

Distinguishing disease impacts from larval supply effects in a lobster fishery collapse

Richard A. Wahle^{1,*}, Mark Gibson², Michael Fogarty³

¹Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, Maine 04575, USA

²Rhode Island Division of Fish and Wildlife, Jamestown, Rhode Island 02835, USA

³Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole, Massachusetts 02835, USA

ABSTRACT: We describe a time series analysis that differentiates the effects of variable larval supply and the mortality impact of shell disease on cohorts of the American lobster *Homarus americanus* in a southern New England, USA, coastal population. Prior to the onset of a shell disease epizootic in 1997, larval settlement alone fully explained 82% of the variation in the numbers of pre-recruit lobsters about to enter the Rhode Island lobster fishery. With the onset of shell disease, however, the model required an additional term for disease prevalence to provide a sufficient statistical fit to the observed data. Neither time trends in bottom temperature nor predatory fish provided significant additional explanatory power for variability in pre-recruit abundance. To our knowledge, this analysis constitutes the first demonstration in which cohorts of a benthic marine invertebrate have been successfully tracked from settlement to the threshold of a fishery by accounting for the joint effects of variable supply of new recruits and subsequent disease during post-settlement years. As such, it illustrates how factors altering the rate of post-settlement mortality over time can obscure predictive relationships between settlement and subsequent recruitment. A tight spawner-to-recruit linkage is therefore unlikely in coastal Rhode Island. The analysis underscores the value of maintaining parallel time series of different life stages, as well as the need to better quantify both pre- and post-settlement mechanisms that influence cohort success in marine populations.

KEY WORDS: *Homarus americanus* · Larval supply · Shell disease · Open population · Recruitment · Forecasting · Stock assessment

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INTRODUCTION

Depletion, disease and degradation of marine ecosystems is on the rise world-wide (Hughes 1994, Ruiz et al. 2000, Jackson et al. 2001, Harvell et al. 2002), but distinguishing among the various factors contributing to the fate of even a single population can be especially problematic in the marine environment. This difficulty arises in part simply because of the absence of appropriate baseline time series for critical life stages (Hunt & Scheibling 1997, Stenseth et al. 2002), but it also stems from the 'open' nature of many marine populations at the scale they are assessed and managed (Caley et al. 1996). Where populations are open, our understanding of the processes determining their dynamics may be confounded by so-called 'supply-

side' effects, whereby the supply of new recruits is derived to varying extents from planktonic larvae broadcast from neighboring populations (Eckman 1983, Lewin 1986, Roughgarden et al. 1988, Doherty & Fowler 1994, Cowen et al. 2000). Here, we evaluate the relationship between the variable supply of new recruits, the onset of disease and the rapid decline of a coastal population of American lobster *Homarus americanus*, in southern New England over the last decade.

The American lobster has undergone dramatic swings in abundance over the last century that have been both local and geographically widespread (Drinkwater et al. 1996, Acheson & Steneck 1997, Castro and Angell 2000, Pearce & Belcom 2005). Explanations for these fluctuations vary from changes in the physical environment to the strength of biologi-

*Email: rwahle@bigelow.org

cal interactions that affect recruitment and mortality. The American lobster occupies a geographic range characterized by steep environmental and biogeographic gradients that are likely to set the stage for dramatic regional differences in the factors driving lobster population dynamics. The recent collapse of the lobster fishery in southern New England, during a time of unprecedented expansion to the north in the Gulf of Maine, provides a poignant example (Castro & Angell 2000, Pearce & Belcom 2005). In the present study, we therefore take the approach of seeking explanations for temporal trends in population change at relatively small regional spatial scales, notwithstanding the degree to which connectivity among subpopulations may buffer these trends.

In southern New England, after a period of increase in the early 1990s, coastal lobster harvests in Rhode Island and neighboring waters of southern Massachusetts and eastern Connecticut fell sharply.

The collapse of the near-shore Rhode Island fishery was preceded by an outbreak of shell disease in coastal southern New England in 1997 (Castro & Angell 2000). Shell disease in American lobster is associated with chitinoclastic bacteria that opportunistically exploit vulnerable animals (Sindermann 1991). Heavy infections can result in abnormal molting and death (Sindermann 1991). In general, the severity of the cases increases as the intermolt period becomes longer with lobster size and age (Glenn & Pugh 2006). By 2003, shell disease had spread to Cape Cod Bay, Boston Harbor and to the nearshore area of the southern Gulf of Maine (Glenn & Pugh 2006) but, as of 2007, had not penetrated coastal Maine or eastern Canada (C. Wilson, Maine Department of Marine Resources, pers. comm.). The shell disease epizootic appears to be unrelated to another much publicized lobster mortality event confined to western Long Island Sound during the summer of 1999, which was induced by warm temperatures, hypoxia and heavy rainfall (Pearce & Belcom 2005). Unclear, however, is the extent to which the lobster decline in the eastern sectors of southern New England is related to shell disease and other environmental factors.

There would be great economic value in foreseeing these trends. The clawed lobster *Homarus* spp. is an international icon of the North American and European fishing industry. In the northwest Atlantic, *H. americanus* is the most commercially valuable single-species fishery, with a combined United States–Canadian landed value of nearly 1 billion USD. To date, however, correlation analyses using single environmental factors such as temperature or predator abundance to explain lobster dynamics have had limited success (Drinkwater et al. 1996, Acheson & Steenack 1997). In addition, although a recent analysis

predicted relative stability for the Rhode Island fishery on the basis of a larval settlement index alone (Wahle et al. 2004), harvests have continued to fall.

We describe a time series analysis that suggests the rapid decline of the Rhode Island lobster population during the late 1990s may be related to the combined effects of a decline in postlarval settlement, followed by the onset of epizootic shell disease, but not to changes in bottom temperatures or predatory fish abundance over the period. To our knowledge, this is the first study in which cohorts of a benthic marine invertebrate have been successfully tracked from settlement to the threshold of a fishery by accounting for the joint effects of variable larval settlement and subsequent disease during the post-settlement years.

MATERIALS AND METHODS

As part of a New England-wide effort to understand the quantitative relationship between larval settlement and subsequent recruitment and the American lobster fishery, we focused on one sub-region where parallel time series of early and later life stages are sufficiently long to evaluate such linkages and where the local outbreak of shell disease is suspected to have caused significant mortality, thereby providing an opportunity to assess a change in natural mortality over the course of the available data set.

Temperature time series. Water temperatures $>20^{\circ}\text{C}$ and their associated low oxygen concentrations are generally considered to be physiologically stressful for the American lobster (McLeese 1956). We examined trends in mean August temperature, typically the warmest month in nearshore waters, for evidence of changes over the period of the lobster decline. Mean monthly bottom water temperatures for Rhode Island's nearshore waters were obtained through the University of Rhode Island Graduate School of Oceanography trawl monitoring program (J. Collie pers. comm.).

Trawl surveys. The Rhode Island Division of Fish and Wildlife (RIDFW) has conducted a seasonal bottom trawl survey in Narragansett Bay and the adjacent Rhode Island and Block Island Sounds since 1979 to monitor groundfish and lobster abundances. Survey cruises were conducted in both spring (May) and autumn (September) using a random sampling design stratified by depth (Lynch 2002). The autumn survey is recognized as the most reliable measure of lobster and groundfish abundances, as water temperatures are less variable than during spring cruises. Therefore, this survey is used in regional stock assessments as well as the present analysis. Per cruise, 42 stations were sampled. For the present analysis, we used trawl data from 1993 to 2006. Lobsters were individually

measured for length and inspected for shell disease. Fishes were counted and weighted in aggregate by species. The trawl collected lobsters both above and below the legal harvestable size of 85.7 mm carapace length. Lobsters >50 mm were sampled well by this gear and those from 60 to 72 mm were included in the pre-recruit index for the present study. This size interval was estimated to correspond to ages of 2.5 to 3.4 yr and would take at least 2 moults to achieve legal size (Gibson et al. 1997). The fish time series comprised species known to be predators of lobsters and other benthic crustaceans from direct observation or from gut content analysis (Ojeda & Dearborn 1991, Wahle & Steneck 1992, Collette & Klein-MacPhee 2002), including black sea bass *Centropristis striata*, striped bass *Morone saxatilis*, silver hake *Merluccius bilinearis*, bluefish *Pomatomus saltatrix*, scup *Stenotomus chrysops*, cunner *Tautoglabrus adspersus*, tautog *Tautoga onitis*, sea raven *Hemitripterus americanus*, goosefish *Lophius americanus*, skate (family: Rajidae), summer flounder *Paralichthys dentatus*, winter flounder *Pseudopleuronectes americanus* and windowpane flounder *Scophthalmus aquosus*. Because the relative predatory impact of the different species is not known, an aggregated abundance index, expressed as biomass (kg) per 20 min tow, was presented in the time series.

Lobster settlement index. Larvae from egg-bearing female lobsters hatch in early summer and spend 6 to 8 wk in the plankton until they metamorphose to the postlarval stage and settle to the sea bed soon thereafter. At the end of the settlement season, young lobsters were sampled by divers using suction samplers in cobble–boulder nurseries between 5 and 10 m below mean low water (Wahle et al. 2004). Standardized diver-based suction sampling surveys have been conducted at fixed locations along the coast of Rhode Island as part of a larger New England-wide survey (Wahle et al. 2004). Settlement surveys were done in shallow cobble–boulder nurseries adjacent to deeper areas in which the trawl survey was conducted. The ‘settlement index’ refers to the population density of young-of-year lobsters collected in a single annual survey at the end of the larval settlement season in late summer to early autumn. As such, it provides an index of the recruitment of 0-group lobsters. Between 12 and 16 quadrats of 0.5 m² were suction-sampled per site. Results from preliminary sampling demonstrated that the variance stabilized at approximately 8 quadrats. Six sites were sampled annually in Rhode Island, and collectively some 65 sites were sampled annually in Rhode Island, Massachusetts and Maine, and New Brunswick, Canada. Settlement indices presented herein represent the means of 3 sites that have been sampled continuously since 1990.

We emphasize that the settlement index should not be misconstrued as a proxy for the local spawning stock because of the small size of the area in question and the likely contribution of an offshore larval subsidy suspected to contribute to southern New England’s inshore recruitment (Katz et al. 1994, Crivello et al. 2005). Thus, the settler-to-pre-recruit relationship described here may not equate to a spawner-to-pre-recruit relationship, which has yet to be evaluated.

Previous research has established that the number of settlers is an accurate reflection of planktonic larval supply (Incze et al. 1997, Wahle & Incze 1997), as well as a predictor of initial year-class strength through the first year of benthic life (Wahle et al. 2004). The persistence of a significant settler-to-1-yr-old relationship in the shell disease years (Wahle et al. 2004) suggests that rates of post-settlement mortality had not changed substantially for lobsters in their first year of life despite increasing prevalence of disease among older lobsters. We reasoned that a lag of 3 yr between settlers and pre-recruits provided sufficient time in which to detect the suspected change in natural mortality that would not be confounded by harvesting.

Model selection. Our previous work revealed a weak density-dependent relationship between the numbers of settlers and resultant 1-yr-old lobsters, which is described by a simple power function (Wahle et al. 2004). This functional relationship seemed reasonable given previous evidence of density dependence in lobsters (Caddy 1986, Fogarty 1995, Wahle et al. 2004). We therefore chose a similar power function as the starting point to evaluate the settler-to-pre-recruit relationship at Year $t + 3$ in the present study. To assess the potential impact of disease on the settler-to-pre-recruit relationship, we examined an extended version of the power function model relating settlement in Year t (S_t) and the resulting recruitment at Age 3 (R_{t+3}) by including the cumulative effects of disease (D) over the 3 yr following settlement (defined here as the sum of the prevalence in a cohort over those years). Because the impact of disease may vary with settlement density, we considered a model including the interaction (I) of disease and settlement (defined as $S_t \times D$). This model structure assumes that disease-related terms have a multiplicative effect on recruitment. Terms for predation (P) and temperature (T) were included as additive effects, but interaction terms were not included for these factors, in part to limit the number of independent variables and therefore the complexity of the model, and because interactions with settlement density were considered less likely.

The full model is then:

$$R_{t+3} = aS_t^b e^{-cD_t - dI_t - gP + hT} \quad (1)$$

where a is the rate of recruitment at low settlement densities, b is a coefficient reflecting compensatory processes, and c , d , g and h are coefficients reflecting the magnitude of disease, interaction, predation and temperature effects, respectively. For estimation, we employed a linearized form of the model:

$$\log_e R_{t+3} = \log_e a + b \log_e S_t - cD_t - dI_t - gP + hT + \xi_t \quad (2)$$

where ξ_t is a normally distributed random error term with mean zero and constant variance. We sequentially added the disease and interaction terms to the basic power function model to test for their effect.

We used the Akaike information criterion (AIC) for model selection (Burnham & Anderson 1998). The AIC is a robust information-theoretic measure that explicitly addresses the issue of model parsimony. Models with a greater number of parameters are assessed a penalty. The model with the lowest AIC score is deemed the most appropriate model among those tested based on the same series. We computed the Durbin-Watson statistic to test for first-order autocorrelation in the residuals to check for violation of the assumption of independence in the error terms. Due to the relatively small number of observations, we used the corrected form (Burnham & Anderson 1998; p. 51):

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1} \quad (3)$$

where AIC is the standard Akaike information criterion measure (Burnham & Anderson 1998; p. 46), K is the number of parameters and n is the number of observations.

RESULTS

The decline in Rhode Island's near-shore commercial lobster *Homarus americanus* landings was preceded by a sharp downturn in the abundance of pre-recruit lobsters as measured by the annual RIDFW autumn near-shore trawl survey (Fig. 1A) (Lynch 2002), a trend corroborated by other surveys in the region (University of Rhode Island Graduate School of Oceanography trawl survey, www.gso.uri.edu/fishtrawl/).

The incidence of shell disease in Rhode Island was extremely low until 1996, when its prevalence increased dramatically, peaking in 2002 at 32% and stabilizing just below 30% thereafter (Wilk et al. 1996; Fig. 1A). During this period, there was no apparent trend in temperature and appreciable increases in predatory fish abundance were only evident after 2002, well after the decrease in lobster pre-recruit numbers (Fig. 1B). Prior to the onset of

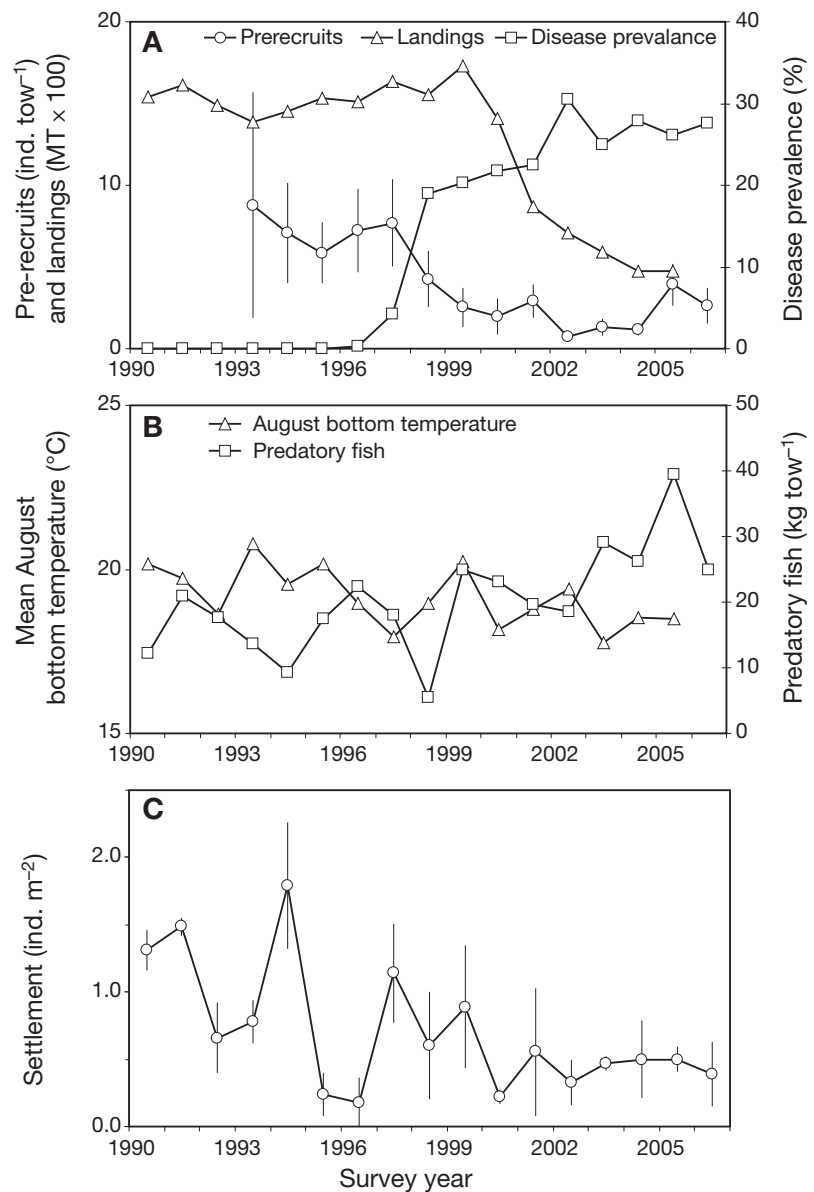


Fig. 1. *Homarus americanus*. Time series of: (A) inshore Rhode Island commercial lobster landings, pre-recruit abundance (mean \pm 1 SE) and shell disease prevalence (percent of lobsters with shell disease) from autumn near-shore trawl surveys ($n = 42$ tows yr^{-1}). The large SE in the 1993 trawl survey is attributed to a single very large catch; (B) bottom temperature and predatory fish abundance in trawl surveys; and (C) newly settled young-of-year lobster (mean \pm 1 SE; $n = 3$ sites sampled annually since 1990). MT: metric tons

shell disease, coastal Rhode Island experienced 3 of the highest settlement years on record between 1990 and 1994, followed by a precipitous drop to 2 of the poorest years on record in 1995 and 1996 (Fig. 1C). Intermediate to low levels of settlement were observed over the remaining years. For the cohorts unaffected by shell disease (1990 to 1996), settlement alone explained 82% of the variability in pre-recruit numbers 3 yr later (Fig. 2, Tables 1 & 2). However, when the 1997 to 2003 cohorts were added, the settlement index alone was no longer sufficient to describe the relationship and the regression was rendered non-significant (Fig. 2, Tables 1 & 2).

The expanded model including the settlement–disease interaction considerably improved the fit to the observed data, while adding temperature and predator abundance added little to the explanatory power of the model. The version of the model with terms for settlement and the settlement–disease interaction had the lowest AIC_c score and the highest adjusted r² value (Table 1; see also Appendix 1). The change in AIC_c relative to the next best-fitting model was greater

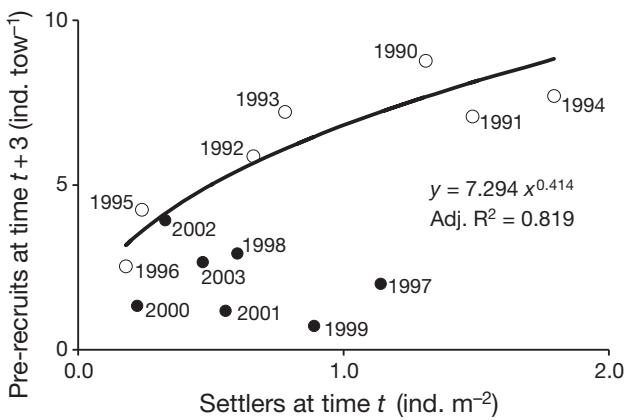


Fig. 2. *Homarus americanus*. Settler-to-pre-recruit linkage decouples. Relationship between abundance of pre-recruits from trawl surveys and settlers from diver surveys, with a lag of 3 yr for the 1990 to 1996 cohorts (O with fitted curve and power function). See ‘Results’ and Tables 1 & 2 for regression statistics. Inclusion of 1997 to 2003 cohorts affected by shell disease (●) render a non-significant regression

than -2 , indicating a significant improvement in fit (Burnham & Anderson 1998). As individual factors, D and I explain $>60\%$ of the variability in the pre-recruit time series, whereas S , P and T alone explain $<22\%$ (Appendix 1). Parameter estimates for the best-fitting model are provided in Table 2, and observed and predicted values of pre-recruit abundance are presented in Fig. 3A,B.

A plot of the relative mortality index ($Z = -\ln[R/S]$) over time suggests elevated mortality rates beginning with the 1997 year class and again in year classes 1999 and 2001 (Fig. 3C). The change in ratio clearly resulted from a decline in pre-recruits (R ; Fig. 1A), not an increase in settlement (S ; Fig. 1B). The relative mortality index has not been as high in recent years, perhaps suggesting a decline in disease severity despite continued high prevalence.

DISCUSSION

The modified power function incorporating settlement and disease terms captures the combined effects of variable settlement and the increasing impact of disease over the years in question reasonably well. We cannot rule out the possibility that an unidentified third factor may have made lobsters *Homarus americanus* in southern New England more susceptible to shell disease than in the past. More data are clearly needed on the mechanism(s) and size-specificity of this syndrome. We also cannot entirely rule out other possible agents of natural mortality or emigration that might explain the disappearance of older lobsters from coastal areas, but it would be difficult to explain the abruptness of the change in lobster numbers on the basis of the time series in predator abundance or bottom temperature.

These findings are significant for reasons both specific to the American lobster fishery and more generally to the development of forecasting tools for open marine populations. First, to our knowledge, this is the first demonstration for a benthic marine invertebrate that local cohort dynamics can largely be explained by the

Table 1. Model fit statistics. Linear least-squares regression statistics, Akaike information criterion (AIC) and first-order correlation statistics for the power function describing the relationship between lobster settlement at time t and pre-recruits 3 yr later at $t + 3$, using defined ranges of cohorts with and without the model parameters for disease and the interaction between settlement and disease. ND: not determined

Independent variables represented	Adjusted r ²	p	AIC	1st order auto-correlation	Durbin-Watson statistic
Settlers 1990–1996 cohorts	0.819	0.005	ND	–0.641	2.870
Settlers 1990–2003 cohorts	0.055	0.192	–4.11	0.379	1.171
Settlers 1990–2003 cohorts + Interaction	0.795	0.0001	–22.36	0.222	1.463

Table 2. Model parameters. Least-squares regression parameter estimates for linearized versions of power models evaluated in Table 1. NA: not applicable. Parentheses: 1 SE

Independent variables represented	$\text{Log}_e a$	b	c	d
Settlers 1990–1996 cohorts	1.987 (-2.538)	0.414 (0.087)	NA	NA
Settlers 1990–2003 cohorts	1.377 (-1.402)	0.394 (0.285)	NA	NA
Settlers 1990–2003 cohorts + Interaction	1.998 (-1.858)	0.428 (0.140)	NA	-2.123 (0.340)

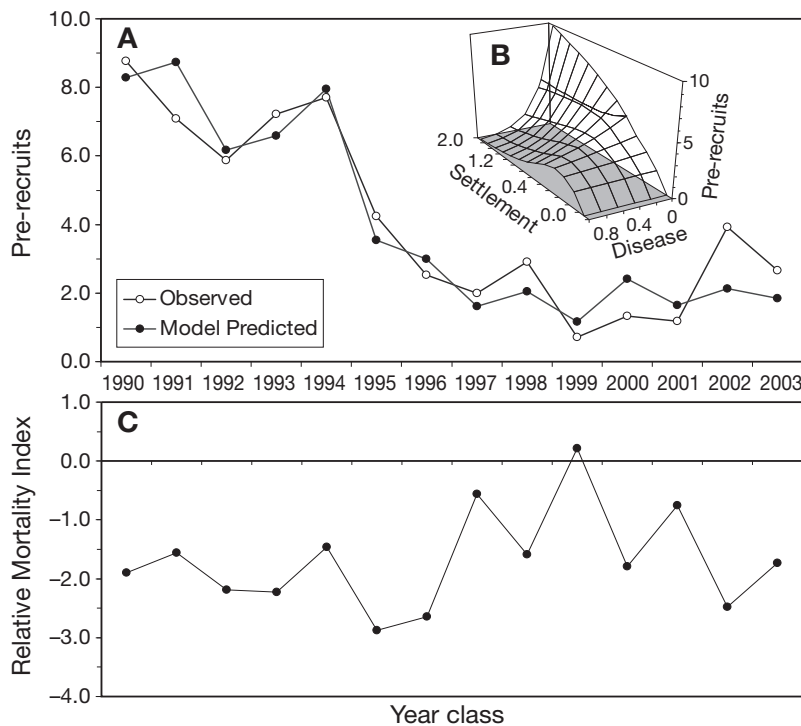


Fig. 3. *Homarus americanus*. Modeling joint effects of settlement and disease. (A) Comparison of observed and model-predicted time trend in pre-recruit abundance. (B) Response surface of the power function employed to model the effects of settlement, disease severity and their interaction on pre-recruit abundance. (C) Estimated relative mortality rate between settlers and pre-recruits from observed data. Relative mortality is expressed as $Z = -\ln(R/S)$, where R is the number of pre-recruits and S the number of settled individuals

joint effects of settlement and disease. The significant interaction term is consistent with the hypothesis of a density-dependent disease transmission mechanism, whereby disease prevalence is higher among cohorts settling at relatively high densities. To date, there is little understanding of the degree to which shell disease is contagious. The mechanism of transmission must therefore be a priority for future research.

Second, the settlement data suggest that not all of the decline in pre-recruits during the late 1990s can be attributed to shell disease. Rather, an earlier drop in settle-

ment appears to have compounded the decline in pre-recruits. Moreover, because the simple settler-to-1-yr-old relationship described by Wahle et al. (2004) has persisted into the shell disease years and larger, older lobsters exhibit the most severe cases of the disease (Glenn & Pugh 2006), it appears that most of the mortality associated with the disease is felt after the first year of life.

Third, this is a prime example of the utility of parallel time series of early juvenile and adult life stages to assess the health of the stock. Parallel monitoring of multiple life stages of marine organisms with complex life histories can provide insights into the influence of pre- and post-settlement processes on the fate of a cohort that would otherwise be unavailable from surveys of only a single stage (Gosselin & Qian 1997, Hunt & Scheibling 1997). For commercially exploited species, multi-stage monitoring can be a powerful tool in assessment, forecasting and management (Caputi et al. 1995, Lipcius & Stockhausen 2002). While we believe the present study is a promising indication for the wider application of a settlement index as a predictive tool for the American lobster, we acknowledge the geographically restricted nature of the current evaluation. Foremost among the challenges that face forecasting and management in the northwest Atlantic is the strong signature that the region's oceanographic heterogeneity and steep thermal gradients leave on lobster demography. The relatively local nature of shell disease and other mortality events contrast strongly with the large-scale transport potential of the planktonic larvae, which by most estimates can disperse 100s if not 1000s

of kilometers and may, to some extent, buffer the effects of local mortality events (Fogarty 1998).

Trends in the western rock lobster *Panulirus cygnus* fishery of Australia have long been forecast on the basis of larval supply and the ocean processes driving that supply (Phillips 1986, Caputi et al. 1995). Such an early warning system has been an elusive goal for most other large decapod fisheries. In the present case, what was developing as a possible first example of a settler-to-recruit predictive linkage for a clawed lobster was obscured by an apparently disease-induced change in

the rate of natural mortality during the years after settlement. While the change in mortality rate of later juvenile stages compromised the predictive utility of the settlement index for this region, it is noteworthy that this is the first demonstration that a settlement index, either alone or in concert with another environmental indicator, is of value in explaining time trends in the abundance of American lobsters within 1 or 2 molts of harvestable-size individuals. The dynamics of Western Australia's rock lobster can be predicted from a settlement index collected at a few sites along several 100 km of coast. In contrast, the steep environmental gradients along the American lobster's geographic range and locally important agents of mortality, such as disease, make it unlikely that future predictive tools will ever be as widely applicable for this species. Rather, it may be necessary to accommodate regionally tailored or spatially structured models that account for such local variability in post-settlement mortality.

Finally, a question likely to be critical to recovery from the region's recent population collapse is the extent to which the local population off Rhode Island's immediate coast is dependent on local versus distant egg production. Developing the appropriate management response to this recent crisis will benefit from a better understanding of larval exchange among regions. It is likely that the effective breeding population for coastal southern New England extends well beyond the area afflicted with shell disease and perhaps to the edge of the continental shelf (Katz et al. 1994, Crivello et al. 2005). Tight spawner-to-recruit coupling is therefore unlikely in coastal Rhode Island. Wind-driven and residual currents are sufficient to transport larvae from as far away as Georges Bank and the southern New England shelf break 100s of kilometers to the south and east, where concentrations of reproductive lobsters exist (Skud & Perkins 1969, Katz et al. 1994), possibly enhancing the resilience and recovery of this local population (Fogarty 1998). Modeling approaches that further evaluate the relative contribution of recruits from local and distant sources continue to be as central to our understanding of lobster population dynamics as they are in other marine systems (e.g. Cowen et al. 2000).

Still, as with disease events in other marine environments, significant uncertainties remain about the causes and future of shell disease in the region. While evidence for the links between climate warming and disease events are emerging in other marine systems from corals to seagrasses (Harvell et al. 2002), the role of increasing sea temperatures on the lobster shell disease epizootic remains speculative (Glenn & Pugh 2006). Expansion of shell disease into the waters of Maine and eastern Canada could be catastrophic for the coastal economies that depend on the lobster fish-

ery. Local episodes of high mortality such as this underscore the need to better understand the implications of spatial and temporal heterogeneity in mortality processes to the productivity of exploited populations (Hilborn & Walters 1992). It will be through our ability to distinguish among the multiple natural and anthropogenic factors influencing population dynamics that sensible management options emerge.

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Appendix 1. Results of model selection runs for models including the log transformed settlement index (*S*), disease index (*D*), interaction between disease and settlement (*I*), predation index (*P*) and temperature (*T*). Models ranked by r^2 values from highest to lowest. Model with the lowest AIC score is deemed the most parsimonious predictive model

Number of variables	Adjusted r^2	AIC	Variables in model	Number of variables	Adjusted r^2	AIC	Variables in model
2	0.7933	-22.36	<i>S, I</i>	3	0.6826	-14.84	<i>I, T, P</i>
3	0.7879	-20.08	<i>S, I, P</i>	4	0.6766	-12.09	<i>S, D, T, P</i>
3	0.7788	-19.54	<i>S, I, T</i>	1	0.6671	-17.68	<i>D</i>
4	0.7737	-16.73	<i>S, I, T, P</i>	2	0.6412	-15.19	<i>D, P</i>
3	0.7707	-19.07	<i>S, D, I</i>	2	0.6339	-14.92	<i>S, D</i>
4	0.7624	-16.09	<i>S, D, I, T</i>	1	0.6240	-16.10	<i>I</i>
4	0.7619	-16.07	<i>S, D, I, P</i>	3	0.6020	-11.90	<i>S, D, P</i>
3	0.7553	-18.23	<i>D, I, T</i>	2	0.5910	-13.51	<i>I, T</i>
5	0.7460	-11.91	<i>S, D, I, T, P</i>	1	0.2140	-6.51	<i>P</i>
4	0.7441	-15.13	<i>D, I, T, P</i>	2	0.1557	-4.07	<i>S, P</i>
2	0.7325	-19.01	<i>D, T</i>	2	0.1356	-3.76	<i>T, P</i>
3	0.7159	-16.28	<i>D, I, P</i>	3	0.0624	-0.76	<i>S, T, P</i>
2	0.7148	-18.17	<i>D, I</i>	1	0.0546	-4.11	<i>S</i>
3	0.7070	-15.88	<i>S, D, T</i>	2	-0.0319	-1.46	<i>S, T</i>
3	0.7055	-15.81	<i>D, T, P</i>	1	-0.0823	-2.36	<i>T</i>
2	0.7031	-17.65	<i>I, P</i>				