (n)	Summer % freq (n)	Fall % freq (n)
Silver Hake	1973-1977	1.59 (2)		
	1978-1982	1.27 (7)	2.94 (5)	1.28 (3)
	1983-1987	0.74 (5)		1.93 (20)
	1988-1992	2.30 (22)	10.06 (53)	6.59 (115)
	1993-1997	6.4 (74)	11.93 (109)	14.15 (247)
Smooth Skate	1978-1982	25.00 (1)	11.77 (2)	100.00 (1)
	1983-1987	16.67 (2)		
	1988-1992	4.88 (2)	46.15 (6)	7.41 (2)
	1993-1997			20.59 (7)
Spiny Dogfish	1983-1987	2.08 (1)		1.17 (6)
	1988-1992		4.42 (29)	2.18 (12)
	1993-1997	5.10 (10)	7.06 (25)	4.69 (30)
Thorny Skate	1973-1977			50.00 (1)
	1978-1982		3.28 (2)	6.25 (1)
	1983-1987	1.67 (2)		1.89 (2)
	1988-1992	3.07 (9)	4.82 (4)	8.15 (19)
	1993-1997	10.43 (12)	12.20 (10)	15.27 (31)
White Hake	1973-1977	6.74 (6)		13.51 (20)
	1978-1982	3.06 (3)	4.13 (5)	
	1983-1987	3.55 (11)		9.86 (63)
	1988-1992	3.55 (12)	22.93 (119)	15.14 (175)
	1993-1997	7.05 (22)	23.01 (127)	22.61 (206)
Windowpane	1993-1997	11.11 (1)		
Winter Skate	1988-1992		44.44 (4)	
	1993-1997	4.00 (1)	10.34 (3)	4.00 (2)
Wrymouth	1978-1982	100.00 (1)		
	1988-1992			50.00 (1)

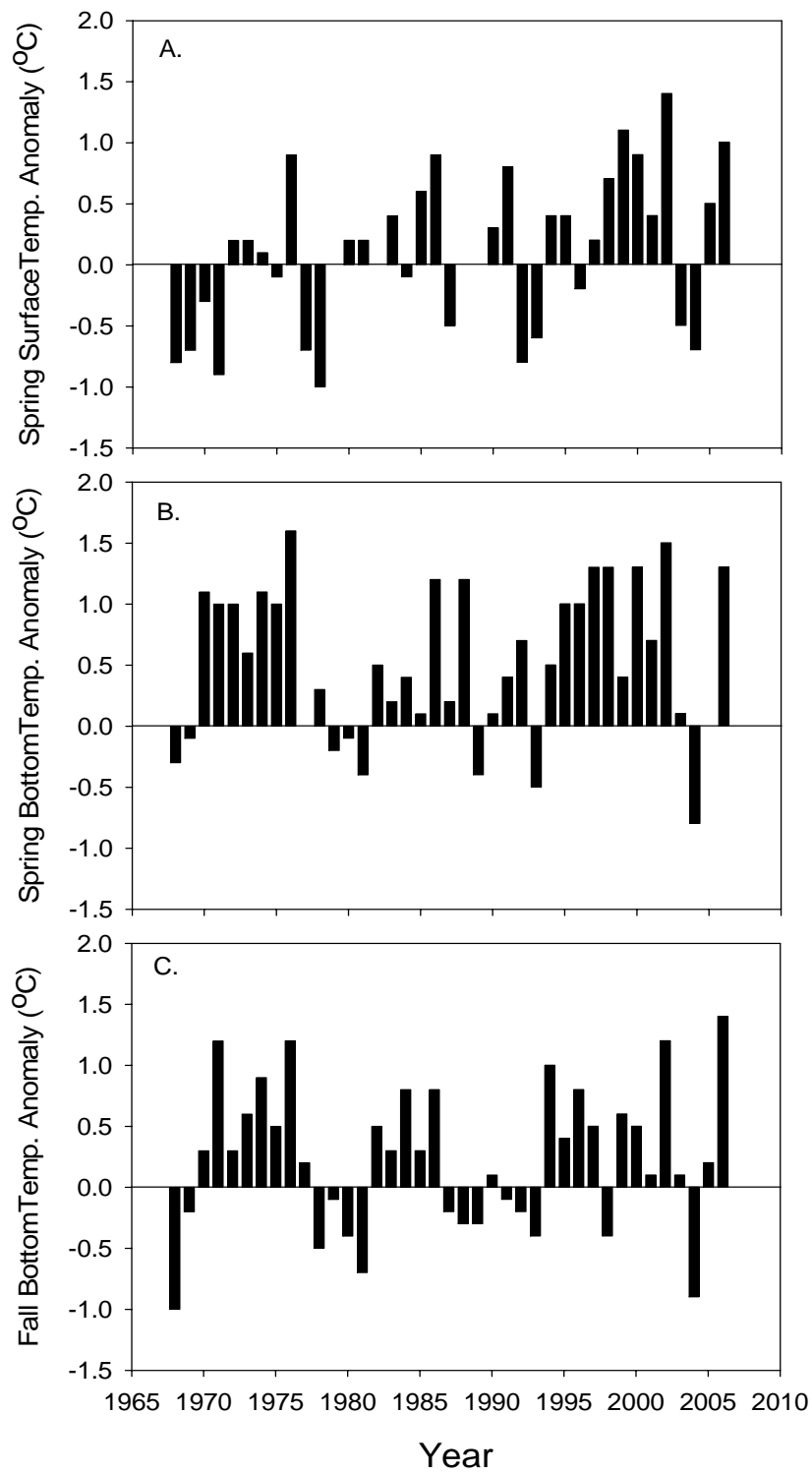


Figure 1. Ocean temperature anomalies, 1968-2006. Spring surface temperature (A), spring bottom temperature (B), fall bottom temperature (C).

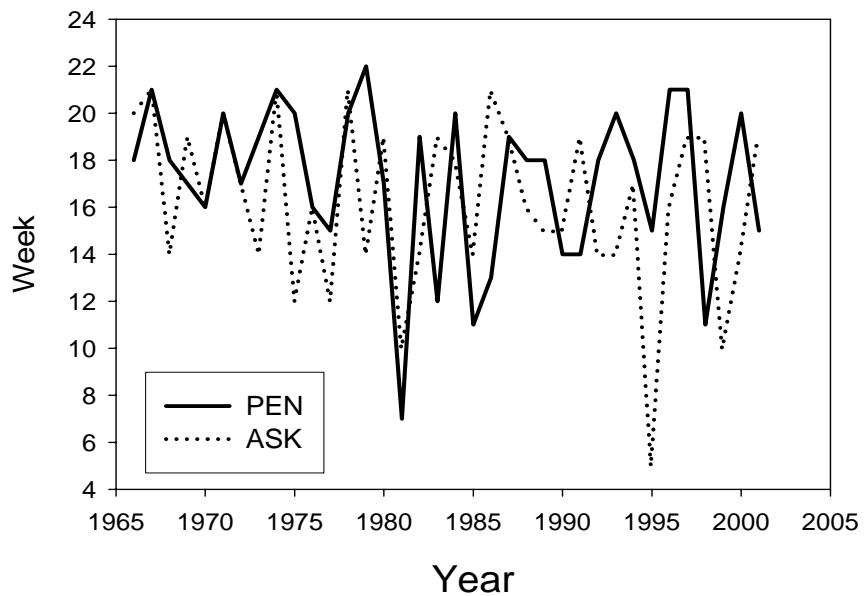
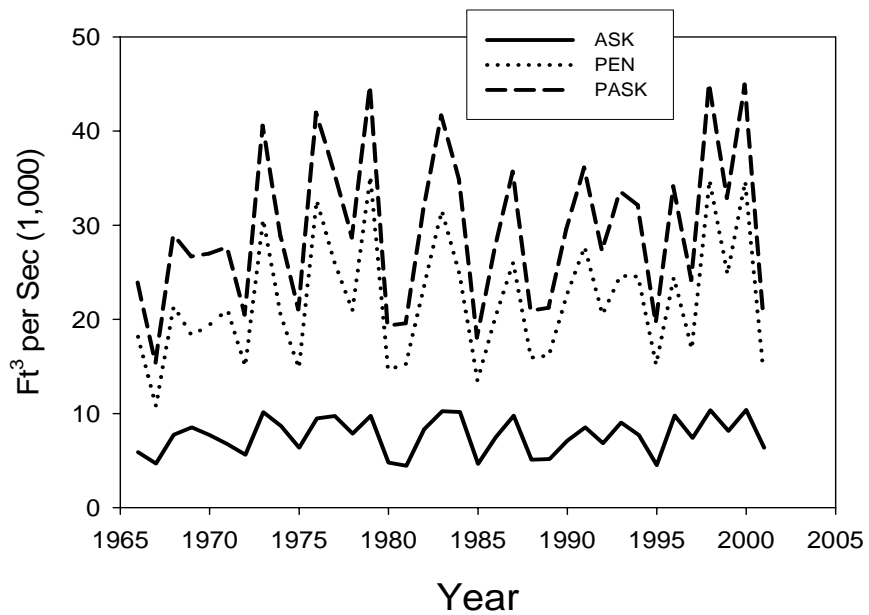


Figure 2. Mean stream flow during March and April (A) and timing of peak stream flow during March-May (B), 1966-2002. PEN is Penobscot River, ASK is Androscoggin, Saco and Kennebec Rivers combined, PASK is Penobscot and ASK combined

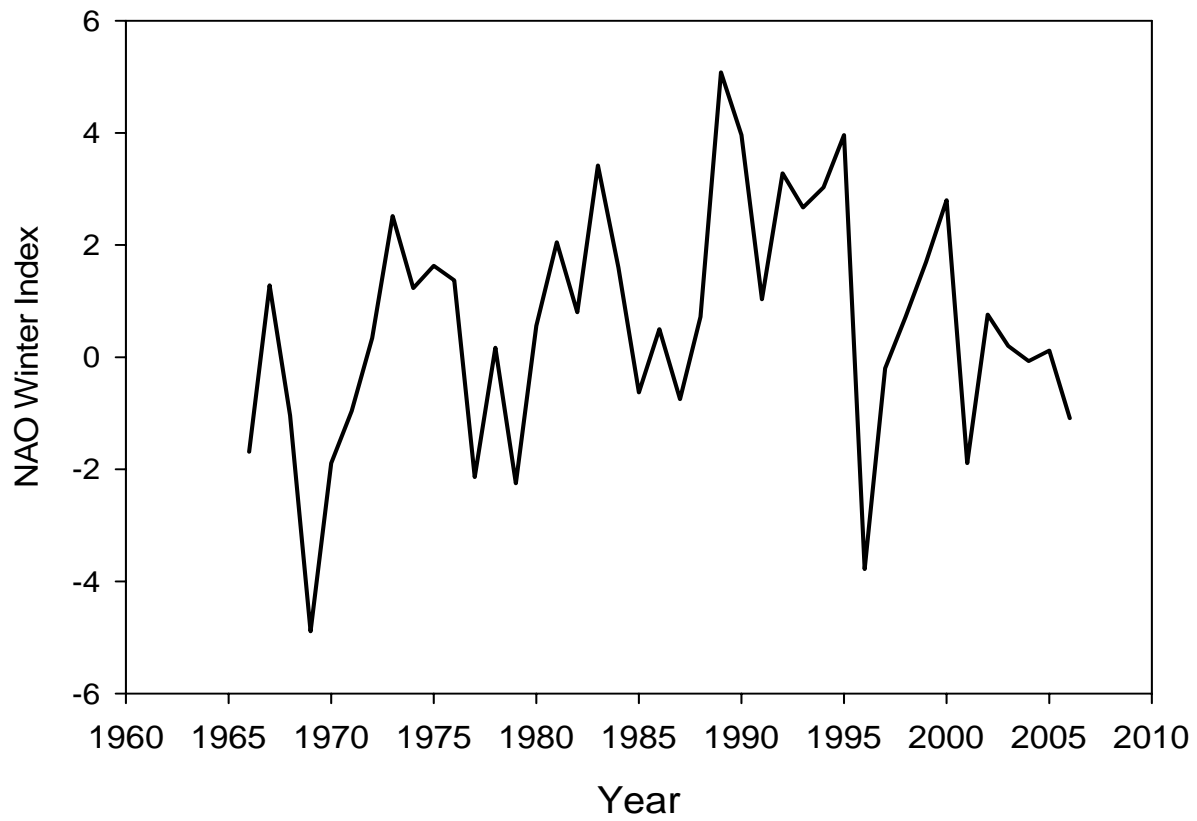


Figure 3 . North Atlantic Oscillation winter index, 1966-2002. Source: <http://www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html#winter>

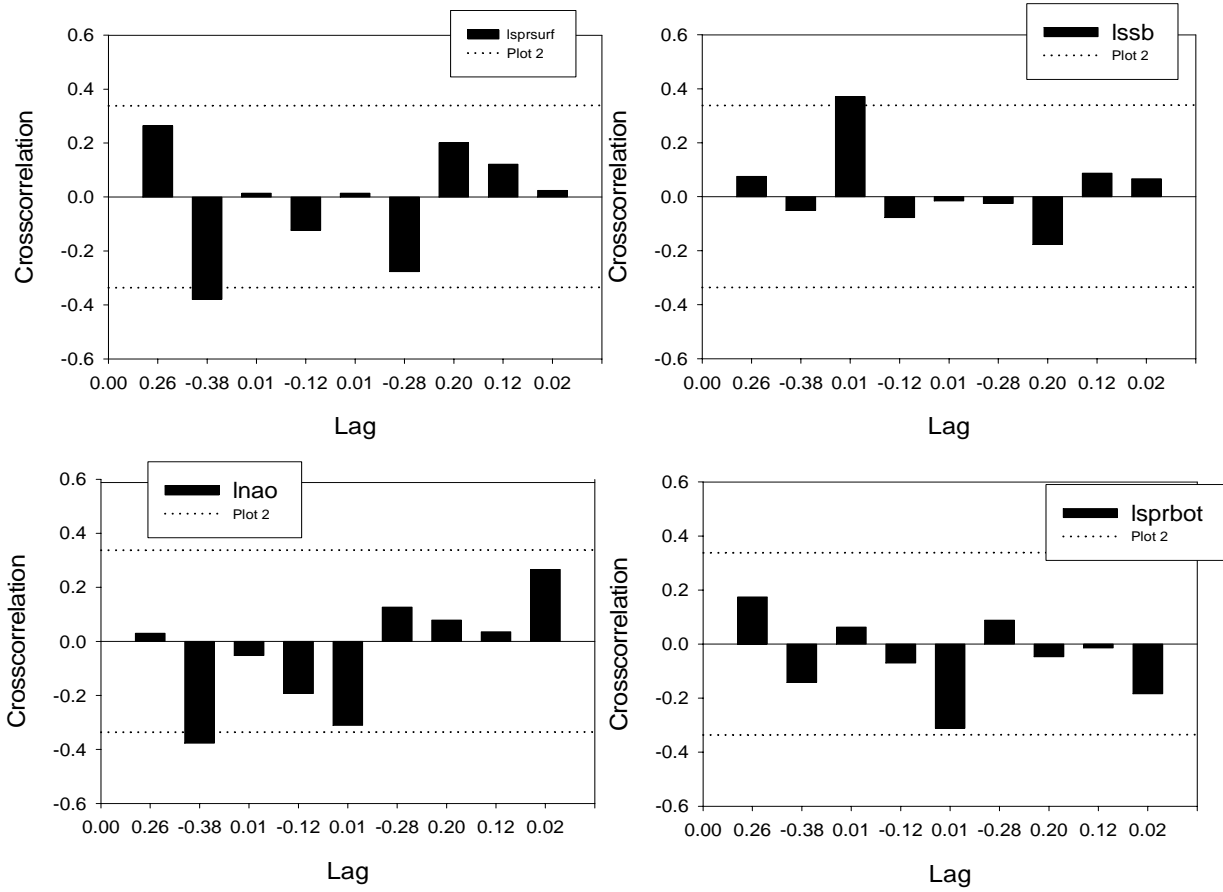


Figure 4 . Crosscorrelations between recruitment and spawner index (A), NAO winter index (B), spring surface temperature anomaly (C), and spring bottom temperature anomaly (D), 1968-2001. Dotted line is approximate 95% confidence interval.

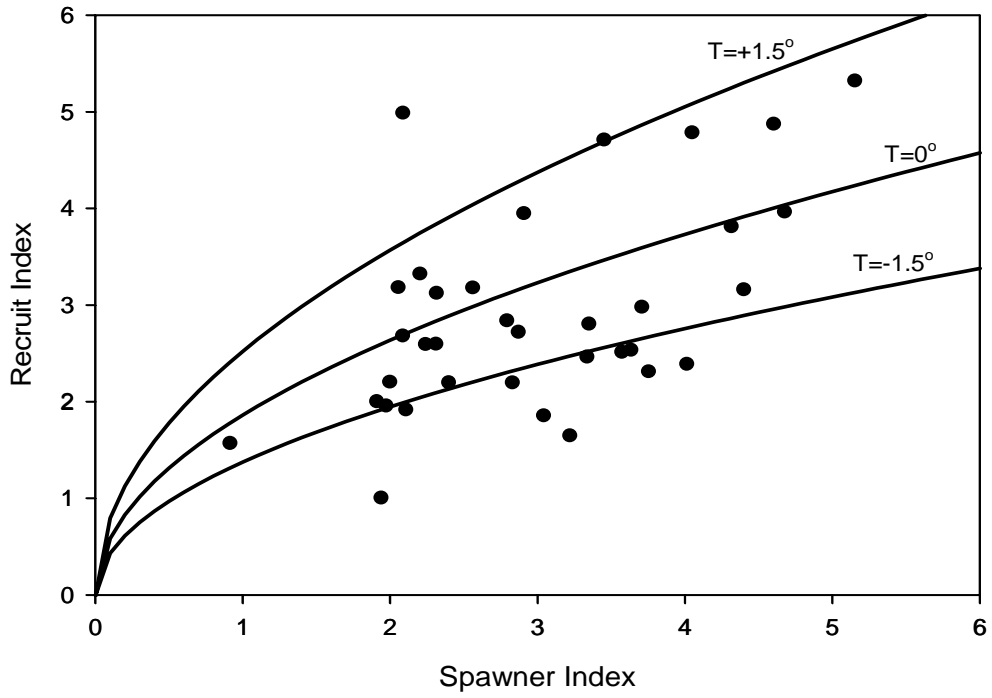


Figure 5. Stock-recruitment models for 1968-2001 with sea surface temperature anomaly ranging from -1.5 to + 1.5. Model depicted does not include spring bottom temperature anomaly.

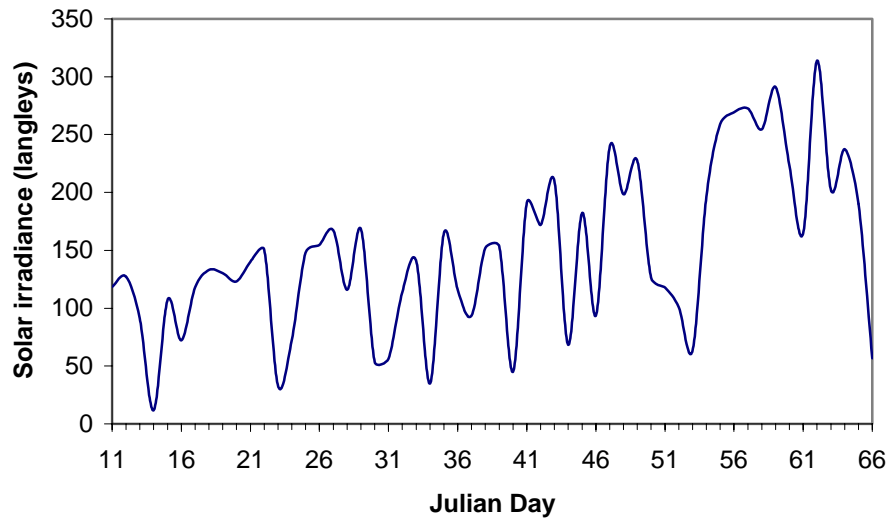


Figure 6. Daily solar insolation (langleys) for mid-January-mid-March 1982 from pyrliometer charts read using the image analysis system.

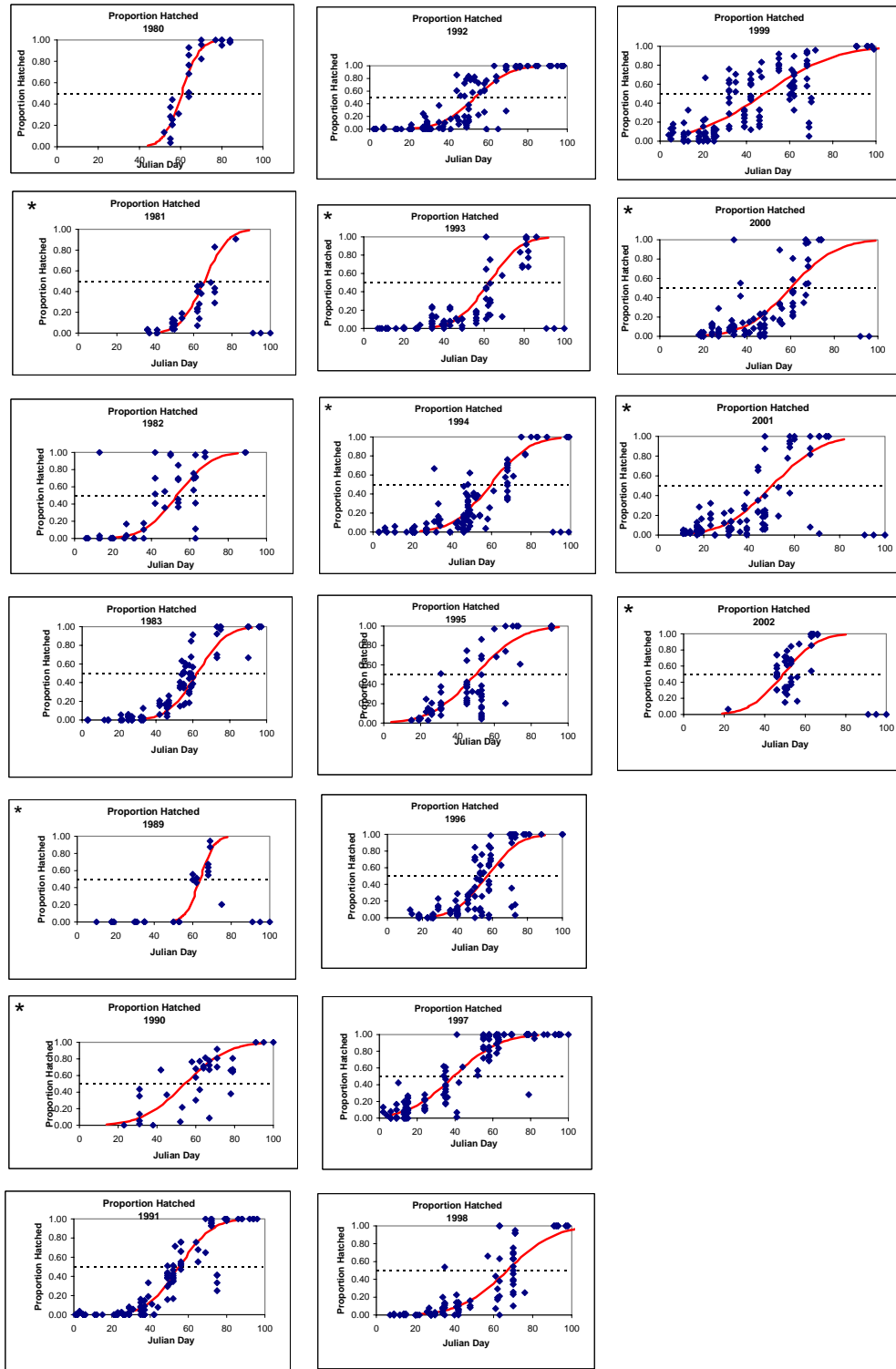


Figure 7. Probit curves for shrimp hatch dates.

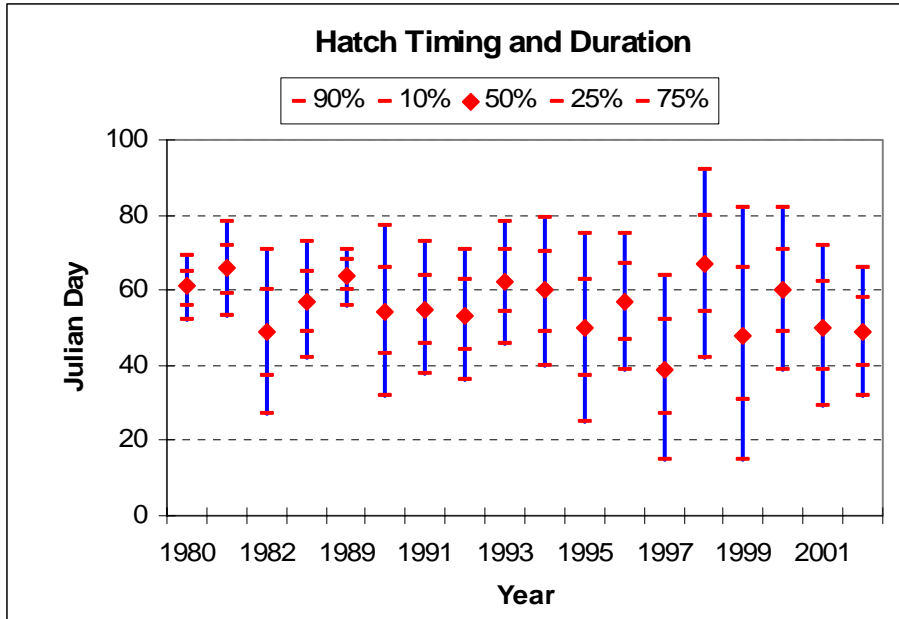


Figure 8. Estimates of hatch timing from probit analysis of proportion of egg-bearing females in samples from the commercial shrimp fishery.

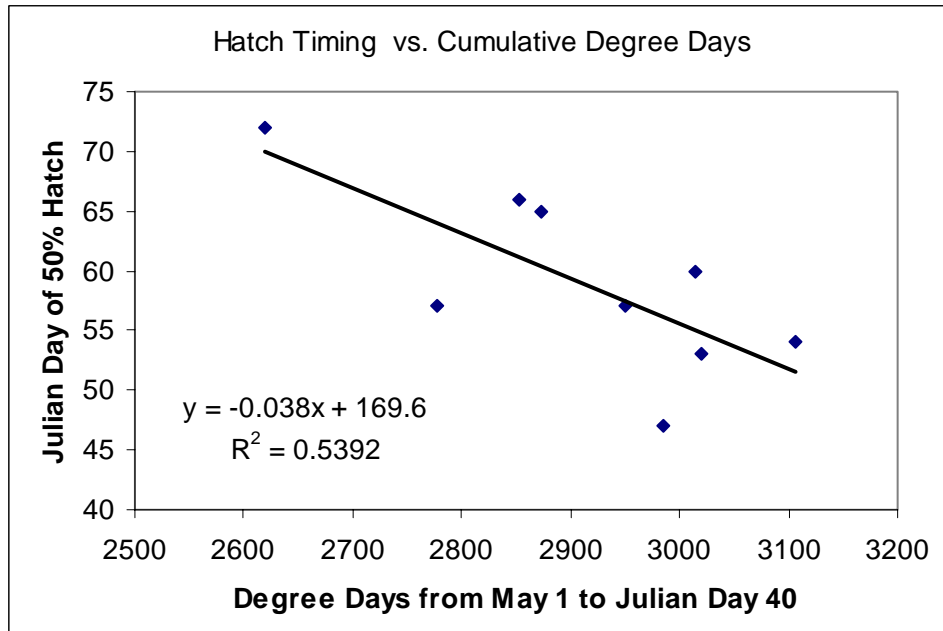


Figure 9. Relationship between estimated date of 50% hatch and the number of degree days during May 1 – February 9 (corresponding to period of oogenesis and embryogenesis).

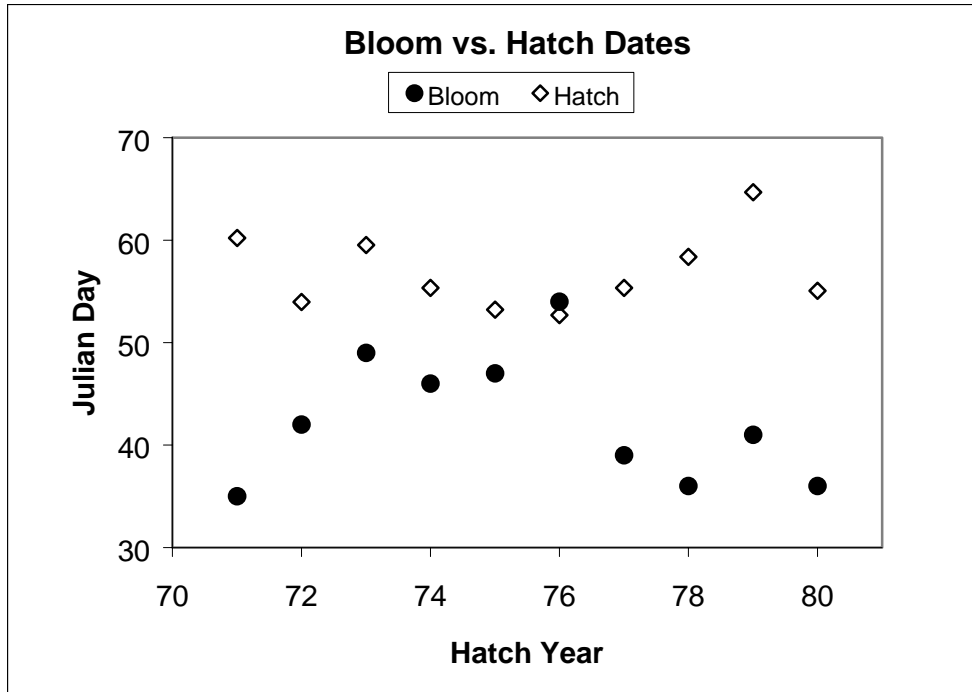


Figure 10. Estimated hatch dates (from relationship with water temperature) and dates of onset of the phytoplankton bloom (Townsend and Cammen 1988) for 1971-1980.

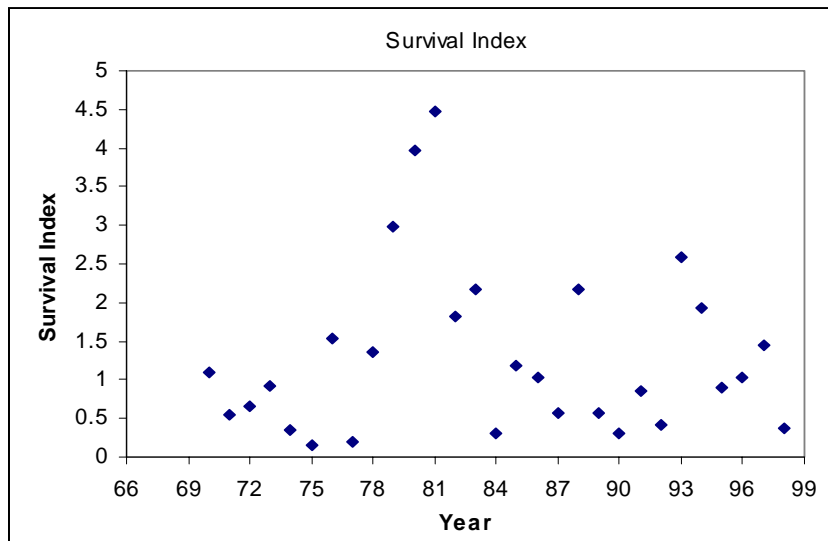


Figure 11. Survival indices for northern shrimp (recruits per spawner).

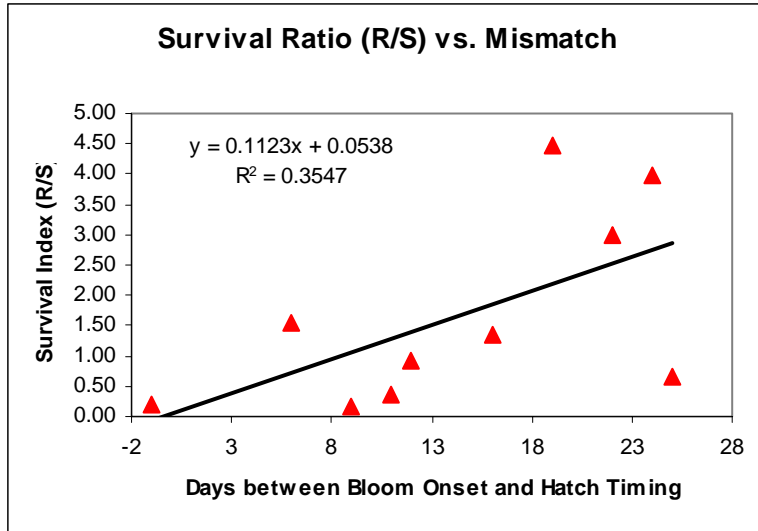


Figure 12. Relationship between degree of mismatch between hatch and bloom onset and early life stage survival of northern shrimp.

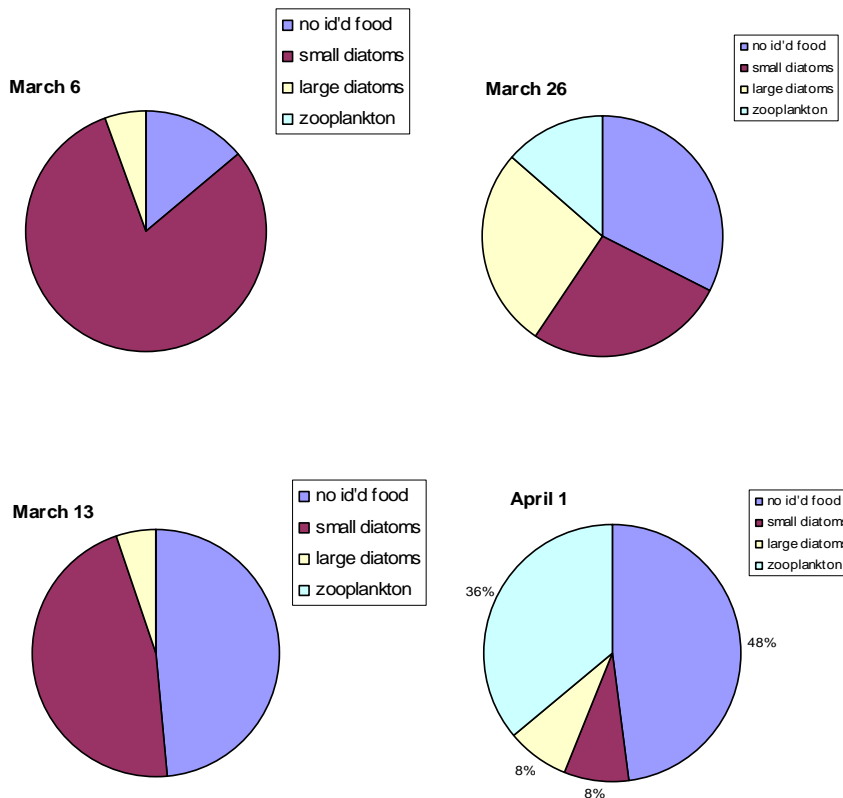


Figure 13. Seasonal progression of diet of larval shrimp (Stickney and Perkins 1980).

Figure 14 Percent frequency of occurrence of shrimp in stomachs by predator size for A. Atlantic cod., B. Red hake; C. Silver hake, D. White hake, E. Spiny dogfish.

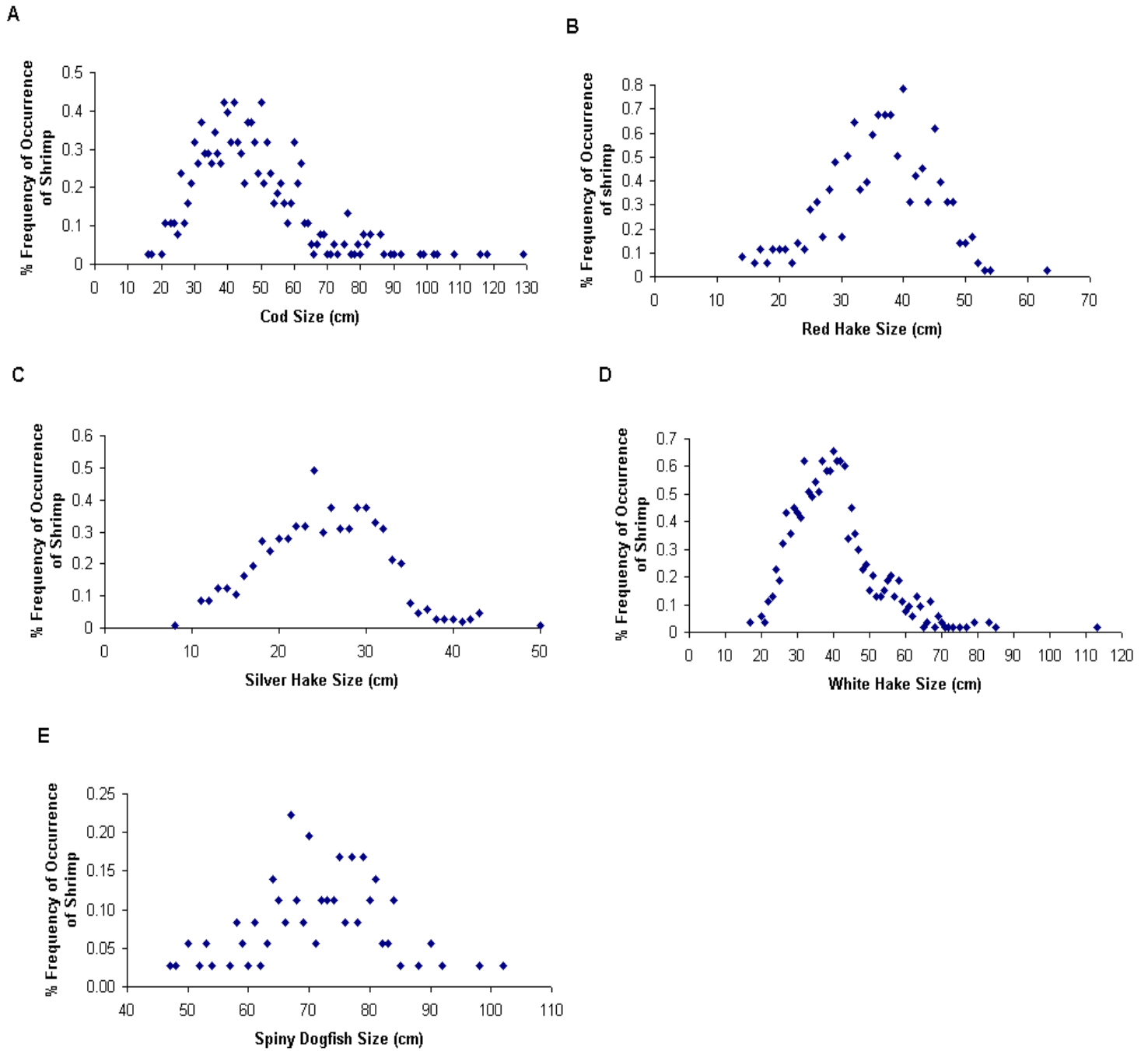


Figure 15. Percent frequency of occurrence of shrimp in stomachs of predators by season
 Number of stomachs examined varies by predator (see Table 2).

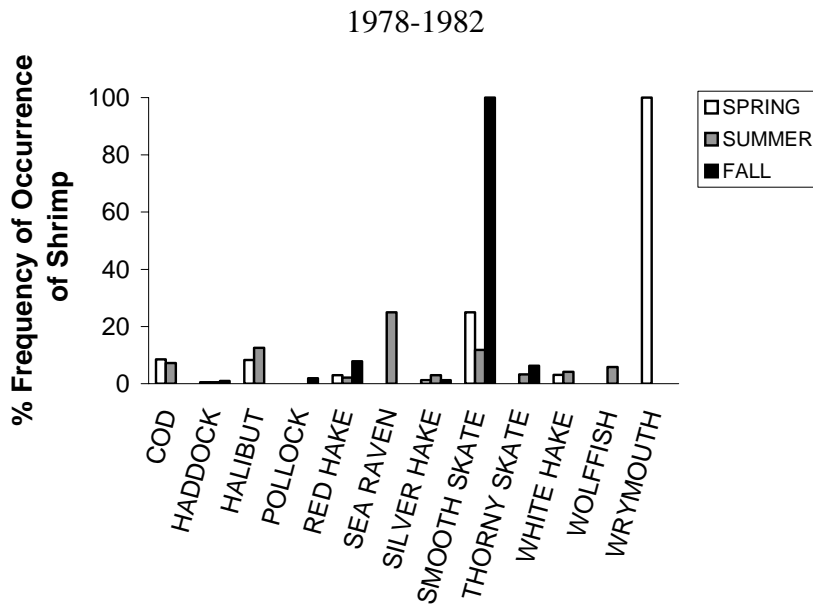
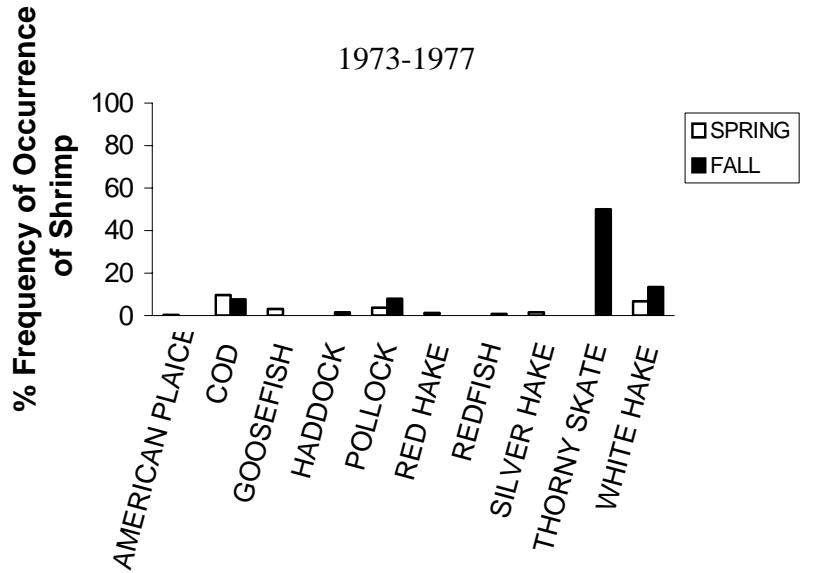


Figure 15, continued.

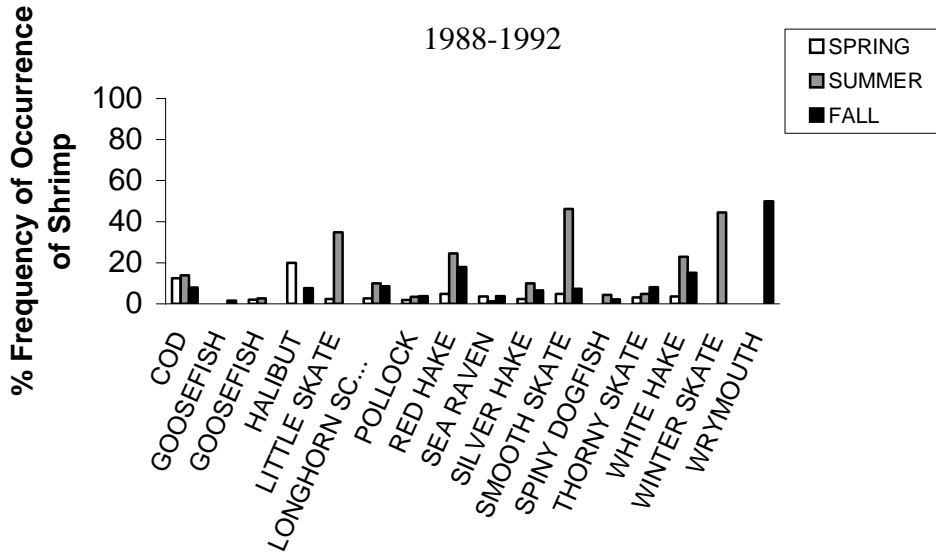
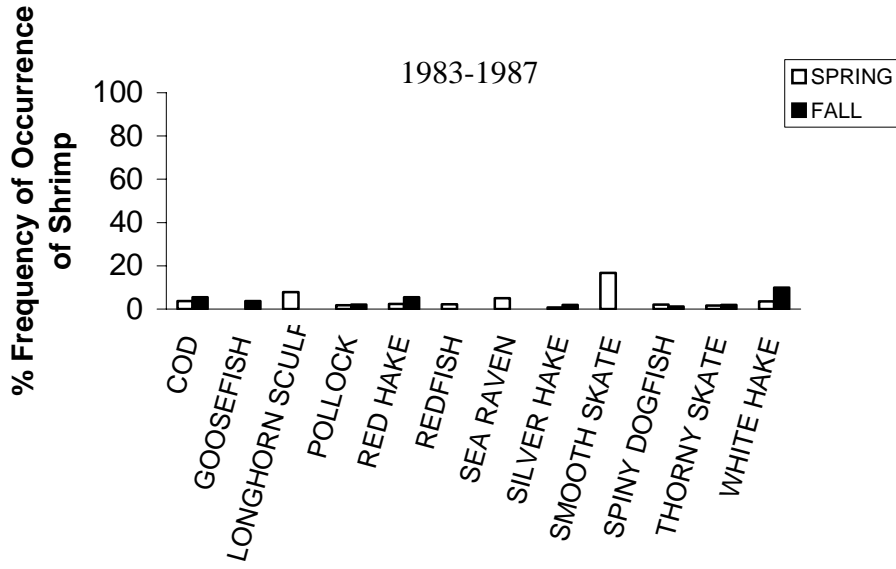


Figure 15, continued.

