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Impact of disease on the survival of three commercially fished species

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Abstract

Recent increases in emergent infectious diseases have raised concerns about the sustainability of some marine species. The complexity and expense of studying diseases in marine systems often dictate that conservation and management decisions are made without quantitative data on population-level impacts of disease. Mark-recapture is a powerful, underutilized, tool for calculating impacts of disease on population size and structure, even in the absence of etiological information.

We applied logistic regression models to mark-recapture data to obtain estimates of disease-associated mortality rates in three commercially-important marine species: snow crab (*Chionoecetes opilio*) in Newfoundland, Canada, that experience sporadic epizootics of bitter crab disease; striped bass (*Morone saxatilis*) in the Chesapeake Bay, USA, that experience chronic dermal and visceral mycobacteriosis; and American lobster (*Homarus americanus*) in the Southern New England stock, that experience chronic epizootic shell disease. All three diseases decreased survival of diseased hosts. Survival of diseased adult male crabs was 1% (0.003 – 0.022, 95% CI) that of uninfected crabs indicating nearly complete mortality of infected crabs in this life stage. Survival of moderately and severely diseased striped bass (which comprised 15% and 11% of the population, respectively) was 84% (70 – 100%, 95% CI), and 54% (42- 68%, 95% CI) and that of healthy striped bass. The disease-adjusted yearly natural mortality rate for striped bass was 0.29, nearly double the previously accepted value, which did not include disease. Survival of moderately and severely diseased lobsters was 30% (15 – 60%, 95% CI) that of healthy lobsters and survival of mildly diseased lobsters was 45% (27 – 75%, 95% CI) that of healthy lobsters. High disease mortality in ovigerous females may explain the poor recruitment and rapid declines observed in this population. Stock assessments should account for disease-related mortality when resource management options are evaluated.

Introduction

Recent reports of frequent and severe disease outbreaks raise questions about how and when marine diseases should be managed (Harvell et al. 1999, Groner et al. 2016). Critical to such decisions are whether, and under what circumstances, disease outbreaks cause significant impacts on marine populations, including commercially important stocks (e.g., Chaloupka et al. 2009, Krkosek et al. 2013). However, evaluating impacts of marine diseases on populations can be challenging because quantitative estimates of disease-related mortality are difficult to obtain, particularly when host species are mobile or experience chronic diseases (Cooch et al. 2012). Although they yield complementary data, studies of the etiology and pathology associated with an emergent disease can be expensive and time-consuming, often taking longer to conduct than the window of time available for early intervention (Burge et al. 2016, Groner et al. 2016, Langwig et al. 2015). The paucity of information on disease impacts in marine systems has made it difficult for government agencies to prioritize research and management actions for many commercially and ecologically important species.

Although underutilized, mark-recapture can be an effective tool for estimating the impacts of disease on host populations (Conn and Cooch 2009, Cooch et al. 2012). Mark-recapture studies that use simple biological marking or conventional tags represent an adaptable method for obtaining data. These studies can be implemented quickly as either a new research program or as an extension to an existing mark-recapture program. In the latter case, adapting the program to the study of disease requires the identification and recording of a non-lethal diagnostic for disease presence such as visual signs or detection of pathogens in bodily fluids. Identification of a pathognomonic diagnostic does not require that the etiology of the disease be fully elucidated, thereby allowing population impacts of the disease to be assessed concurrently with fundamental epidemiological and pathological research, rather than after its completion. Moreover, mark-recapture methods are applicable to the study of a wide range of diseases that are diverse in their epidemiology and population impacts. Although complex multi-state mark recapture methods are the ideal approach for determining survival, disease incidence and disease progression, these methods frequently require *a priori* knowledge about the disease in order to correctly specify state-transition matrices, and can suffer from convergence issues (i.e. Choquet et al. 2009). In contrast, logistic regressions comparing the recapture rates of initially healthy and diseased individuals can be used to quantify relative survival of diseased versus healthy individuals without *a priori* knowledge of the disease. Mark-recapture methods are being increasingly used to estimate epidemiological processes in diseases of terrestrial wildlife, including badgers with tuberculosis (Graham et al. 2013), little brown bats with white-nose syndrome (Maslo et al. 2015) and gorillas with Ebola virus disease (Genton et al. 2015).

However, they are not well-used in marine systems, even though mark-recapture is a common method for estimating population sizes in such systems (i.e. Chaloupka et al. 2009).

We used logistic regressions to conduct prospective, case-control studies to estimate disease-associated mortality rates in three commercially important species that show visual signs of chronic disease: snow crab (*Chionoecetes opilio*), striped bass (*Morone saxatilis*), and American lobster (*Homarus americanus*). These diseases range in severity and phenology, and include a rapidly-progressing, unresolvable, parasitic infection causing bitter crab disease (BCD) in snow crabs; a slowly-progressing, rarely-resolved disease caused by mycobacteria resulting in visceral and dermal mycobacteriosis in striped bass; and a rapidly-progressing, resolvable bacterial dysbiosis causing epizootic shell disease (ESD) in lobsters. In all cases, populations are hypothesized to be declining in parts of their ranges due to disease (Shields et al. 2005, Wahle et al. 2009, Vogelbein et al. 2012). We applied logistic regression to mark-recapture data to estimate relative survival of animals released in different disease severity states compared to presumably healthy conspecifics (Jennelle et al. 2007, Cooch et al. 2012). We interpreted these results in terms of their impacts on natural mortality, management practices and, in the case of the American lobster, impacts on spawning potential.

Methods

Study systems and tagging method

Case 1: Snow crabs and BCD

Study system: Snow crab support the most valuable fishery in Atlantic Canada with exports valued at CAN $500 million annually (Fisheries and Oceans Canada, 2016). In 1992, a parasitic dinoflagellate (*Hematodinium* sp.*)* was discovered in crabs from the northern bays of Newfoundland. The parasite causes bitter crab disease (BCD) and renders the meat of the crabs unfit for consumption (Taylor and Khan 1995). Disease prevalence in large-clawed male crabs, which are favored by the industry, has generally been low (< 3.5%) with occasional pulses of increased disease that have been associated with warmer temperatures, and increases in densities of small and intermediated sized crabs (Shields et al. 2005, 2007, Mullowney et al. 2011). In 2005, prevalence reached 35% in large-clawed males, leading resource managers and the industry to question the role of the parasite in crab mortalities (Shields et al. 2007). The fishing industry elected to reduce the quota in the affected areas in 2006 as a precautionary measure, however population estimates of the impact of BCD are not available and it is unclear if these management strategies increase the resiliency of these populations to disease outbreaks.

Tagging: To estimate disease mortality, 361 diseased crabs and 361 crabs without external signs of the disease (Figure 1a) were tagged in Conception Bay, Newfoundland, Canada (lat. 47° 45‘ N, long. 53° 10’ W), in October, 2006, by tying a uniquely-labelled vinyl tube (spaghetti tag) laterally around the carapace. All crabs in the study were large-clawed males in terminal molt conditions 2 (i.e., with a new hard shell), ranging in size from 95 to 139 mm carapace width. Crabs in the terminal molt instar will not molt and hence will not lose the tag to molting. Although it would have been informative to tag other stages, this was not feasible due to the risk of tag-loss during molting and the absence of a fishery for other sizes and stages. Most recaptures were made by commercial fishermen and occurred during the fishing season, in late spring (April-June) in the two years after release. A few additional crabs were recaptured during research cruises in the spring and fall. For all recaptures, a reward of CAN $10 was offered for return of a tag. To check for differential survival between diseased and healthy crabs that resulted from tagging, tagged crabs with and without BCD infection (five of each) were held in commercial crab traps at sea for 24 hrs and then examined for differential mortality. Survival was 100% in both groups (Taylor, D. M. unpubl. data). A 24 hr acute test is considered sufficient to test tagging mortality in this species.

Case 2: Striped bass

Study system: The striped bass fishery supports both recreational and commercial fishing, with US landings between 2005 and 2014 averaging 26.2 million pounds annually for recreational efforts and 6.7 million pounds for commercial efforts (ASMFC 2016). In the 1990s, striped bass in Chesapeake Bay recovered from a significant population decline associated with over-exploitation, environmental degradation and low recruitment (Richards and Rago 1999). Since 1997, granulomatous dermatitis (Figure 1b) and granulomatous inflammation of the visceral organs have been noted in striped bass from the region; the disease lesions are associated with two newly described species of *Mycobacterium* as well as other undescribed species (Gauthier et al. 2011, Rhodes et al. 2003, 2005). As is typical for infections with *Mycobacterium* spp. in fishes, disease in striped bass develops slowly and some individuals appear to persist for long periods with low-level infections (Colorni 1992). Despite recognition of its potential to cause mortality or alter fecundity, it is unclear how disease is affecting population size and restoration efforts for striped bass (Vogelbein et al. 2012).

Tagging: Tagging took place in September through November every year from 2005 to 2012 and in May for some years. Approximately one to three thousand fish were obtained from pound nets at the mouth of the Rappahannock River, Virginia (lat. 37° 36.67' N, long. 76° 17.49' W) and upriver (lat. 37° 58.73' N, long. 76° 53.04' W) each year. All fish were greater than 457 mm in total length (minimum legal size), and 95% were between 457 and 610 mm total length) which, in the Chesapeake Bay, typically corresponds to between three and six years of age. Upon tagging, fish were measured for fork length and both sides of each fish were photographed for a direct comparison of disease signs at the times of tagging and recapture. Disease status of released and recaptured individuals was assessed in photos using the following classification: *healthy* – no visible external signs of mycobacteriosis; *mild disease* – up to 10 pigmented foci per side or a single, small focal skin ulcer (< 2 cm^2) per side of the fish; *moderate disease* – from 11 to 50 pigmented foci or multifocal ulcers all less than 2 cm^2; and *severe disease* – more than 50 pigmented foci per side or focal or multifocal ulcers greater than 2 cm^2. A pigmented focus is a small, external, brown focal lesion appearing as a dot on a scale that we considered to be the earliest manifestation of the disease. Histologically, each pigmented focus is associated with epidermal/dermal granulomatous inflammation, often containing acid-fast bacteria (Vogelbein et al. 2012). Approximately one thousand to fifteen hundred fish obtained from gill nets from a variety of locations were tagged annually in Maryland waters. Anchor tags were inserted into the body cavity through a small incision cut into the abdomen; a vinyl streamer remained external to the body with a unique number and a message offering a $20 US reward for return of the fish and a $5 reward for return of the tag. Recaptured animals were obtained from commercial or recreational fishers or by research personnel. Fish were handled according to approved IACUC procedures (project assurance number VA-A3713-01) and were immediately released back into the water at the tagging location.

Case 3: American Lobsters

Study system: The American lobster is one of the most valuable fisheries in the United States, with annual dockside revenues as high as USD $567 million (NMFS, 2016). Although lobster populations appear to be growing over most of their range, abundance of lobsters in the southernmost stock, the southern New England stock, is the lowest since the 1980s despite declining exploitation rates over the last 10 years (Wahle et al. 2015, Howell 2012). Recruitment has been low since 1998 and the natural mortality rate appears to have increased (Howell 2012, Castro et al. 2012). In 1997, epizootic shell disease appeared on lobsters off southern New England (Castro and Angell 2000). The etiology of the disease remains undetermined, but there is evidence for the involvement of chitinolytic bacteria in a dysbiosis facilitated by environmental stressors such as temperature and contaminants (Castro et al. 2012, Chistoserdov et al. 2005). The disease is characterized by an extensive erosion and melanization of the cuticle (Smolowitz et al. 2005, Figure 1c). Mortality often occurs during molting, which can be incomplete if cuticle damage is too extensive. However, if molting is successful, lobsters can rid themselves of the disease when they shed their damaged exoskeleton.

Tagging: Tagging took place from May to October every year from 1982 through 2015. The original purpose of the tagging study was to monitor population size; however, data on ESD were collected as well. For the purposes of this study, data was only examined for the time period where ESD was present (1999 and later). We also excluded recaptures that occurred within 21 days or less after tagging, as exploratory analyses revealed diseased animals were more likely to be recaptured during this period. Tagging took place off eastern Connecticut near Jordan Cove, Niantic Bay, and Twotree Island (lat. 41° 18' N, long. 72° 10' W). Lobsters (73.0 ± 12.72, mean ± 95% CI carapace length in mm) were caught in traps and moved to continuous flow-through seawater tanks until the end of each sampling week at which time carapace length, sex, reproductive condition, molt stage, and disease state were recorded. Thereafter lobsters were tagged with serially numbered, international orange, sphyrion tags and released at the site of capture. Lobsters were assigned to one of four disease states: *Healthy* – no signs of disease; *mild disease* – active shell disease covering < 10 % of the carapace; *moderate disease*– active disease covering 11 – 50% of the carapace; *severe disease* – active disease covering > 50% of the carapace. Lobsters recaptured during subsequent research cruises were examined for growth, maturity and disease state and returned to the water immediately. A $2 US reward was offered to commercial fishers for return of a tag. Tag loss due to molting is low (< 4%) for sphyrion tags (Moriyasu et al. 1995) and would only be a problem for relative survival estimation if there were a differential loss of tags by disease state.

Analyses

Relative survival estimation

We used logistic regression models of recaptured animals to conduct case-control studies to estimate disease-associated mortality rates in our three study systems. These models work as follows: Assume two cohorts were tagged and released at the same time and place. One cohort had external signs of disease ("*D*") and the other had no visible signs of disease ("*H*"). If the size of each cohort declined exponentially with time, at any given time *t*, the abundance of the i^{th} cohort would be

$$N_{it} = N_{i0}\mathrm{e}^{-Z_i t}, \quad i \in \{D, H\}, \; (1)$$

where N_{i0} is the initial abundance of cohort *D* or *H*, and Z_i is the total instantaneous mortality rate (hazard rate) for cohort *i*. Suppose that catch, *C*, in a short time interval beginning at time *t* is proportional to abundance at time *t*

$$C_{it} = q_{it} N_{it}, \; (2)$$

where q_{it} is a cohort- and time-specific catchability coefficient. The ratio of the catches at time *t*, R_t would be proportional to the ratio of the survival rates of the two cohorts. By substituting equation 1 into equation 2 and taking the ratio we obtain the following relationship:

$$R_t = \frac{C_{Dt}}{C_{Ht}} = \frac{q_{Dt}\, N_{D0}\, \mathrm{e}^{-Z_D t}}{q_{Ht}\, N_{H0}\, \mathrm{e}^{-Z_H t}}, \; (3)$$

We can simplify equation 3 if we assume that the ratio of catchability coefficients (*q*) is constant throughout the course of the study. This assumption does not require the cohort-specific catchability coefficients to be equal or constant through time as long as the ratio remains constant. Thus, the model implicitly allows for disease-associated differences in vulnerability to capture, and in rates of tag reporting, tag-induced mortality and tag shedding. Rearranging equation 3 produces

$$R_t = \varphi e^{(Z_H - Z_D)t}, \; (4)$$

where φ is a proportionality constant equal to the ratio of the products of the cohort-specific catchability coefficients and the initial cohort abundances, i.e., $\varphi = \frac{q_{Dt}N_{D0}}{q_{Ht}N_{H0}}$. Taking the logarithms of (4) results in the linear relationship

$$\log(R_t) = \log(\varphi) + \beta t, \quad (5)$$

where β is equal to the difference in total instantaneous mortality rates ($Z_H - Z_D$) of the two cohorts. The variable R_t is equivalent to the odds of catching an animal from the diseased cohort, given a tagged fish has been caught, and thus estimates of β can be obtained using logistic regression. Exponentiation of $\hat{\beta}$, provides an estimate of the relative survival rate ($\widehat{RS}$) for the two cohorts. Additional variables can be added to these logistic regressions to understand how discrete demographic variables such as sex affect relative survival and initial disease prevalence. For example, to understand the effect of sex (s) on relative survival and initial disease prevalence, equation (5) could be modified such that

$$\log(R_t) = \log(\varphi) + \beta_1 s + \beta_2 t + \beta_3(t * s), \quad (6)$$

where exponentiation of $\beta_2 + \beta_3$ is the sex-dependent relative survival rate, and exponentiation of β_1 added to φ is the sex-specific proportionality constant.

In our studies, logistic regressions were fitted to exact times-at-liberty. Confidence intervals for the regression parameters were calculated by the profile likelihood method. For striped bass and American lobster, the log of the intercept parameter (which can be thought of as prevalence * catchability) was estimated within the model. For snow crabs the intercept was fixed at 0.5 because half of the animals tagged were diseased and half appeared free of the disease at the time of tagging. Striped bass and American lobster were tagged and released over successive years; however, year effects on β were not estimated for either species. This was necessary because annual sample sizes (stage-specific recaptures) were small and was further justified by the lack of support for year effects in more general models. Thus, time-at-liberty was calculated as days between release and recapture regardless of what year, or time of year, the striped bass or American lobster was tagged. Because we quantified different stages of disease severity in striped bass and lobsters, we conducted separate logistic regressions comparing recaptures of animals at level of disease severity to animals without disease. In the case of lobsters, we also included the effects of gender and life stage (male, non-ovigerous females and ovigerous females) in our logistic regressions. We included interaction terms between all variables (time at large and gender/life stage) in a full model and also calculated models with all possible subsets of these terms. We then used Akaike Information Criteria to pick the best model for each stage of disease.

To infer if there was an association between health and body size, we analyzed the effect of disease status and severity on body size. We used an analysis of variance for each case study.

Disease prevalence

We calculated disease prevalence from our tagging data for lobsters and striped bass. In both cases, these calculations required the assumption that the proportion of diseased individuals in our catch reflected the disease prevalence of the population.

For striped bass, there was no evidence for seasonal variation in disease. Therefore we calculated disease prevalence as the proportion of diseased individuals caught (tagged or recaptured) in each disease class (healthy, mild, moderate or severe) per year. We calculated the mean prevalence across years and used the year to year variation to calculate confidence intervals around the prevalence.

For lobsters with epizootic shell disease, prevalence varied with time and by sex. Therefore we calculated disease prevalence separately for males, non-ovigerous females and ovigerous females for each month that tagging occurred. We did this separately for each year and we also calculated mean monthly prevalence levels for males, non-ovigerous females and ovigerous females by averaging monthly prevalence levels across years. As with the striped bass analysis, we also used all caught (i.e., tagged or recaptured) animals to determine prevalence.

Disease-associated changes in natural mortality rate

By assuming that natural mortality (including fishing mortality) rates prior to disease were additive to mortality from disease, we interpreted the relative survival rate estimate obtained for any individual or group of severity stages as an estimate of the change in natural mortality rate ($\widehat{\Delta M}$, equivalent to $\hat{\beta}$) for that severity stage or group. The estimate, $\widehat{\Delta M_J}$, did not depend on the natural mortality rate for uninfected individuals; however, to interpret the magnitude and management implications of $\widehat{\Delta M_J}$, we required an outside estimate of natural mortality rate for the component of the population that is negative for disease. For this purpose, natural mortality rates in the absence of disease were obtained from the most recent assessment of the population status of the stock for striped bass. The Atlantic States Marine Fisheries

Commission estimated that natural mortality rates were $M = 0.15\ yr^{-1}$ in areas with little or no disease (ASMFC 2003). The disease-adjusted, population-level, natural mortality rate was estimated as a weighted average of the stage-specific natural mortality rates where each weight was equal to the stage-specific prevalence. Bootstrapped changes in mortality rate were obtained by sampling from the distribution of $\widehat{RS}_j$ for each disease stage and multiplying it by the disease prevalence for that stage. In the case of striped bass, there was little seasonal variation in disease prevalence, so we used the average yearly prevalence in this calculation. Epizootic shell disease in lobsters, on the other hand, was highly seasonal, with peaks in the spring and autumn. Disease prevalence in all seasons and seasonal mortality rates would be required to estimate the disease-associated changes in natural mortality rates due to epizootic shell disease. Therefore we could not estimate disease associated changes in mortality rates for this species.

All analyses were run in R (v. 3.3.1). R-code for relative survival analyses are available as supplemental documents (DS1). Data are available in dryad.

Results

Case 1: Snow crabs

Of the 722 tagged crabs released, half were healthy and half were diseased. Recaptures were obtained from 219 crabs that were healthy at release and 14 crabs that were diseased at release. At the time of tagging, the mean size of diseased crabs was statistically greater than healthy crabs (t_{720}= -3.53, p = 0.0005); however the mean difference (2.03 mm) was not considered biologically significant because the animals were in the terminal molt instar. The logistic regression model showed that large-clawed, male snow crabs with bitter crab disease had a significantly lower survival rate than their healthy counterparts (z-value = -9.364, p < 0.001). The survival rate of diseased males was 0.009 % (0.003 – 0.022, 95% CI) that of uninfected crabs (Figure 2).

Case 2: Striped Bass

Striped bass tagging programs in Virginia and Maryland released totals of 22,629 and 4,712 fish, respectively. These fish had average prevalence levels of 39.4 ± 1.0% (mean ± standard error) for mildly diseased striped bass, 15.2 ± 1.0% for moderately diseased striped bass and 10.5 ± 0.5% for severely diseased striped bass (Figure 3). A one-way ANOVA was used to test for differences in mean length across the four disease stages. Mean length differed significantly by disease stage ($F_{3, 26951} = 172$, $p < 0.001$), with severely diseased fish having on average the largest size followed by moderately diseased, mildly diseased and healthy fish. The mean length of fish with stage 3 (severe) disease was 19.3 mm larger than that of fish at stage 0 (healthy).

Of the tagged striped bass, 1,880 and 236 of the striped bass released by Virginia and Maryland, respectively, were recaptured and used in the analyses. Combined recaptures for both tagging programs were 912, 966, 393, and 299 for healthy, mild, moderate and severely diseased individuals, respectively. Time from release to recapture for striped bass ranged from 0 days (recaptured on the day of tagging) to 1,824 days (nearly 5 years). Striped bass were recaptured in every month with the majority of recaptures occurring in October and November corresponding with tagging activity and the annual period of peak fishing activity. Approximately 80% of striped bass were recaptured within a year of release and 95% of all recaptures occurred within 712 days of release.

Logistic regression showed that relative survival decreased with increasing disease severity state and was marginally or significantly lower than that of healthy animals for moderately and severely diseased animals respectively (Table 1, Figure 4). Relative survival was 84% (95% CI 70 – 100%), and 54% (42- 68%) that of healthy animals for these stages. Weighting the distribution of relative survivals by the prevalence of each disease state gives an overall relative survival during this period of 86.4 ± 8.7% (mean ± 95% confidence interval based on 1000 bootstraps) for fish exhibiting dermal disease relative to fish without signs of disease. If the mortality associated with disease is additional to pre-disease estimates of natural mortality, this is equivalent to a change of natural mortality from 0.15, as estimated by ASMFC (2009) to 0.29 (95% CI: 0.20 - 0.37), or almost a doubling of the natural mortality rate in the population.

Case 3: Lobsters

During the study period (1999 – 2015), 60,212 lobsters were tagged. Time between release and recapture ranged from 2 days to 789 days, with the mean time at large being 97 days. Preliminary analyses of lobster tagging data showed strong seasonal differences in the overall prevalence and severity of epizootic shell disease. Seasonal patterns of disease varied by sex and, for females, by reproductive status (Figure 5). For males and non-ovigerous females, the highest disease prevalence occurred in October, where it was 56.9 ± 8.1% for males and 42.8 ± 5.5% for non-ovigerous females. Ovigerous females had much higher overall prevalence levels of disease and their highest disease prevalence was in May, 84.7 ± 12.3%.

In order to quantify seasonal patterns, we partitioned the dataset based on time of release. The release data for October was eliminated from the full data set so as to stabilize stage-specific estimates of relative survival. Stabilization of the estimates was indicative of having reduced the full data set to a homogenous subset that captured the warm water disease dynamics. The sample size for the excluded month (n=298 tagged and recaptured individuals) was too small to analyze for stage-specific relative survival. The remaining dataset, which also excluded animals that were at large for less than 21 days was 6,904 animals. An ANOVA of recaptured individuals for the summer dataset indicated that moderately and severely diseased lobsters were slightly larger than healthy lobsters ($F_{3,6603}$= 6.55, p = 0.003); however, the differences were small (2.1 and 1.9 mm respectively) and deemed not biologically significant.

Model selection of logistic regressions showed that the best fitting model of mild ESD included time at large and ovigerous females (Table 2, Figure 6). The relative survival of mildly diseased animals was 45% (95% CI: 27 – 75%). Prevalence of mild ESD at tagging was 12.8 times higher in ovigerous females than in all other groups at the time of tagging.

Separate logistic regressions of moderately and severely diseased lobsters revealed that these disease states had similar estimates of relative survival. Therefore, we combined these data into a single (moderate/severe) model. The best fitting model of moderate/severe ESD included time at large and whether a female was ovigerous (but sex as a factor was not significant) (Table 2, Figure 6). The survival of moderately and severely diseased lobsters (combined) relative to healthy lobsters was 30% (95% CI: 15 – 60%). The prevalence of moderate/severe disease at the time of tagging was 16 times greater in ovigerous females than in all other lobsters.

Discussion

This study demonstrates the value of mark-recapture data for estimating impacts of poorly understood, chronic diseases on fished populations. In all cases, mortality resulting from disease was substantial. It reached nearly 100% in diseased snow crabs. Natural mortality in diseased populations of the striped bass we examined was approximately two times higher than the AFMSC estimate for natural mortality (0.15, AFMSC 2003). Mortality of diseased lobsters was more than double that of healthy lobsters. These findings suggest that these emergent diseases are substantial drivers of population dynamics. In such cases, disease mortality should incorporated into population models that inform fisheries management plans for these species.

Although we were only able to examine adult male snow crabs in our study, the logistic regression clearly showed that, consistent with lab studies of this species (Shields et al. 2005) and observations in other crustacean species (e.g., Meyers et al. 1987), bitter crab disease can rapidly devastate snow crab populations. Our results support the industry's conservative reduction in the catch quota in 2006. The sporadic nature of severe epizootics in Newfoundland suggests that monitoring disease prevalence, particularly when warmer temperatures may contribute to outbreaks, would be prudent in order to forecast impacts on the fishery and protect adequate reproductive potential (Shields et al. 2007). Further studies evaluating other stages, particularly adult females, would assist with population projections and estimating potential reproductive loss. Field surveys in Newfoundland show that BCD prevalence in juvenile males and females can be higher than in adult males, suggesting that estimations of population impacts in this study may be conservative (Shields et al. 2005).

Prevalence of ulcerative dermal mycobacteriosis in our study frequently exceeded 50% in striped bass from Maryland and Virginia waters. This is higher than previously reported. However, this is likely due, in part, to under-reporting in previous studies that did not quantify early signs of disease (i.e., presence of pigmented foci). Previous estimates were reported to be up to 16% in striped bass in the Rappahannock River, Virginia, and 29% in the York River, Virginia (Cardinal 2001). While survival of mildly infected individuals was not different from that of healthy animals, survival of moderately and severely diseased individuals was reduced relative to healthy fish. Combined with this disease's negative impact on growth (Latour et al. 2012), its high prevalence in adults and its increased severity in larger fish, the mortality rate from mycobacteriosis raises concerns about potential impacts on fecundity. The Generally Although Chesapeake Bay populations of striped bass have rebounded considerably from over-harvesting in the 1980s, our results indicate a doubling of the natural mortality rate and support concerns about the impact this disease may be having on this population (e.g., Gauthier et al. 2008, Vogelbein et al. 2012). Collectively, these results suggest that chronic disease now needs to be considered as an important component of mortality, and the biological reference points need to be recalculated to improve the management goals for these fisheries in light of new levels of non-fishing mortality.

Analyses of epizootic shell disease in the Southern New England stock of American lobster show that this relatively new, chronic disease can be contributing substantially to the collapse of the stock. Our models suggest that mortality of moderately or severely diseased individuals can be high. Of great concern is the impact of epizootic shell disease on ovigerous females. Ovigerous females have nearly 85% disease prevalence and molt less frequently than males and non-ovigerous females. It has been hypothesized that they have higher mortality rates because the disease can progress further between molts and molting is less likely to be successful (Glenn and Pugh 2006). In addition, female lobsters rarely molt when ovigerous (Campbell 1983) and, because they cannot shed the disease unless they molt, this likely contributes to disease mortality at this stage (Stevens 2009). A reduction in survival of ovigerous females is consistent with results from Wahle et al. (2009) that associate declines in settlement and recruitment to ESD. Lobsters above the legal size limit experience high fishing mortality and have little chance to reproduce. Combined with decreased reproductive output due to ESD, mortality of ovigerous lobsters may explain at least part of the rapid declines of the Southern New England stock. The current management strategy for lobsters includes protecting females until at least one reproductive event has occurred before they reach the legal size (ASMFC 2009). Low survival of ovigerous females may be undermining the success of this strategy.

As with striped bass, chronic disease in American lobster must now be considered an important component of mortality in southern New England. It is encouraging that the biological reference point for mortality for the Southern New England stock was increased to 0.285 from 0.15. Further analyses are necessary to calculate disease-associated mortality across the year. A recent, peer-reviewed assessment of the status of the lobster fishery recommended a five-year fishing moratorium for southern New England because of low abundance and poor recruitment (ASMFC 2009). Increased non-fishing mortality, possibly due to disease and increased temperatures, have been implicated (ASMFC 2009, 2015, Howell 2012). The Atlantic States Marine Fisheries Commission, (the agency responsible for American lobster management), declined to impose a moratorium and the stock in southern New England has declined further. Our analysis of the tagging data, in combination with data on catch indices (Wahle et al. 2009), give mechanistic explanations of increased natural mortality, shifts in sex ratios and reduced recruitment in southern New England lobsters. Increased mortality in diseased relative to healthy individuals is particularly high in ovigerous females. Taken together, these analyses further substantiate the need for management actions focusing on protecting female lobsters.

The degree to which an emergent disease should affect management of an exploited resource is controversial (Legault and Palmer 2015, Johnson et al. 2015) and depends upon the specific dynamics of the host-disease interaction. In the case where a disease is novel to a system, we favor a conservative approach. In these cases, the host population has not yet co-evolved with the pathogen so the stress of disease should be added to the stress of fishing mortality to compute the maximum potential impact on the host population. While a reference point such as the biomass producing maximum production might not change with the introduction of the disease, the amount of sustainable yield that can be achieved and the rate of fishing that produces maximum yield should be reduced by the amount of new disease mortality. However, in cases where the degree of change in natural mortality is poorly estimated, a status quo approach may be the best option (Legault and Palmer 2015).

Several factors need to be taken into consideration when employing logistic regressions on mark-recapture data to understand disease. First, the ability to establish a pathognomonic non-lethal diagnostic can be a challenging aspect of studying disease via mark-recapture; however, this task can be accomplished by pathologists familiar with the affected species or by using molecular methods to detect pathogen presence. Although the former case may result in missed detection of diseased individuals, the latter case may be too sensitive, indicating the presence of a pathogen but not necessarily disease. Thus, diagnostic approaches must be considered with the research question and disease progression in mind (Burge et al. 2016). Secondly, the model assumes that the ratio of catchability for diseased and healthy individuals is constant over time and only dependent upon the grouping factor (e.g., disease status). Numerous factors could lead to the violation of this assumption including differential behavior of diseased and healthy animals in relation to variable environmental conditions, change in disease state after tagging, differential migratory patterns in diseased and healthy individuals, or differential tag reporting. Although such factors are frequently unknown in marine organisms, simulations can be used to understand how violations of these assumptions can affect results, and laboratory experiments may help quantify such effects. Given the value of mark-recapture for understanding disease in poorly studied populations, these considerations should not hinder the approach, but, when possible, should be accounted for in the study design and interpretation.

Logistic regression may not be appropriate for analyzing all mark-recapture data. Particularly when there is suspected error in diagnosis, or cases where diagnoses are not possible, multi-state mark recapture methods are more appropriate because they can account for imperfect detection (e.g., Conn and Cooch 2009). In addition, in cases where there are unidentified sources of heterogeneity within the dataset, for example, due to different life history strategies within a population, multi-state mark-recapture may be a better approach. In contrast to logistic regression models, multi-state mark recapture analyses use all tagging data, not just recaptures, to estimate parameters, which may be a major advantage, depending on the dataset of interest (e.g., Choquet et al. 2009). The snow crab and striped bass datasets were well-suited to analysis with logistic regression because, in both cases, the disease progression was linear; it was not strongly seasonal and recovery did not occur. In contrast, analysis of epizootic shell disease in the American lobster was less straightforward due to complex seasonal dynamics of epizootic shell disease and recovery from disease as a result of molting. While the logistic regression provides a useful first approach to understanding mortality due to this disease, seasonal estimates are necessary to quantify the temporal dynamics of the disease and its time-dependent impacts on survival. This next-step could be accommodated through multi-state mark recapture analysis. In cases where more epidemiological processes need to be estimated (i.e., disease incidence, progression and recovery), multi-state mark-recapture is a preferred method of analysis. The trade-offs, as discussed above, are the *a priori* knowledge required to specify state-transitions and potential challenges in convergence for these complex models. On the other hand, the logistic regression models, demonstrated here, are useful alternatives, particularly when little is known about the disease in question.

Collectively, these studies demonstrate the value of using simple analytical tools (i.e. logistic regression) on mark-recapture data to assess the population impacts of chronic marine diseases on host populations. Despite substantial differences in disease progression, disease mortality, and host life history, this approach was successful in elucidating challenging yet critical estimates of the population-level impacts of disease. One of the advantages of this approach is that additional demographic data can be incorporated in order to identify vulnerable groups or adjust fisheries management to account for additional disease-related mortality. These data can also be used to parameterize population projections. For example, for two of our study species, snow crab and American lobster, increased temperature is associated with disease. The data collected from our mark-recapture studies can be used to predict disease impacts in different environmental regimes (Maynard et al. 2016). We expect to see more studies using mark-recapture data to quantity the effects of disease on marine organisms. The increasingly sophisticated and flexible methods for evaluating disease with mark-recapture data (Calvert et al. 2009, Conn and Cooch 2009, Cooch et al. 2012) leverage the capacity of the research community to quantify disease impacts in marine organisms (Shields 2012, Stentiford et al. 2012, Groner et al. 2016)

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.f56v8

Tables

Table 1. **Estimated relative survival of striped bass with dermal mycobacteriosis.** Relative survival is measured against survival of fish with no signs of disease. CI = 95% confidence interval. Data includes fish tagged in Fall and Spring from Maryland (2007-2009) and Virginia (2005-2012).

Disease state	Relative survival	Confidence Interval (95%)	p-value	Sample size	Percent of recaptures
None				912	35.5 %
Mild	0.96	0.84 – 1.09	0.50	966	37.6 %
Moderate	0.84	0.70 – 1.00	0.06	393	15.3 %
Severe	0.54	0.42 – 0.68	<0.01	299	11.6 %

Table 2. Akaike information criteria to pick the best fit logistic regressions examining the effects of sex and time at large on recaptures of (A) mild and (B) moderate to severe epizootic shell disease in lobsters relative to healthy lobsters. Best models are shown below (C and D). The index, or base model, is for male lobsters.

Model	df	AICc
A) Model selection for mild epizootic shell disease		
Time + Ovigerous	3	2236.0
Time * Ovigerous	4	2237.4
Time + Ovigerous + Female	4	2237.6
Time * Female + Ovigerous	5	2238.8
Time * Ovigerous + Female	5	2239.0
B) Model selection for mild moderate shell disease		
Time + Ovigerous	3	1567.9
Time * Ovigerous	4	1568.7
Time + Ovigerous + Female	4	1569.6
Time * Ovigerous + Female	5	1570.3

	Coefficient	Standard Error	z value	p-value
C) Best model: Mild epizootic shell disease				
Intercept	-3.017	0.085	-35.508	<0.00001
Time (years)	-0.795	0.256	-3.098	0.002
Ovigerous	2.551	0.198	12.894	<0.00001
D) Best model: Moderate to severe epizootic shell disease				
Intercept	-3.412	0.107	-31.911	<0.00001
Time (years)	-1.204	0.354	-3.405	0.001
Ovigerous	2.830	0.220	12.867	<0.00001

Figure legends

Figure 1. Pathognomonic signs of disease in snow crab, striped bass and American Lobster. Shown are, snow crabs with bitter crab disease show characteristic 'cooked' appearance (left side of figures a and b), Striped bass with dermal lesions from mycobacteriosis and a green tag (c), and American lobster with severe lesions to the carapace due to epizootic shell disease (d). Photo credits: PC Beck (DFO, a, b), VIMS mycobacteriosis project staff (c), Jeff Shields (d).

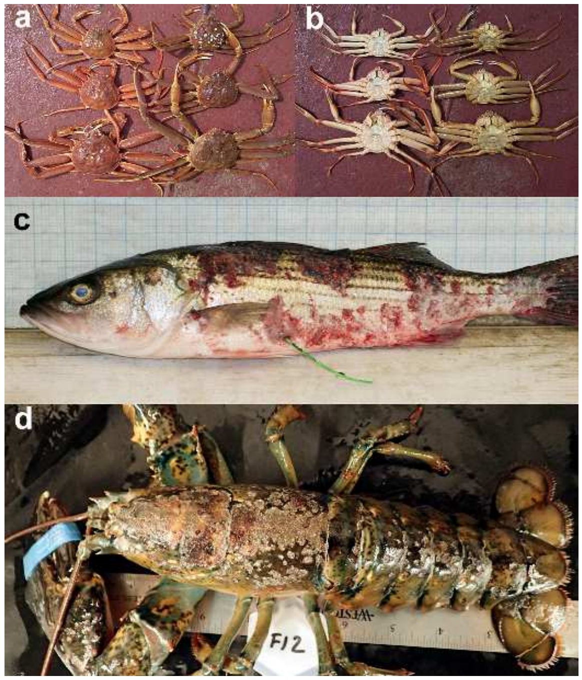
Figure 2. Logistic regression to estimate survival of adult male snow crabs with disease relative to those with no signs of disease. Rug display shows individual recaptures (disease positive on top, disease negative on bottom). Sample size is shown and also given as proportional circles during each period. Shaded areas indicate 95% confidence intervals.

Figure 3. Proportion of sampled striped bass population from the Chesapeake Bay that is healthy or has mild, moderate or severe dermal mycobacteriosis. Means are average yearly proportions and bars indicate standard errors around yearly estimates.

Figure 4. Logistic regression to estimate survival of striped bass with mild, moderate and severe disease relative to those with no signs of disease (a-c). Rug displays and confidence intervals are as in Figure 2.

Figure 5. Seasonal variation in the prevalence of epizootic shell disease for males, non-ovigerous females and ovigerous females. Estimates are mean monthly prevalence levels from 1999-2015 and standard errors around those means are indicated with shading.

Figure 6. Logistic regression to estimate the relative survival of male and non-ovigerous female lobsters (a, b), and ovigerous female lobsters (c, d), with mild or moderate to severe epizootic shell disease relative to lobsters with no signs of disease. Rug displays and confidence intervals are as above.



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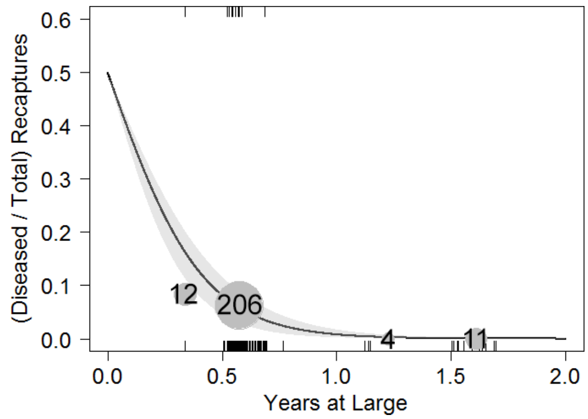

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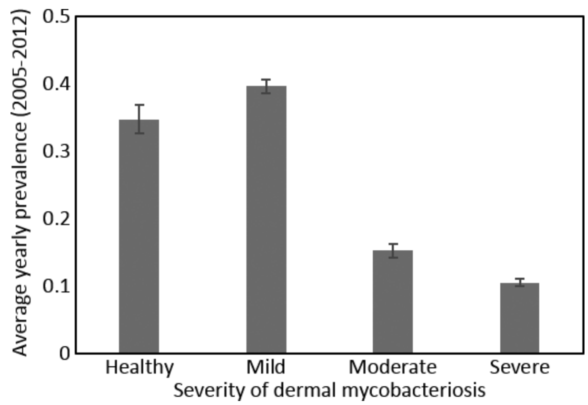

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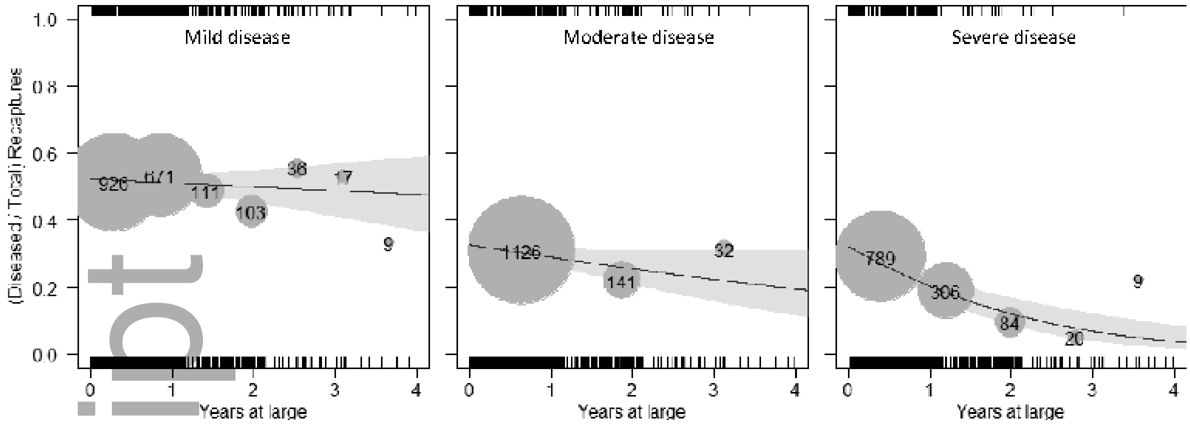

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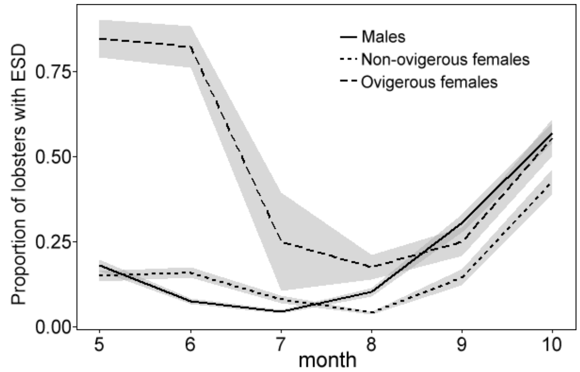

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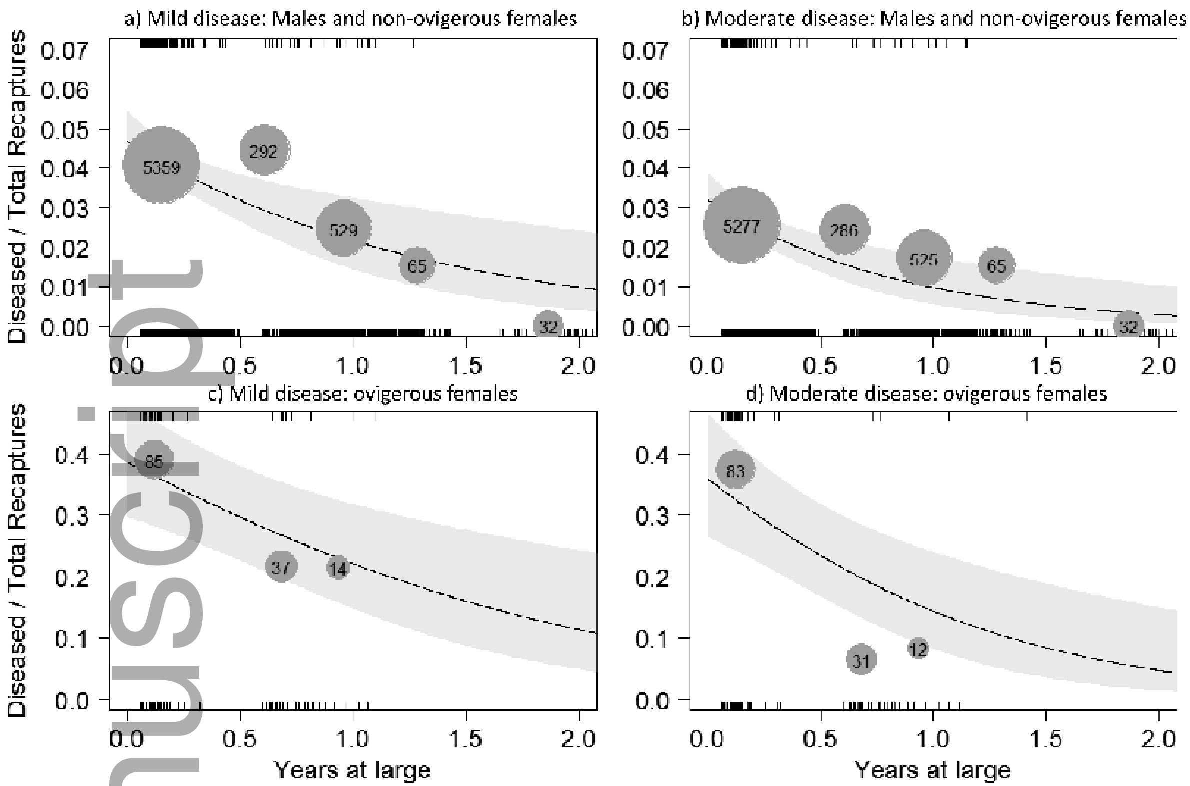

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