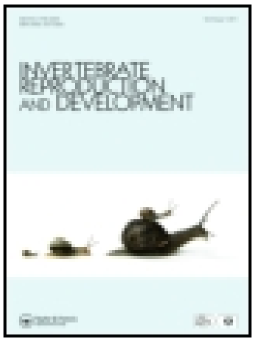

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Patterns and possible causes of skewed sex ratios in American lobster (*Homarus americanus*) populations

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ABSTRACT

Multiple studies have identified sex ratios in adult American lobster (*Homarus americanus*) populations that are skewed toward males in some locations and females in others. The mechanisms leading to these differences, and the subsequent ecological implications, have been reported to be a result of sexual differences in fishing mortality due to sex specific regulations, catchability, or behaviour. In particular, seasonal migrations in response to fluctuating environmental conditions, including temperature and salinity, can lead to skewed sex ratios of lobsters in estuaries, nearshore coastal and offshore habitats. In this review we focus on four relatively well-studied American lobster populations that are consistently male or female dominated: 1) The Great Bay Estuary, New Hampshire; 2) The Isles of Shoals, off the coast of New Hampshire and southern Maine; 3) Buzzard's Bay, Massachusetts and; 4) Georges Bank. We review the available data and discuss the various hypotheses that have been put forth to explain the underlying causes of the skewed sex ratios in each area. We then outline possible changes in reproduction that may be expected if sex-specific changes in local distributions of lobsters shift further due to climate change.

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Sex ratio; crustacean; lobster; behavioural thermoregulation; migration; climate change

Introduction

It is not necessary to have equal numbers of males and females to sustain healthy lobster populations, but changes in sex ratios may influence mating dynamics, which could subsequently influence reproductive output. American lobster (*Homarus americanus*) sex ratios are approximately 1:1 throughout much of their range, particularly for newly settled and early stage juveniles (Krouse 1973; Lawton and Lavalli 1995; Howell et al. 1999). However, there are also multiple reports of locally skewed sex ratios of adults, with either more males than females (Munro and Therriault 1983; Karnofsky et al. 1989a; Howell et al. 1999), or more females than males (Skud and Perkins 1969; Estrella and McKiernan 1989; Carloni and Watson 2018). Adults are defined here as reproductively mature and are generally >70 mm in carapace length (CL) depending on the location. However, it should be noted that the legal harvestable size is usually somewhat larger (i.e. >83 mm CL) and it also varies by location (Ennis 1980; Little and Watson 2003; Glenn and Pugh 2006; Haarr et al. 2018).

The causes of these skewed American lobster sex ratios are poorly understood, but in other decapod species variable sex ratios occur in early life-history phases due to recruitment or developmental factors, or in later life history phases due to differences in: 1) mortality or catchability (Miller 1990; Estrella and Morrissey 1997; Sordalen et al. 2018); 2) sex-specific fisheries regulations (e.g. single-species fisheries or protection of reproductive females) and/or; 3) spatial segregation of the sexes (e.g. *Callinectes* spp., *Cancer* spp., *Carcinus* spp., *Chionecetes* spp.; see Taggart et al. 2004; Sainte-Marie et al. 2008; Fulton et al. 2013). We will address potential causes of skewed sex ratios in adult lobsters first, then present case studies concerning four different lobster populations that have well-documented skewed sex ratios.

Catchability

Differences in sex-specific catchability, or the probability of capture relative to effort and actual density, can influence the ability of a sampling program to detect a true sex ratio skew. If one sex is more likely to be captured than the other, estimates of the sex ratio at that location may be biased. Differences in sex-specific catchability can also produce skewed sex ratios, since it results in differential fishery removal rates of males and females. Trap-based measurements of sex ratios can be

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particularly complicated to interpret because catchability in traps is not only determined by the spatial and temporal overlap of the lobsters and the gear (influenced primarily by environmental variables and lobster demographics, see Miller 1990 and below), but also by 'decisions' made by individuals to interact (or not) with the gear (see Karnofsky and Price 1989). Differential catchability of males vs. females due to moulting effects (Miller 1990; Tremblay and Smith 2001), female reproductive status (Miller 1990), intraspecific competition (Karnofsky et al. 1989b), individual behaviour, or motivational status (Karnofsky and Price 1989; Waddy et al. 1995; Cowan et al. 2007) have been presented as possible explanations for differences in observed adult lobster sex ratios. For example, Tremblay and Smith (2001) demonstrated that males are generally more catchable than females in the autumn (fall), particularly over certain bottom types, and attributed this to the fact that males moult earlier in the season than females and subsequently exhibit increased post-moult foraging behaviour in comparison to females. Ultimately catch is based on the combination of lobsters that are 'available' to be captured as well as their catchability (Karnofsky and Price 1989; Miller 1990; Tremblay and Eagles 1997; Watson and Jury 2013) and thus sex-dependent movements as well as interaction with traps are likely to influence catch composition.

Mortality

Mortality can be divided into fishing mortality and natural mortality. Not only can sex-specific fishing mortality be influenced by differences in catchability (see above), it can also be biased by sex-specific management regulations intending to conserve reproductive females. This has been reported for Dungeness crabs (*Metacarcinus magister*), snow crabs (*Chionoecetes opilio*) and Chilean crabs (*Metacarcinus edwardsii*) (Pardo et al. 2015). Both sexes of American lobsters are protected by size limits in the U.S. and Canada, and egg-bearing (ovigerous) females are also illegal to harvest. Additionally, V-notched females (lobstermen put a V-notch in the tails of ovigerous lobsters before releasing them) are not legal to harvest in all U.S. management areas and some Canadian management areas. As a result reproductive females have a lower fishing mortality than males and this allows them to accumulate in the population, which can lead to a female-dominated catch, which has been observed in the Canadian offshore fishery (DFO 2000, 2009). During the late 1970s and early 1980s, when fishing pressure was increasing in Canadian offshore waters, sex ratios were between 40% and 60% male based on at-sea sampling data, but then they decreased to 10–40% in the 1990s.

One factor that can lead to sex-specific differences in natural mortality is differential susceptibility to disease. While most lobster diseases appear to impact the sexes indiscriminately, there is one exception: epizootic shell disease. This disease is common in inshore Southern New England, and it has been shown to primarily affect mature females, in part due to their increased intermoult duration (Castro and Angell 2000; Glenn and Pugh 2006; Stevens 2009; Castro and Somers 2012). Recent work, based on a long-term mark-recapture study in eastern Long Island Sound, has added further support to this hypothesis by demonstrating that ovigerous females experience much higher disease-related mortality than non-ovigerous females or males (Hoenig et al. 2017).

Movement

A primary reason for skewed adult sex ratios appears to be sex-specific differences in movement patterns (Krouse 1973; Robichaud and Cambell 1991; Cowan et al. 2007). Sex ratios do not depart sharply from 1:1 in smaller juvenile size classes (Figure 2), but as size and mobility increase, and predation susceptibility decreases, male and female lobsters move more (Cobb 1995; Lawton and Lavalli 1995). At this point differences in habitat, temperature, and salinity preferences cause males and females to move to different areas, which can lead to skewed sex ratios (Jury and Watson 2013; Boudreau et al. 2015). Lobsters are capable of sensing small changes in temperature (Jury and Watson 2000) and behaviourally thermoregulate by moving away from water that is too warm or cold and toward water of a preferred temperature (Crossin et al. 1998; Jury and Watson 2013; Nielsen and McGaw 2016). Importantly, adult males and females appear to respond differently to temperature (Jury and Watson 2013).

Salinity in some habitats may also affect lobster movements and thus sex ratios. Lobsters are limited osmoregulators and generally avoid low salinity water (Jury et al. 1994b). However, they are present in many estuaries and in the laboratory it has been shown that females expend more energy osmoregulating at low salinities than males (Jury et al. 1994a), and are more likely to avoid low salinity than males (Jury et al. 1994b). This might be particularly true for ovigerous females because low salinities likely influence egg, larval or post-larval survival (Charmantier et al. 2001). Thus, males may be more likely than females to use lower salinity habitats or remain in nearshore and estuarine habitats that have fluctuating salinity due to run-off, melting snow and storm events (Jury et al. 1995).

Further details about differential movements and the manner in which these lead to skewed sex ratios are presented in the case studies below.

Case studies

In this review, we summarize data that are available from four different locations where skewed sex ratios have been documented in American lobster populations (Figure 1). These locations were chosen because they span a large portion of the geographic range of lobsters in the U.S. northeast, and they represent a range of habitat types, including estuarine, coastal, nearshore, and offshore areas. Finally, we selected these areas because in some of them the population is skewed towards males and in some it is skewed towards females. These case studies are intended to be representative examples of how the conditions in certain areas can lead to skewed sex ratios.

Estuarine-Great Bay Estuary New Hampshire (NH)

While lobsters are not particularly abundant in estuaries, as compared to coastal habitats (Howell et al. 1999; Moriyasu et al. 1999; Watson et al. 1999), they are present in sufficient numbers in some estuaries, like the Great Bay Estuary (GBE) in NH (Figure 1), to support lobster fisheries. In contrast to adjacent coastal environments, estuaries (as well as some other near-shore habitats (e.g. island lagoons, Munro and Therriault 1983)) are characterized by fluctuating salinities and water temperatures. The biggest changes in temperature and salinity occur during the spring, when shallow estuarine and river waters warm rapidly and spring run-off lowers the salinity; and the autumn, when the estuary cools faster than coastal waters. Moreover, there are occasional storms that cause the salinity to drop close to, or below, physiologically stressful (and potentially lethal) limits of lobsters (McLeese 1956; Jury et al. 1995). Nevertheless, during a majority of the lobster fishing season, from April to October, the GBE tends to be warmer than coastal waters and this might be one advantage of this otherwise challenging habitat.

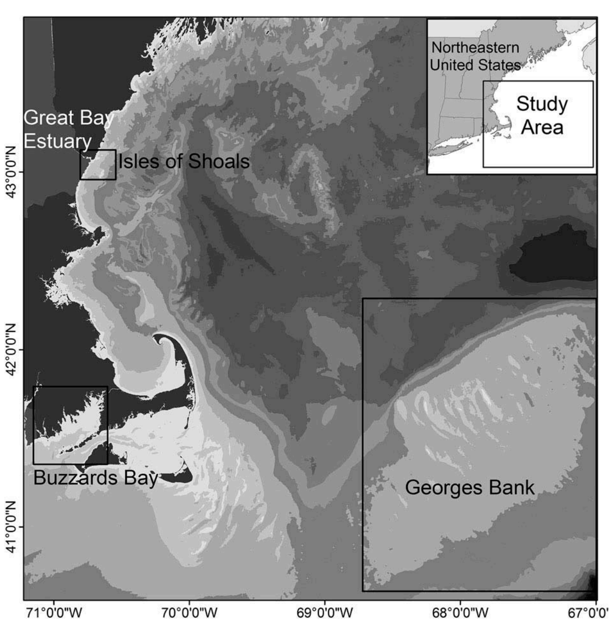

Figure 1. Map of case study sites.

The four case study locations were selected based on their documented skewed sex ratios. The Great Bay Estuary is an estuarine site leading to the Isles of Shoals off the coast of New Hampshire. Buzzards Bay is a coastal site in the Southern New England lobster stock unit in Massachusetts. Georges Bank is an offshore area consisting of shoal and adjacent deeper water areas in the Gulf of Maine.

Howell et al. (1999) demonstrated that catch (n = 19,485; captured with standard traps fished by researchers, as well as by commercial lobster fishers) in the GBE was consistently dominated by male lobsters and that the ratio of adult males to females increased further into the estuary. However, analysis of both trap and SCUBA survey data revealed that the sex ratio of juvenile lobsters (<60 mm CL) was approximately 1:1 in areas with male skewed adult sex ratios (Figure 2). Furthermore, they noted that in the upper reaches of the estuary there were few, if any, reproductive females (although they are present in the middle of the estuary). Thus, it appears that the skewed sex ratio in the GBE does not develop until lobsters approach sexual maturity and become more mobile.

Because skewed sex ratios in the estuary only appear to develop as lobsters grow large enough to move long distances, our working hypothesis is that as lobsters approach sexual maturity, males and females respond differently to temperature and salinity gradients which triggers the differential movements that lead to the skewed sex ratios documented in GBE (Howell et al. 1999; Watson et al. 1999; Jury and Watson 2013). The evidence in support of this is: 1) American lobsters can sense small changes in temperature and salinity (Jury and Watson 2000), 2) Females find low salinities more aversive than males (Jury et al. 1994b), and expend more energy than males osmoregulating when exposed to low salinity water (Jury et al. 1994a) and, 3) Females find higher water temperatures more aversive than males (Jury and Watson 2013). Models using these parameters in GBE, as well as the broader Gulf of Maine, yield skewed distributions of males and females similar to those obtained with fishery independent trap surveys or trawl surveys (Jury 1999; Chang et al. 2010; Tanaka and Chen 2016; Le Bris et al. 2018; Tanaka et al. 2018). Thus, the available data indicate that female lobsters

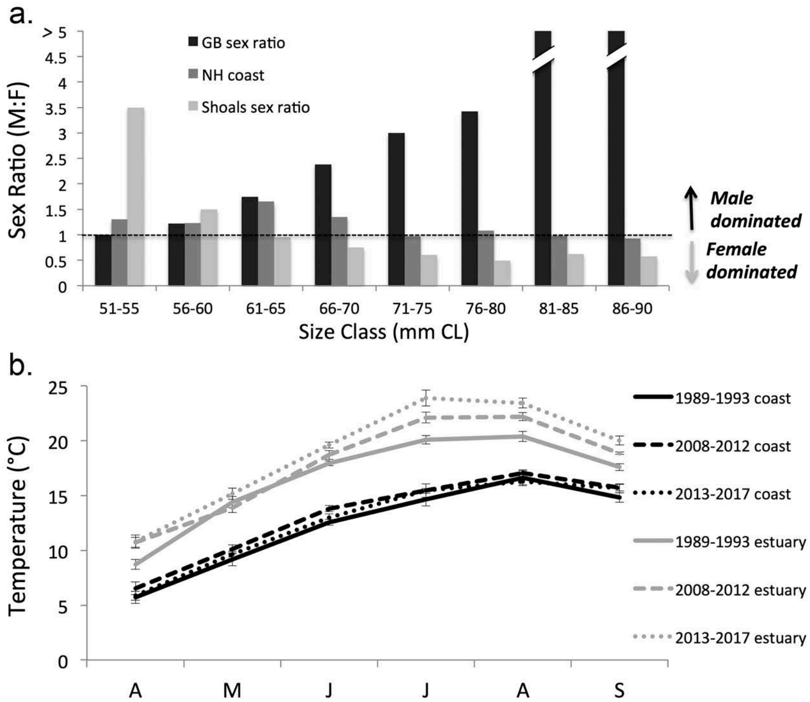

Figure 2. Great Bay Estuary and Isles of Shoals sex ratios.

(a). Sex ratio (M:F) vs. size (mm CL) of lobsters in the Great Bay estuary (GBE) (n = 707), the adjacent NH coast (n = 2488) and at the Isles of Shoals (n = 3316) (see Figure 1 for locations) show consistent differences by location and size. Data were adapted from Howell et al. (1999) such that values >1 show male-dominated sex ratios and values <1 show female dominated sex ratios. (b). Monthly temperatures (mean ± SEM) from the GBE and the coast. Data from panel A. were obtained from studies from 1989–1992. Temperature data from the 5-year periods 2008–2012 and 2013–2017 were extracted from the Great Bay Estuary National Estuarine Research Reserve buoy database (Pennock et al. 2008–2017) and show that some monthly temperatures within the GBE regularly exceed 20°C.

tend to avoid the warmer, lower salinity water that is present in the upper reaches of the GBE, while males do not, leading to the observed skewed sex ratios. This pattern is similar to those of some other decapod crustaceans (Gutermuth and Armstrong 1989; Taggart et al. 2004; Rains et al. 2016; Reiser et al. 2017).

However, it is important to note that more recent studies within the GBE using tag/recapture (Jury and Watson 2013) or telemetry data (Langley 2016) did not show significant differences in the movement patterns *between* adult males vs. females. Both sexes moved further into the estuary in the spring, after the time when the spring run-off typically ends, and towards the coast when the estuarine waters begin to cool faster than the coastal waters in the autumn (Watson et al. 1999). Furthermore, in another telemetry study, we found that seven out of nine ovigerous females tracked in 2007–2009 remained within the estuary during the winter and their eggs hatched there the following spring/summer (Moore et al. in prep.). The timing of these more recent studies coincided with a period of relatively low freshwater input. Historically, periods of high freshwater input tend to drive lobsters into deeper water and toward the coast (Jury et al. 1995). Thus, while most of our data, and other data presented in this review, indicate that temperature gradients probably play a key role in causing skewed sex ratios, in estuaries seasonal and storm-induced changes in salinity might also be important.

Coastal-Buzzards Bay, Massachusetts (MA)

Buzzards Bay is a large and relatively shallow coastal embayment in southern MA (Figure 1). It is part of the Southern New England (SNE) lobster stock (Atlantic States Marine Fisheries Commission (ASMFC) 2015) and at its peak (1994–1998) the catch averaged >180 metric tons; but catch has since declined dramatically to an average of <41 metric tons over the last five years (2013–2017). As a result, there has been significant attrition in the industry, with a 73% reduction in permit holders fishing within Buzzards Bay, a reduction of 61% in overall MA SNE permit holders, and concomitant reductions in effort (trap hauls) (Massachusetts Division of Marine Fisheries (MADMF) unpublished data). These local declines in landings and participants coincide with the recruitment failure and collapse of the SNE lobster stock (ASMFC 2010 & 2015).

One of the major drivers behind the collapse of the SNE lobster stock appears to be the 'loss' of thermally suitable inshore habitat. Warming waters have resulted in large portions of the inshore environment exceeding lobsters' preferred temperature range (see Crossin et al. 1998; Jury and Watson 2013; Nielsen and McGaw 2016), and reaching physiologically stressful temperatures for extended periods of time (ASMFC 2010, ASMFC 2015, see Figure 3(c–d)). This warming of the inshore habitat has been linked to the observed declines in recruitment (ASMFC 2015). Evidence suggests that increased temperature has resulted in a redistribution of the remaining stock into cooler, deeper waters further from shore (Glenn et al. 2011; ASMFC 2015). Buzzards Bay in particular has experienced increases in annual mean bottom water temperatures (rate of 0.048°C/yr from 1986–2016, at 9 m depth, MADMF unpublished data), as well as an increased number of days during the summer when temperatures have exceeded 20°C (from an average of 61 days/year from 1986–1990, to an average of 93 days/year from 2012–2016, MADMF unpublished data), which is considered to be a thermal threshold for changes in blood chemistry and optimal phagocyte function in lobsters (Steenbergen et al. 1978; Powers et al. 2004; Dove et al. 2005).

The available data suggest that the large thermal differences between warm, shallow inshore areas and cooler, deeper offshore habitats are causing a redistribution of mobile sexually mature male and female lobsters, with more females than males moving deeper. For example, data from a fishery-independent survey in Buzzards Bay from 2005 to 2006 show that the deeper strata sampling stations were female-skewed in the larger 'mature' size classes (Size-at-maturity ≥76 mm CL, Estrella and McKiernan 1989), and this was consistent throughout the spring, summer, and autumn of both survey years (Figure 3(b); MADMF unpublished data). In contrast, sex ratios were close to 1:1 for the smaller size class (<76 mm CL, Figure 3(a)). Survey catch rates in the shallow interior portions of Buzzards Bay tended to be much lower than at the outer, deeper stations, however it was apparent that of those few lobsters that remained within Buzzards Bay, most of them were males. Interestingly, this same trend has been observed historically in the Great Bay Estuary in NH, where the sex ratio was mostly male-skewed in the spring (see prior case study, Howell et al. 1999).

Ongoing survey work in Buzzards Bay shows the persistence of the patterns in sex ratio skew described above (MADMF Ventless Lobster Trap Survey; see Pugh and Glenn Forthcoming). A similar depth-related pattern in sex ratio skew has also been reported from a monitoring program in nearby Eastern Long Island Sound, with male-dominated catches at shallower sampling depths (DNC 2016).

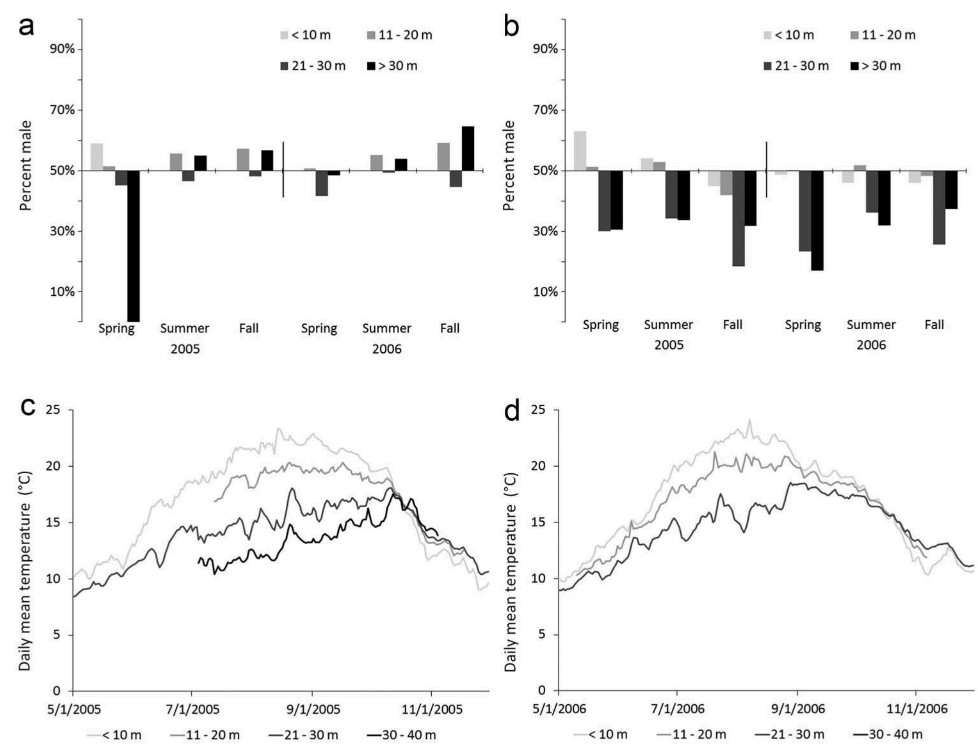

Figure 3. Buzzards Bay sex ratios and temperatures by depth.

Sex ratio (shown as per cent of the catch that was male) for: (a). immature lobsters (<76 mm carapace length, n = 7,334 (2005), n = 8,229 (2006)) and (b). mature lobsters (≥76 mm carapace length, n = 7,307 (2005), n = 8,165 (2006)) by depth for each season of a fishery-independent ventless trap survey in Buzzards Bay, MA. Survey seasons were defined as spring (May–June), summer (July–September), and fall (October–November). Daily mean bottom water temperatures (°C) by depth from May 1–November 31 for (c). 2005 and (d). 2006 (Massachusetts Division of Marine Fisheries (MADMF), unpublished data).

Offshore-Georges Bank (GBK) and Gulf of Maine

Lobster landings have been recorded in U.S. offshore waters (New England to the mid-Atlantic) dating back to the 1940s when lobsters were caught almost exclusively as by-catch in the otter trawl fishery (Skud and Perkins 1969; ASMFC 2015). Landings by trawl nets in offshore waters increased from 1943–1968 from 30 to 2,500 metric tons. By 1968, offshore landings accounted for 17% of lobster landings in the U.S. Beginning in the 1970s traps began to emerge as a way to fish for lobsters in offshore areas and they quickly became the dominant method of harvesting. In anticipation of the expansion of the offshore fishery, Skud and Perkins (1969) documented baseline population dynamics via fisheries dependent and fisheries independent methods around GBK and other offshore canyons farther to the west from 1965–1967 (Figure 1). Although some exploitation had already begun prior to their work, areas on GBK (Oceanographer, Lydonia and Corsair Canyons) showed somewhat female skewed sex ratios (51–67% female), suggesting that this slightly skewed sex ratio was not the result of fishing pressure.

At present, GBK and adjacent deep-water areas of the Gulf of Maine (GOM) continue to show female-dominated catch, based on both fisheries dependent and independent data sources (ASMFC 2015; Henninger and Carloni 2016). Henninger and Carloni (2016) documented heavily female dominated catch (87% female) from July through October on Georges Bank and nearby deep-water portions of the GOM via fisheries observer data. Although a direct comparison between these recent data and early work by Skud and Perkins (1969) has not been conducted, the apparent increase in the proportion of catch composed of females suggests that increased fishing pressure has influenced sex ratios on Georges Bank. This is corroborated by data from the Northeast Fisheries Science Center's (NEFSC) otter trawl surveys that show an increasing trend in the proportion of catch made up of females over the time series (ASMFC 2015). This is consistent with the influence of fishing pressure on sex ratios in other crustacean fisheries .

With protections given to egg-bearing and v-notched female lobsters throughout the GOM and GBK, fishing pressure appears to heavily influence the population structure around GBK, and elsewhere throughout the species range. Female skewed sex ratios in these offshore areas are likely compounded by the fact that inshore, where greater than 98% of GOM landings occur (ASMFC 2015), approximately 35% of legal-sized females are protected with a v-notch (NHF&G 2015; Carl Wilson, Maine Dept. of Marine Resources, personal communication). There is also some evidence suggesting that lobsters disperse away from these inshore habitats to less competitive offshore areas as they mature (Steneck 2006; Steneck and Wahle 2013), which likely contributes to the highly skewed sex ratios observed offshore.

Behavioural differences between males and females also appear to be playing an important role in the observed skewed sex ratios around GBK and GOM. Several studies have shown that adult lobsters tend to exhibit seasonal movement patterns, migrating to deeper water in the colder months and to shoal waters in the warmer months (Cooper and Uzmann 1971; Krouse 1973; Campbell 1986; Campbell and Stasko 1986). These directed movements may increase the rate of egg development, by increasing the degree-days they accumulate, or they might take place for other reasons. For, example, Cowan et al. (2007) demonstrated, by fitting ovigerous females with temperature data loggers, that seasonal migrations did not significantly increase degree days, but rather led to more gradual changes in water temperatures experienced, which could benefit developing eggs. More recently, Goldstein and Watson (2015) showed that the movements of ovigerous females from nearshore to offshore areas also did not lead to a significant increase in degree days, however, due to the rapid increases in water temperature in the spring, eggs carried by inshore lobsters hatched before those carried by females that moved offshore. Thus, ovigerous females might, instead, migrate offshore so that when their eggs hatch in the spring, the larvae are in the best possible location for their survival and dispersal to optimal areas for settlement.

Aggregations of egg-bearing lobsters have been documented on GBK (Campbell and Pezzack 1986; Henninger and Carloni 2016), as well as other offshore shoals in close proximity to deeper basins (Campbell 1990; Carloni and Watson 2018). Campbell (1990) found that a specific area around Grand Manan, Canada had a higher abundance of egg-bearing lobsters and he theorized that females may aggregate in shallow water due to warmer temperatures and/or to be near currents that may aid in larval dispersion during egg hatch.

Nearshore-Isles of Shoals

Carloni and Watson (2018) recently documented similar aggregations of mature lobsters at the Isles of Shoals, a group of Islands located 10 km off the coast of NH/ME (Figure 1). They compared catch rates between the east and west side at three different depths and found the catch on the east side, which was closer to deeper water and higher currents, was composed of 82% females (legal-size range), while on the west side it was only 40% females. Catch of egg-bearing lobsters was also three-times higher on the east side. Given the proximity of these areas, these differences in sex ratios were likely not the result of differential exploitation of males vs females. Furthermore, trap and acoustic telemetry data showed that ovigerous lobsters tended to move to deeper water just before their eggs hatched (Carloni 2018). Thus, our working hypothesis is that offshore areas in close proximity to deep water are attractive to mature females (particularly large ones), as well as egg-bearing females, because they are ideal places to brood eggs (shallow water) and release larvae (adjacent deep water). Therefore, GBK, Grand Manan, Canada and the Isles of Shoals, USA appear to have female dominated populations because sexually mature females move there because they are very suitable for reproduction. However, at the present time, the cues that attract female lobsters to these locations are not known. Identification of these cues is of great importance because these aggregations have far-reaching implications for larval recruitment, population dynamics, and fishery management, particularly in light of changing oceanographic conditions.

Summary of factors leading to skewed sex ratios of American lobsters

The aforementioned case studies demonstrate how temperature and/or depth gradients can result in skewed sex ratios in different estuarine and nearshore habitats. In Buzzards Bay, MA and the Great Bay Estuary, NH out to the Isles of Shoals, the gradient from shallow, seasonally warmer water areas into deeper cooler areas resulted in a transition from male to female dominated sex ratios. Furthermore, some American lobster populations are consistently dominated by females (George's Bank and offshore GOM). The male-dominated populations discussed above occur in shallow, warm water areas that are adjacent to cooler, deeper areas. Due to the fact that female lobsters tend to avoid warm water more than males, we conclude that the skewed sex ratios in these regions are due to the differential movements of adult males and females in response to thermal cues. Furthermore, in estuaries, salinity may also cause differential movements and further influence the skewed sex ratios.

Temperature may also be a primary driver of female-dominated populations found in the two offshore lobster populations summarized in this review. It appears as if reproductive females are attracted to some areas to incubate their eggs, and adjacent locations, around the time when their eggs are due to hatch. It is not clear if temperature is a cue used to identify these areas, or if other factors such as depth and prevailing currents also play a role.

In most of case studies we have presented, there are adjacent populations that experience a similar fishing pressure and are sampled using similar gear, and yet they do not have major differences in the sex ratios. Furthermore, even in areas where the sex ratio is skewed in the adult size classes, it is generally 1:1 in the smaller juvenile size classes (although this is not known explicitly in all areas presented). Therefore, while fishing pressure and the associated regulations favouring exploitation of males over females can impact the sex ratios of American lobster populations, it appears as if the differential movements of males and females, in response to various physiochemical features of the environment, can also greatly influence sex ratios in particular areas.

Discussion

Skewed adult American lobster sex ratios may have significant ecological and evolutionary consequences, especially with respect to mating behaviour and reproductive success (Emlen and Oring 1977; Pugh 2014; Sordalen et al. 2018). Protections afforded to reproductive females ensure that females experience lower fishing mortality rates than males, often allowing them to achieve larger sizes. This can result in not only a generally female-skewed sex ratio for harvestable-sized lobsters, but in some cases a skewed size structure as well. The skewed size structure could complicate mating dynamics, as females seek out and prefer large dominant males as mating partners (reviewed in Atema and Voigt 1995; Debuse et al. 1999; Atema and Steinbach 2007; Sordalen et al. 2017). Larger males tend to cohabit longer with females (Gosselin et al. 2003) and produce larger ejaculates with more sperm (Gosselin et al. 2003; Pugh et al. 2015). However, if sex ratios are female-skewed and large males are relatively rare, pre-moult females may not be able to locate a larger male and have to settle with a smaller mate. If the size difference between a female and a smaller male partner is too great (e.g. ≥25% difference), the male's ejaculate may not completely fill the female's receptacle and smaller males may be unwilling or incapable of mating with larger females (Pugh 2014). While individual males can successfully inseminate large numbers of females (Waddy et al. 2017), male size and moult stage affect male reproductive capacity (Pugh et al. 2015; Waddy et al. 2017). Conditions of female-skewed sex ratios and a synchronous female moult may also negatively impact male capacity for multiple matings, disrupt cohabitation patterns, and thus have a negative impact on female reproductive success (Pugh 2014). Clearly, more work is required to fully understand the impact of skewed sex ratios on lobster reproductive success.

While skewed sex ratios may result from the differential protections of adult females, it is also clear that lobster movements in response to temperature and salinity gradients, and perhaps other environmental factors as well, play an important role. Mature lobsters typically move offshore during the winter months, returning to warmer inshore waters in the spring and summer (Cooper and Uzmann 1971; Fogarty et al. 1980; Ennis 1984; Campbell and Stasko 1986). If the extent of lobster movements is dictated by thermal preferences, and those preferences differ by sex, then recent changes in these thermal gradients have likely been a key component in the observed changes in distribution patterns. More importantly, the trend towards steadily increasing water temperatures throughout SNE and the GOM (Pershing et al. 2015; Kleisner et al. 2017; LeBris et al. 2017, 2018) are likely to create more areas with large thermal gradients and more habitats that are warm enough that females avoid them. This, in turn, could cause further separation of the sexes, alterations to seasonal migrations and shifts in their distribution (Fogarty et al. 2007; Pinsky et al. 2013; Le Bris et al. 2018). For example, as lobsters are driven from warmer waters >18–20°C in the southern end of their range (e.g. Buzzards Bay), or in the upper regions of estuaries (e.g. Great Bay Estuary), their distribution is likely to shift towards deeper waters that are closer to their preferred temperature of 16°C (Crossin et al. 1998; Jury and Watson 2013). Differences in the sex-specific responses to these environmentally driven changes will likely exacerbate existing skewed sex ratios, particularly when coupled with fishing pressure.

Currently, it appears as if some ovigerous lobsters aggregate in specific areas that appear to have the optimal combination of water temperature for incubating their eggs, and local currents to aid in the distribution of the larvae once they hatch (Campbell 1990; Carloni and Watson 2018). However, if females start to aggregate in different areas, because of shifts in water temperatures, it could impact recruitment. For example, in Southern New England (see above) the distribution of egg-bearing lobsters has changed as the waters have warmed (ASMFC 2010; Glenn et al. 2011). These changing distributions, even on scales of just a few kilometres, can influence transport pathways and the eventual locations of larval settlement (Glenn et al. 2011; Goldstein and Watson 2015), and thus could have profound effects on survivorship and recruitment.

Climate change is undoubtedly influencing lobster biology and their habitats. Elevated water temperatures have been shown to result in large-scale latitudinal shifts in the geographic distributions of many marine species (Fogarty et al. 2007; Le Bris et al. 2018), while at more local scales this changing environment may influence population characteristics such as adult lobster sex ratios via differential responses by males and females. An upper thermal limit of 20°C (Powers et al. 2004; Dove et al. 2005; Watson and Jury 2013;) has been exceeded in multiple coastal habitats in southern New England (Figure 3) and temperatures this high regularly occur seasonally in many Gulf of Maine estuaries, including the Great Bay estuary (Figure 2). We have shown above that sexual differences in the responses of lobsters to environmental conditions can lead to skewed sex ratios. Therefore, while it remains to be seen how climate change will ultimately affect the distribution and abundance of American lobsters as a whole, it is likely to have a profound influence over smaller spatial scales on adult sex ratios specifically, and lobster ecology and fisheries in general, under future warming scenarios.

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