









Measures of habitat quality for Black Sea Bass using oyster aquaculture cages

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ABSTRACT

Objective: Black Sea Bass *Centropristis striata* are a temperate reef finfish that occupy natural and artificial structured habitats. This study used fish behavior, condition indices, and production estimates to evaluate how oyster aquaculture cages serve as artificial reefs for Black Sea Bass in central Long Island Sound, USA.

Methods: Underwater video was recorded on oyster farms and a natural rock reef to identify and quantify the behavior of Black Sea Bass that is associated with oyster aquaculture cages and boulders. Juvenile Black Sea Bass were sampled from farms and reefs in Clinton and Milford, Connecticut, to assess individual energy density and relative condition factor as measures of habitat quality. Proximate analysis was conducted to develop a predictive regression for percentage of dry weight and energy density in juvenile Black Sea Bass, which was then applied to estimate energy density in fish that were collected from farms and reefs. The abundance of young-of-the-year Black Sea Bass was used to quantify fish production on the oyster farms.

Results: Significantly greater shelter and grouping activity were observed on cages than were observed among boulders. Instances of courtship/reproduction in mature fish, escape, foraging, and territorial behavior were statistically similar across the cage and boulder habitats. The condition metrics of energy density and relative condition factor showed no difference in the physiological status of juvenile fish that inhabited farms versus reefs. The enhanced production of Black Sea Bass was estimated to be 4.1 kg/100 cages per year based on higher abundance of young-of-the-year fish on farms relative to the rock reef reference habitat.

Conclusions: Our results suggest that aquaculture gear provides valuable habitat services that are similar to those obtained via other man-made structures that are considered essential fish habitat for Black Sea Bass throughout their life history.

KEYWORDS: Black Sea Bass, fish production enhancement, habitat, natural rock reef, oyster aquaculture cages, relative fish condition

LAY SUMMARY

Oyster aquaculture cage farms demonstrably function as artificial reefs and valuable habitat for Black Sea Bass. Information on the quality of habitat services and local population enhancement that are provided to this species by oyster gear can inform resource managers who make decisions about aquaculture permitting and designations of essential fish habitat.

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INTRODUCTION

The Black Sea Bass *Centropristis striata* is a commercially and recreationally valued finfish that is distributed from the Gulf of Mexico to the Gulf of Maine (e.g., Drohan et al., 2007; Secor et al., 2021). Black Sea Bass are seasonal migrants that are found in coastal waters from spring to fall, which provide inshore spawning and nursery habitat (Drohan et al., 2007; Moser & Shepherd, 2010). A temperate reef species, Black Sea Bass are strongly associated with complex habitats, including naturally occurring seafloor features and man-made structures (Drohan et al., 2007; Jech et al., 2023). For this reason, essential fish habitat (EFH) designations for Black Sea Bass have traditionally included both natural and artificial structures. Areas that are defined as EFH for Black Sea Bass are known to support their habitat requirements during their life history, based on data for categories that include presence/absence, abundance, ecological functions (growth/survival/reproduction), and production (Magnuson–Stevens Fishery Conservation and Management Act, 2007).

Oyster farms may effectively function much like artificial reefs and thus may represent EFH for Black Sea Bass. Black Sea Bass have been observed in high abundance on farms in southern New England where multitiered cages are used to grow the eastern oyster *Crassostrea virginica* and add vertical structure to otherwise low-relief sediments (e.g., DeAlteris et al., 2004; Mercaldo-Allen, Clark, Liu, et al., 2020; Mercaldo-Allen et al., 2021, 2023; Tallman & Forrester, 2007). Black Sea Bass, particularly juveniles, show high site fidelity to complex hard-substrate habitats (Able & Hales, 1997; Drohan et al., 2007), and their observed association with cages at multiple life stages suggests that these structures may offer habitat services to this species (Mercaldo-Allen et al., 2023). Artificial structures may aggregate fish from neighboring natural hard substrate or enhance production through the creation of new habitat where structure-oriented recruits settle and become established (Bohnsack, 1989; Bohnsack & Sutherland, 1985). Although abundance is one indicator of habitat services, other metrics such as fish behavior, fish condition, and fish production enhancement can provide better insight into the quality of the habitat that is provided by artificial structures and potential beneficial effects at the population scale.

Fish behavior can provide detailed information on habitat use and preferences and help identify the ecological benefits that are provided to fish by aquaculture gear (Armbruster et al., 2024). The architecture of oyster cages, composed of interstices of varying sizes and elevated relief above the seafloor, creates a complex three-dimensional habitat. For structure-oriented fish like Black Sea Bass, cages may provide food and shelter, protection from predators, and refuge from current flow and may be a site for courtship and spawning behavior. Underwater video on shellfish farms can be used to quantify fish–habitat interactions and behaviors that are related to habitat use (Muething et al., 2020; Shinn et al., 2021; Struthers et al., 2015; Tsuyuki & Umino, 2018).

Biochemical and morphological condition indices can provide useful quantitative measures of the health of fish and enable comparisons of relative habitat quality between aquaculture gear and natural structured habitat based on a fish's ability to allocate excess energy to fat reserves (Barrett et al.,

2022). These condition metrics are common proxies for the general health, fitness, or nutritional status of a fish (e.g., Hayes & Shonkwiler, 2001; Lloret et al., 2014). Relative condition factor (K_n) is a nondestructive index that essentially compares fish weight at length on the premise that a heavier fish contains fat reserves (e.g., Hayes & Shonkwiler, 2001; Wuenschel et al., 2019) in excess of those required for homeostasis and growth. Energy density (ED) is an indicator of nutritional and physiological condition and energy reserves (Johnson et al., 2017). One method to estimate ED is proximate composition analysis, which determines the amount of lipid and protein present. This metric can be estimated from models that relate the percentage of dry weight (% DW) to ED, as whole-body water content is inversely related to ED (Breck, 2008). Energy storage and utilization varies over ontogeny such that ED and % DW relationships should be determined for each life stage (Wuenschel et al., 2006). Tissue-specific (muscle, liver, gonad) ED values have been measured previously in reproductive adult Black Sea Bass (Slesinger et al., 2022; Wuenschel et al., 2013); however, baseline data are not yet available for young of the year and juveniles. Whole-body condition indices may be particularly useful measures of fitness in Black Sea Bass at the early life stages.

Fish production is thought to be a robust indicator of habitat quality (Searcy et al., 2007), particularly for territorial, philopatric, and shelter-oriented fish species (Bohnsack, 1989) such as Black Sea Bass. In the United States and Europe, habitat that is created by adding aquaculture gear to the seafloor has been shown to enhance fish production at an estimated 348 to 1,110 kg/ha per year of fish biomass in addition to that found on natural reference habitats (Barrett et al., 2022). Research is needed to determine whether the high abundance of Black Sea Bass that is associated with oyster farms represents enhanced fish production or attraction of fish from adjacent habitats (Gentry et al., 2020; Martínez-Baena et al., 2022). Calculating population enhancement estimates for Black Sea Bass on farms relative to reefs may help to resolve the question of whether population or production enhancement contributes to the high fish abundance that is observed on cages relative to that observed among boulders.

Understanding and quantifying the habitat value of aquaculture gear on managed species can provide resource managers with a basis for a synergistic view of the positive and adverse effects associated with aquaculture development in coastal waters. In the United States, the federal aquaculture review and permitting process requires consideration of the benefits of an aquaculture farm proposal to be balanced against its reasonably foreseeable detriments as part of the permit application review process (General regulatory policies, 2025). This includes the consideration of the effects on EFH and fish and wildlife values. Uncertainty that is related to how and to what extent aquaculture structures function similarly to comparable natural habitats has impeded the consideration of the habitat provisioning that is provided by aquaculture into the regulatory decision-making process. A comparison of fish behavior, relative condition, and production enhancement of a managed species, the Black Sea Bass, on cage farms and natural reefs provides an evaluation of farm habitat quality and function. Information on quality of habitat that is provided to this species by oyster gear can inform resource managers

who make decisions about aquaculture permitting and designations of essential fish habitat.

We employed three metrics to evaluate the habitat quality that is provided by oyster farms relative to that provided by natural rock reef habitat (1) to identify and quantify behaviors that are associated with the habitat use by Black Sea Bass in underwater video that was collected on two oyster cage farms and a rock reef; (2) to test whether fish condition indices, including ED and K_m , differed between Black Sea Bass that were collected on farms versus reefs; and (3) to use abundance of young-of-the-year Black Sea Bass to estimate population enhancement on farms relative to that in a rock reef reference habitat.

METHODS

Study sites

We collected underwater video during 2018 to document the behavior of Black Sea Bass and estimate fish production on shellfish farms with high (dense) and low (sparse) cage abundance versus boulders on a rock reef. The three study sites were located west of Charles Island, near Milford, Connecticut, USA, within central Long Island Sound (northwest Atlantic; Figure 1A). Detailed methods and fish abundance were previously reported in [Mercaldo-Allen et al. \(2023\)](#).

The dense cage farm site, with 40–100 commercial cages, was located on a 0.11-km² shellfish lease, permitted for up to 200 multitiered off-bottom cages. An adjacent 0.25-km² lease, permitted for up to 250 off-bottom cages, was colocated at the dense cage farm site. As working commercial farms, the number of cages in the area varied on any particular day and across the spring–fall study period and limited our ability to test the effect of specific cage density itself. We placed four study cages that were identical to those that are used on the commercial farms at the dense cage farm site, spaced 47.5 m apart.

The sparse cage farm site was located at the intersection of two large shellfish leases, each 0.20 km² in size, where traditional on-bottom oyster aquaculture with no off-bottom gear was underway. Here, the sand-and-shell bottom was characterized by low vertical relief and contained areas of live oysters and empty shell valves and was devoid of rocks or boulders. We placed five study cages in a line along the delineation between the two on-bottom aquaculture leases 82 m apart. This small “farm” of five study cages was designated a “sparse” cage farm relative to the “dense” cage farm that had up to 100 cages in the study area.

The rock reef site, containing 70% cobble and boulder substrate, served as a structured control site for natural hard-bottom habitat. The reef was horseshoe-shaped, patchy, and covered 0.25 km² of seafloor. We selected four boulders that were interspersed on the reef for study that were located a minimum of 10 m apart and out of visual range of one another.

The distances between the Milford study sites (dense cage farm, sparse cage farm, and rock reef) ranged from 745 to 1,537 m ([Mercaldo-Allen, Clark, Liu, et al., 2020](#); [Mercaldo-Allen, Clark, Redman, et al., 2020](#)). The water depths at high tide measured 4.6 m at the dense cage farm and 6.1 m at the sparse cage farm and rock reef sites.

During 2023, we collected juvenile Black Sea Bass from oyster farms and natural rock reefs in the coastal waters of Clinton and Milford, Connecticut, in Long Island Sound to compare

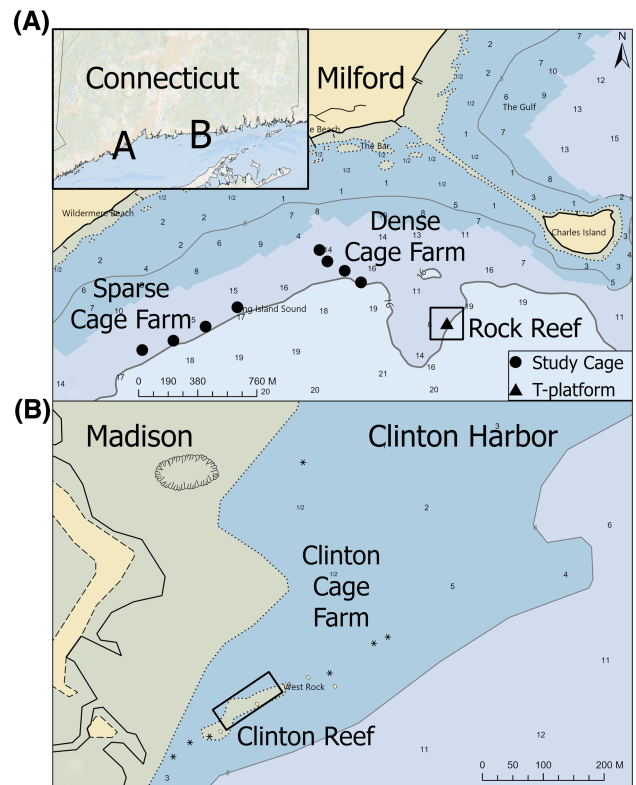


Figure 1. Map of study sites: (A) Natural cobble and boulder rock reef (rock reef), five single study cages (sparse cage farm), and five study cages that were deployed adjacent to a commercial oyster farm (dense cage farm) near Milford, Connecticut. (B) Commercial oyster farm and rock reef near Clinton, Connecticut. The inset map shows the locations of that sites that were within Long Island Sound, USA. Water depths in feet are shown at mean lower low-water values.

the relative condition of fish that is related to cages and boulders. The Milford farm and rock reef sites were at the same locations as were the dense cage farm and rock reef sites that were studied in 2018, described above. The Clinton cage farm site, approved for up to 100 cages, was located farther east on a shallow 0.338-km² shellfish lease in outer Clinton Harbor adjacent to Cedar Island ([Figure 1B](#)). The Clinton Reef was located in the same embayment, northeast of Hammonasset State Park toward West Rock and approximately 650+ m away from the cage farm. The reef was discontinuous and extended 300 m in a relatively narrow line of intertidal and subtidal cobble and boulders that were interspersed with open bottom. Both Clinton sites experienced high tidal energy, with water depths of 2.1 m at high tide.

Oyster aquaculture cages, camera deployments, and recording methods (2018)

We studied commercially available shelf-and-bag-style oyster aquaculture bottom cages (Ketcham Supply, New Bedford, Massachusetts, USA) that were constructed of 11.43-cm mesh, heavy-duty 8-gauge vinyl coated wire, with two reinforced 3.81-cm wire-mesh feet. The wire-mesh feet elevated the cages 15.2 cm off the seafloor, with 10 bricks added to each cage foot for ballast. The cages measured 1.22 × 0.91 × 0.61 m and had

three shelves, each holding two bags of oysters (six bags per cage). The bags, made from 2.3-cm plastic mesh, measured 1.07 m in length by 0.52 m in width. We stocked each cage with 150–200 seed oysters measuring 2.5–4.5 cm in size. We used cage-handling methods and oyster-stocking densities that were consistent with general industry practices. The management of the cages was generally consistent regardless of cage number or farm size. The cages are hauled intermittently for maintenance and to cull or harvest oysters. To the extent possible, we adhered to the typical farming practices that are used by the growers in our region to replicate the conditions on a working farm.

Detailed methods for the deployment and retrieval of the video cameras on the oyster cages and adjacent to boulders at the Milford study sites are described in [Mercaldo-Allen et al. \(2021, 2023\)](#). Briefly, we attached two cameras to each of the four study cages, one camera positioned to record across the cage top and the other with a view across two cage sides and the interface between the cage and the seafloor. We also constructed T-platform stands to mount cameras among boulders that provided a perspective similar to that of the cage-mounted cameras and minimized added structure to the rock reef site, as described previously in [Mercaldo-Allen et al. \(2021\)](#). The height of each T-platform was customized to match the elevation of the boulders. Three boulders had similar heights and were paired with T-platforms that measured 45.7 cm in height. The fourth boulder was taller and required a T-platform that measured 71 cm in height. Each T-platform was placed 40 to 60 cm from a boulder to ensure a similar field of view across boulders of slightly varying heights. Divers manually attached and detached the cameras from the mounting clips on each T-platform stand. One camera was positioned to record across the top boulder surface, and the other camera captured the side of the boulder and the boulder–seafloor interface.

Camera recording followed the methods that are outlined in [Mercaldo-Allen et al. \(2021, 2023\)](#). Briefly, we programmed time-synched GoPro Hero Silver 3+ cameras to record video at 30 frames per second, 1,920 × 1,080 resolution, and 10 megapixel, with a wide-angle lens (firmware v03.02). We placed the cameras inside a polycarbonate waterproof case with BacPac attachment, which accommodated a timer. Each camera lens was fitted with a Polar Pro magenta filter, with a 0.50 stop reduction in exposure, to reduce the natural green coloration in the video. Intervalometer blink timers (CamDo) that were paired with GoPro cameras were used to delay the onset of video recording and extend battery life. The cameras were unbaited. Video recording began approximately 24 h after the cameras were deployed, which was intended to reduce deployment-related disturbance effects on the behavior of the fish. To collect footage over a complete tidal cycle and most daylight hours, video was recorded for 8 min every hour from 0700 to 1900 hours, yielding 13 recordings per camera deployment.

We collected video on the dense cage farm during all weekly camera deployments over the 17-week study period from May to September 2018. We recorded during alternate weeks at the other two sites, with eight deployments on the sparse cage farm and nine deployments on the rock reef. An analysis of these videos for fish abundance and community composition was

previously reported ([Mercaldo-Allen et al., 2023](#)). Seawater temperature (°C) was measured over the 3 d of each camera deployment using a HOBO pendant temperature data logger (Onset Computer) that recorded over 5-min intervals. Salinity (psu) was measured at each site during both camera deployment and retrieval using a handheld YSI Pro30 salinity, conductivity, and temperature meter.

Video analysis of fish behavior (2018)

The behavioral-coding software Observer XT (v14.2 and 15.0; Noldus Information Technology) was used for reviewing and scoring the time-synched video that was recorded simultaneously with the top and side cameras. Fish abundance, calculated as MaxN, was previously reported ([Mercaldo-Allen et al., 2023](#)) and defined as the maximum number of fish of a given species that is present in a single frame within each 8-min video segment. Water clarity varied between deployments and among hours within a single deployment; however, visibility generally extended the full length of the cage/boulder. To minimize the effect of variable water clarity across videos, only fish within the immediate cage or boulder vicinity were included regardless of the total extent of field of view within any single video clip.

We used fish body size and morphological characteristics to identify Black Sea Bass by life history stage as described in [Armbruster et al. \(2024\)](#). Age-0 fish were readily distinguished from other small fish by a black lateral stripe extending their body length from behind the eye to the caudal fin. Juveniles (1 year old) were identified by the absence of a visible nuchal hump or black lateral stripe and a lighter/brighter body coloration but could not be differentiated as male or female because they appear physically identical at this stage ([Keigwin et al., 2016](#); [Northeast Fisheries Science Center, 2012](#)). Dominant adult males were distinguished by their large body size, iridescent coloration, and bright blue nuchal hump, whereas secondary males that lacked the nuchal hump and bright coloration could not be differentiated from females ([Keigwin et al., 2016](#)).

We developed an ethogram for describing the Black Sea Bass behaviors that are associated with oyster cages and boulders ([Table 1](#)), including courtship/reproduction (swimming in unison while caudal fins are in close contact, tail touching, spawning runs, release of gametes, and swimming in tandem/touching in close proximity), escape (when a predator or another fish chased a fish into the cage or boulder structure), foraging (fish picking food out of the water column and/or consuming colonizing organisms from the lines, bags, and cage surfaces), grouping (aggregation of fish in numbers of two or more individuals of the same species), sheltering (fish resting or holding position in, on, or around the cage or boulder using small fin movements, often defined as station-keeping), and territoriality (agnostic displays, such as large fish chasing another fish off the cage or boulder, nipping), yawning (mouth opened widely), or fin flaring. A subset of video data that were collected from four dates on three cages and three boulders at the Milford dense cage farm and rock reef sites were analyzed previously to catalog specific ambush, agonistic, displacement, and occupancy behaviors ([Armbruster et al., 2024](#)).

A daily index was calculated for each behavior (courtship/reproduction, escape, foraging, grouping, shelter, and territoriality) by summing events across all the video records: 8 min

Table 1. Ethogram describing behavior of Black Sea Bass observed on oyster cages at shellfish farms and adjacent to boulders on rock reefs.

Behavior type	Definition
Courtship/reproduction	Tail touching, spawning runs, release of gametes, swimming in close proximity, flanks touching
Escape	Fish retreats into structure associated with a predator or another fish
Foraging	Fish picking food (out of water column, off lines/bags/cages)
Grouping	Fish of the same species aggregating in numbers of two or more
Shelter	Fish retreats to structure; not predator/territory associated
	Station-keeping or resting, using small fin movements to maintain position
Territoriality	Defense of space or resources. Fish chases another from an area, displacement, agonistic displays, fin flaring, yawning

per hourly interval $\times 13 \text{ h} = 104$ total minutes per day. This daily index was calculated for each cage/boulder replicate at each study site. The daily indices were normalized to the daily average MaxN for each cage–date combination to remove the effect of fish abundance on the occurrence of behavior events. Normalized daily indices for each behavior were compared across the sampling time series. A global repeated-measures analysis was first performed to compare fish behavior between the habitats—that is, two cage sites that were considered replicates and compared with the single rock reef site. When the global tests were significant, pairwise comparisons across the study sites were performed. Due to logistical constraints, not all three study sites could be sampled simultaneously, so the data were pooled by month prior to the analysis. The repeated-measures analysis used marginal distributions and a percentile bootstrapping method, with 20% trimmed means as the measure of central tendency, as this approach has no assumptions of normality or homoscedasticity, both of which are common problems in ecological data (Wilcox, 2023). Hochberg's sequentially rejective approach was used to control familywise error within pairwise comparisons (Wilcox, 2023).

Field collection and processing of fish to assess relative condition (2023)

We used fish traps to sample juvenile Black Sea Bass on rock reef sites in Clinton and Milford using previously established protocols (Mercaldo-Allen, Clark, Liu, et al., 2020; Mercaldo-Allen, Clark, Redman, et al., 2020). The traps consisted of a wire outer frame that was lined with 3-mm mesh, measured $46 \times 23 \times 23$ cm, and contained a single central chamber and double entries. Each trap was fitted with a flexible 6.4-cm-diameter ring opening at both entrances, which limited the size of fish that gained entry. A 5-kg steel plate along the base of each trap provided ballast and stability. We baited each trap with a perforated plastic cup containing one frozen squid to provide an attractant. Ten traps were soaked for 24 h, three times per week for 1–2 weeks per month from June to September 2023. Fish traps were deployed on the south side of the Clinton Reef on and among the boulder substrate. At Milford, the traps were distributed across the cobble and boulders on the northern portion of the reef. Monthly, during the same period, we collected juvenile Black Sea Bass from oyster aquaculture cages that were retrieved and placed on the boat deck. At the Clinton Farm, we collected fish from inside stacked-tray cages. At the Milford farm, we collected the fish that fell out of the shelf-and-bag

cages onto the deck. Seawater temperature ($^{\circ}\text{C}$) and salinity (psu) were measured during each fish collection using a handheld YSI Pro30 salinity, conductivity, and a temperature meter.

The live Black Sea Bass that were collected from the reefs or farms were transported to the laboratory in aerated buckets of seawater and kept chilled using cool-it blocks. The fish were transferred to static aerated seawater tanks ($55.9 \times 40.6 \times 33.0$ cm) and held overnight to allow their guts to clear. The following day, the fish were removed one at a time from the tank, blotted dry, measured for standard and total length (mm) and wet weight (g), and released. For the ED measurements, we humanely euthanized the fish by placing them in a saltwater slurry ($2\text{--}4^{\circ}\text{C}$) for 10 min until cold stunned and then severing the vertebral just beyond the skull using a scalpel (Use of Fishes in Research Committee, 2014). Throughout the summer, 3 to 10 fish were randomly sampled each week from among the fish that were collected from all the sites, frozen, and then shipped overnight to the biology department at University of Massachusetts at Dartmouth for analysis. Because energy is also allocated to reproduction in mature fish (Slesinger et al., 2022) and can vary with body size and/or ontogenetic stage (Johnson et al., 2017), we sampled juvenile Black Sea Bass <1 year old for the ED measurements. Regressions of ED versus % DW enable the estimation of energy using only dry weight values, without the need for a biochemical analysis of all the collected fish (Wuenschel et al., 2006).

Proximate composition, energy density, and relative condition factor (2023)

In total, 137 juvenile Black Sea Bass ranging in size from 57 to 174 mm (TL) were processed for proximate composition and ED analysis. Whole fish were weighed in preweighed aluminum trays to obtain a fish wet weight (g). The fish were then dried in a convection oven at 60°C for approximately 1 week. An original dry weight (g) was recorded, and the samples were returned to the convection oven and weighed 2–3 more times intermittently (every 1–2 d) until no change in weight (<0.01 g) was observed to obtain a final dry weight. The difference between the wet weight and the final dry weight, or water content, was then used to calculate the percentage of water weight:

$$\text{Percent water} = \text{water content(g)}/\text{wet weight(g)} \times 100.$$

Soxhlet extraction was used to determine the lipid content of each dried sample. The dried fish were placed in preweighed

alundum thimbles and extracted for 3 h in petroleum ether as the solvent. Alundum thimbles were used during the extractions due to their porosity, which allows the sample inside to be continually exposed to the petroleum ether. Larger samples that were unable to fit into one alundum thimble were split into subsamples and placed into multiple thimbles. Following Soxhlet extraction, the thimbles were returned to the drying oven at 60°C overnight to ensure complete dryness, after which they were weighed to determine the lipid content that was lost. Lipid content (g) and wet weight were then used to calculate the percentage of lipid of each sample:

$$\begin{aligned} \text{Percent lipid} \\ = \text{lipid content (g)} / \text{wet weight (g)} \times 100. \end{aligned}$$

To determine the protein content of each sample, the thimbles containing the lipid-free (lean) tissue were then placed into a muffle furnace at 600°C for 3 h to combust any remaining organic material. The resulting ash from this process, consisting of inorganic material, was then weighed and subtracted from the post-Soxhlet value (lipid free, lean weight) to determine the amount of protein content (g) that was lost from the sample. Protein content (g) and wet weight were used to calculate the percentage of protein of each sample:

$$\text{Percent protein} = \text{protein content (g)} / \text{wet weight (g)} \times 100.$$

The % DW of each sample was calculated by dividing the final dry weight by the wet weight and multiplying by 100. Both lipid and protein weights were used to calculate the total energy (kJ) of each sample using common energy values for fish lipids (39.54 kJ/g) and fish proteins (23.64 kJ/g; [Henken et al., 1986](#)). All of the lipid-free (lean) organic matter that was combusted was assumed to be primarily protein, as fish are very low in carbohydrates, generally less than 5% of wet mass in fishes ([Anthony et al., 2000](#); [Nurnadia et al., 2011](#); [Payne et al., 1999](#); [Sinclair et al., 2015](#)).

Total energy was calculated using the values for lipid and protein for each sample:

$$\begin{aligned} \text{Total energy} = [\text{lipid (g)} \times 39.54 \text{ kJ/g}] + [\text{protein (g)} \\ \times 23.64 \text{ kJ/g}]. \end{aligned}$$

The values for ED (kJ/g wet weight) were calculated using the total energy and wet weight of each sample:

$$\text{ED} = \text{total energy (kJ)} / \text{wet weight (g)}.$$

The linear regression relationship between % DW and ED was used to predict ED from % DW without the need for all the proximate composition data ([Hartman & Brandt, 1995](#); [Rand et al., 1993](#)). Seven small fish (50–56 mm) with lipid values that were below the minimum detectable range of 0.5 g were excluded from the analysis. After analysis, the ED values were regressed on % DW to generate an equation for estimating the ED of fish based on dry weight alone for fish ranging from 57 to 174 mm TL.

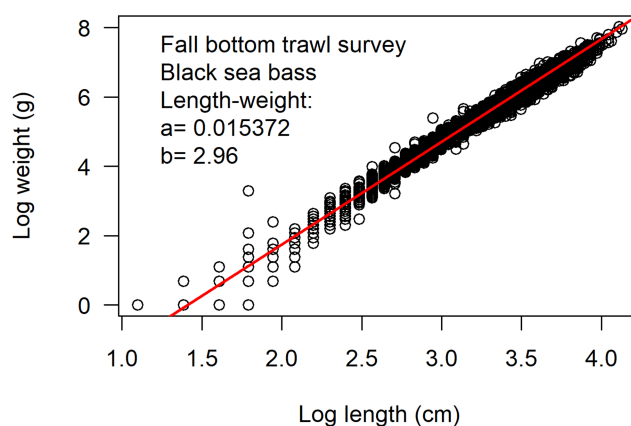


Figure 2. Log length–weight relationship for Black Sea Bass collected during the fall bottom trawl survey between 1983 and 2023.

Additional fish in the same size range were collected from the farms and reefs, sacrificed, and then frozen at Milford Laboratory. The fish were then dried to obtain % DW for predicting ED values without proximate analysis. After an initial 7-d drying period, the samples were weighed at intervals of 1–5 d until reaching a final dry weight. A final dry weight was achieved when two successive dry weights differed by <0.01 ([Wuenschel et al., 2024](#)). The estimated ED values were then determined using % DW in the regression equation.

The K_n for juvenile Black Sea Bass was estimated by first fitting a length–weight relationship to the available data using total length in centimeters (TL) and measured weight in grams (W_{obs}) and calculating the predicted weight in grams (W_{est}) based on length. The value for K_n was then calculated as

$$K_n = W_{\text{obs}} / W_{\text{est}},$$

where K_n with a value of 1 indicates average condition ([Wuenschel et al., 2019](#)). The equation $W_{\text{est}} = 0.015372 \times (\text{TL})^{2.96}$ was used to estimate predicted weights and uses the coefficient values in [Figure 2](#).

The K_n metric is consistent across fish body size, does not assume isometric growth, and is suitable for population-level and regional analyses ([Lloret et al., 2014](#)). The estimated values for ED and K_n were tested for normality using histogram plots and a Shapiro–Wilk test in R ([R Core Team, 2023](#)). The mean values for ED and K_n were compared for the farm versus reef sites at the Milford and Clinton locations and between the reef versus farm for both sites combined. The means were tested for significance in R using a nonparametric Wilcoxon rank sum test.

Fish production calculations

Life history parameters for Black Sea Bass were obtained using the Northeast Fishery Science Center’s fall bottom trawl survey data ([Azarovitz, 1981](#); [Despres-Pajano et al., 1988](#)). Data for length, weight, and catch from 1983 through 2023 were used to determine length–weight relationships ([Figure 2](#)) and construct a von Bertalanffy growth model for Black Sea Bass using the FSA package in R ([Ogle, 2016](#); [Figure 3](#)). The parameters from these

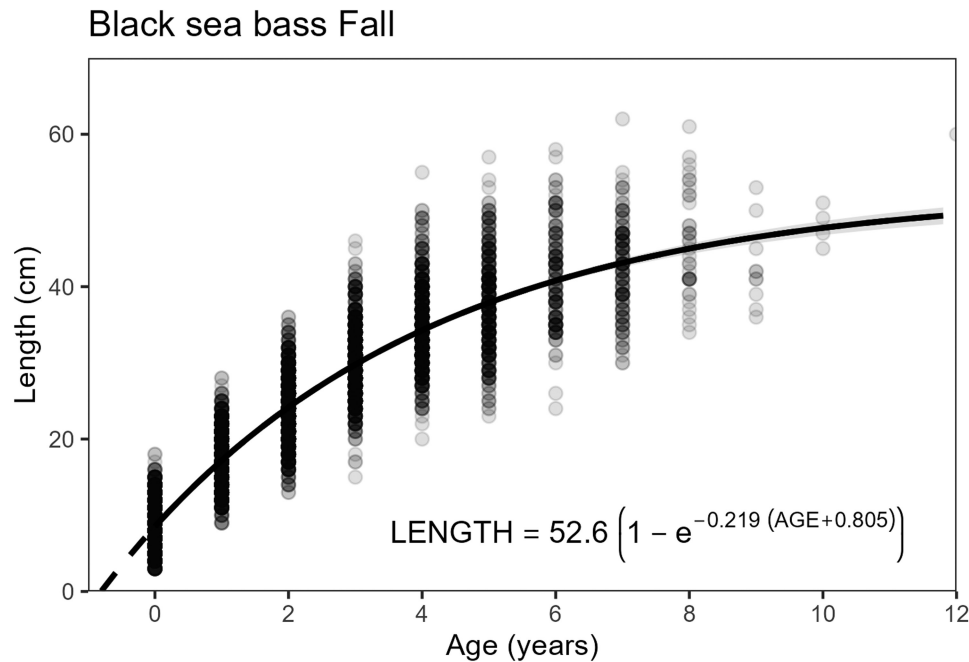


Figure 3. Length-at-age plot and von Bertalanffy model fit for Black Sea Bass collected during the fall bottom trawl survey between 1983 and 2023.

models were used to estimate the age-based natural mortality rate (M) for age 0.5 to age 12 following [Cope and Hamel \(2022\)](#). The life-history parameters from the von Bertalanffy model were used as input to calculate M at age using the Chen–Watt, Gislissen, and Charnov methods. The mortality at terminal age, M_{Linf} , was calculated as the mean of these three M values for age-12 fish. We estimated the age-based Lorenzen mortality for ages 0.5 to 12 using the previously determined M_{Linf} and parameters K and A_0 from the von Bertalanffy model:

$$M_i = M_{\text{Linf}} \times \left\{ 1 - e^{\left[-K \times (A_i - A_0) \right] - 1} \right\},$$

where M_i is the mortality at age for age i , M_{Linf} is the mortality at the terminal age, K is the growth coefficient from the von Bertalanffy model, A_i is the age-class i , and A_0 is age 0.5. The estimates of length at age, weight at age, age-specific mortality, abundance at age, and total enhanced biomass of Black Sea Bass that are associated with cages are shown in [Table 2](#).

We used a mechanistic life history-based approach to estimate Black Sea Bass production according to the methods of [zu Ermgassen et al. \(2016\)](#). This method is based on an estimate of enhanced young-of-the-year abundance relative to a reference site and applies established life history parameters to account for mortality over the assumed lifetime of the cohort. We used the Milford rock reef as our reference habitat. Estimates of habitat value generally assume equal mortality rates at farms and natural reference habitats ([Barrett et al., 2022](#)). The assumption here and in [zu Ermgassen et al. \(2016\)](#) is that the enhanced abundance on farm structures is due to the addition of habitat where previously there was none, leading to improved recruitment success and enhanced production.

The MaxN values for young-of-the-year Black Sea Bass at the Milford dense cage farm and rock reef were obtained from

our data that were collected from June to September 2018 ([Mercaldo-Allen et al., 2023](#)). We used the monthly maximum MaxN value of young-of-the-year Black Sea Bass for each cage at the Milford farm and for each T-platform at the rock reef reference site for August and September. We used the mean for each of these 2 months per cage or per T-platform at each site to estimate seasonal mean values per cage or T-platform. Next, we calculated the mean of those four values to generate the mean seasonal abundance for each habitat. Finally, we calculated the difference between the mean MaxN value at the farm site and the mean MaxN value for the rock reef reference site to generate an enhanced abundance of young-of-the-year Black Sea Bass per cage at the farm site.

Using the Lorenzen mortality at age M_i and the enhanced abundance N_o divided by the area of the cage, we applied the number at age N_i and the standard length and weights to estimate the biomass of cohorts ages 0.5 through 12 to get a total enhanced biomass per cage.

$$N_i = (N_o / A_{\text{cage}}) \times e^{(-M_i)}.$$

The upper and lower confidence intervals of production were estimated using bootstrap values of the von Bertalanffy growth coefficient and intercept. The Lorenzen mortality at age that was calculated for these fish ranged from 0.92 for age-0.5 fish to 0.24 for age-12 fish ([Table 2](#)). The higher mortality at age that was experienced by fish at the early life stages contributed to a reduction in the production estimate.

RESULTS

Fish behavior

Sheltering events were the most common behavior that we observed and occurred more frequently at the cage habitat than

Table 2. Estimates of length at age, weight at age, age-specific mortality (*M* at age), abundance at age (Number at age), and total biomass of Black Sea Bass based on enhanced abundance that was related to oyster aquaculture gear.

Age	Length (cm)	Weight (g)	<i>M</i> at age	Number at age	Biomass (g/m)
0.5	13.1	31.0	0.92	0.7	20.7
1	17.2	69.5	0.70	0.3	23.0
2	24.1	190.4	0.50	0.2	38.3
3	29.7	353.0	0.41	0.1	47.3
4	34.2	535.5	0.35	0.1	50.4
5	37.8	720.6	0.32	0.1	49.3
6	40.7	896.8	0.30	0.1	45.6
7	43.1	1,057.3	0.28	0.0	40.7
8	45.0	1,199.1	0.27	0.0	35.3
9	46.5	1,321.9	0.26	0.0	30.0
10	47.7	1,426.2	0.25	0.0	25.1
11	48.6	1,513.9	0.25	0.0	20.8
12	49.4	1,586.9	0.24	0.0	17.1

at the boulder habitat ($P < 0.001$; [Figure 4A](#)). Significantly more sheltering events were observed at the dense cage farm and the sparse cage farm than were observed at the rock reef ($P = 0.012$ and $P < 0.001$, respectively). There were no significant differences in the number of sheltering events between the sparse cage farm and the dense cage farm ($P = 0.680$). Grouping events occurred more often at the cage habitat than at the boulder habitat ($P = 0.003$; [Figure 4B](#)). The highest occurrence of grouping events occurred at the sparse cage farm, with significantly greater occurrence than at the dense cage farm or rock reef sites (both $P < 0.001$), and the dense cage farm also had significantly more grouping events than the rock reef site ($P < 0.001$). In general, both territorial and escape behavior were also often observed across study sites and dates ([Figure 4C and 4D](#)). Courtship/reproductive behaviors were rarely observed ([Figure 4E](#)). Overall, limited foraging activity was observed, although when foraging did occur, there was a high level of activity ([Figure 4F](#)). There were no significant differences in courtship/reproduction, territoriality, escape, or foraging events between the boulder and the cage habitats over the course of the time series ($P = 0.054$, 0.790 , 0.650 , and 0.065 , respectively).

Relative fish condition

We observed a positive predictive relationship between the ED and % DW values based on a proximate analysis of 137 juvenile Black Sea Bass ranging from 21% to 28% DW ([Figure 5](#)). The ED values were regressed against % DW to yield an equation for estimating ED from % DW values: $Y = 25.85x - 1.37$ ($r^2 = 0.8368$). The ED values for fish from the farm and reef sites represent a combination of both measured and estimated ED values.

The mean values for ED and K_n and the number of Black Sea Bass collected on the farm or rock reef at the Clinton or Milford sites are shown in [Table 3](#). We found that juvenile Black Sea Bass from the oyster farms and rock reefs at the Clinton and Milford sites, respectively, were in similar condition based on both the ED and K_n estimates ([Table 4](#)). When the fish from the Clinton and Milford sites were combined, the values for ED and K_n also showed no difference in relative condition between fish that inhabited the farm and reef habitats ([Table 4](#)).

Fish production estimates

The number of young-of-the-year Black Sea Bass documented on cages at the Milford dense cage farm was consistently higher than the that observed at the rock reef ([Mercaldo-Allen et al., 2023](#)). Using these young-of-the-year values, we estimated the enhanced abundance at the farm site relative to the rock reef reference site to be 1.875 young-of-the-year Black Sea Bass per cage. Extrapolating this value to 100 cages, a typical number of cages deployed at the Milford dense cage farm results in an estimated Black Sea Bass production of 4.1 kg/100 cages per year, with upper and lower confidence intervals of 3.5–4.9/100 cages per year ([Table 5](#)). Black Sea Bass production on aquaculture gear per square meter of cage habitat was estimated at 0.037 kg/m² per year, with upper and lower confidence intervals ranging from 0.031 to 0.044 kg/m² year ([Table 5](#)).

Environmental conditions

Temperature and salinity in Clinton ranged from 16.7°C to 22.3°C and from 28.5 to 30.0 psu, respectively, during the June to September study period. During the May to September study period, temperature and salinity in the Milford embayment ranged from 11.9°C to 24.7°C and from 20.1 to 28.2 psu, respectively.

DISCUSSION

Fish behavior

Black Sea Bass demonstrated a variety of habitat-use behaviors on both the cages and natural boulders, including courtship/reproduction, escape, foraging, grouping, sheltering, and territoriality. Reproductive males, females/immature males, juveniles (1+), and young-of-the-year fish were observed interacting with the aquaculture gear, natural structure, and one another.

Sheltering was the most common behavior observed and occurred more frequently on cages at the dense and sparse cage farms than among the boulders on the reef. Maintaining a position on top, alongside, inside, or beneath cages and adjacent to boulders may be a type of station-keeping behavior, where fish hold position without active swimming and use emergent substrate as flow refuge from the currents ([Cullen & Stevens, 2017](#); [Gerstner, 1998](#); [Liao, 2007](#)). Similarly, underwater video data that were collected in Maryland waters found that Black Sea Bass intermittently cease swimming and rest near rocky outcroppings or boulders ([Cullen & Stevens, 2017](#)). High-relief aquaculture gear and natural bedforms can affect the movement of water and slow the current speed ([Dumbauld et al., 2009](#)). Activities, such as swimming, account for much of a fish's overall energy expenditure ([Jørgensen et al., 2016](#)). Sheltering or station-keeping behavior may provide fish with a respite from active swimming, which allows for physiological recovery at an energetic savings ([Auster et al., 2003](#)). In addition to reducing bioenergetic costs, association with cages as refuge may increase the likelihood of survival, especially at the early life stages. By becoming sedentary, fish can allocate energy to physiological processes other than swimming, such as growth and reproduction ([Reebs, 2008](#); [Secor et al., 2021](#)). Sheltering under oyster-rearing structures has also been documented among

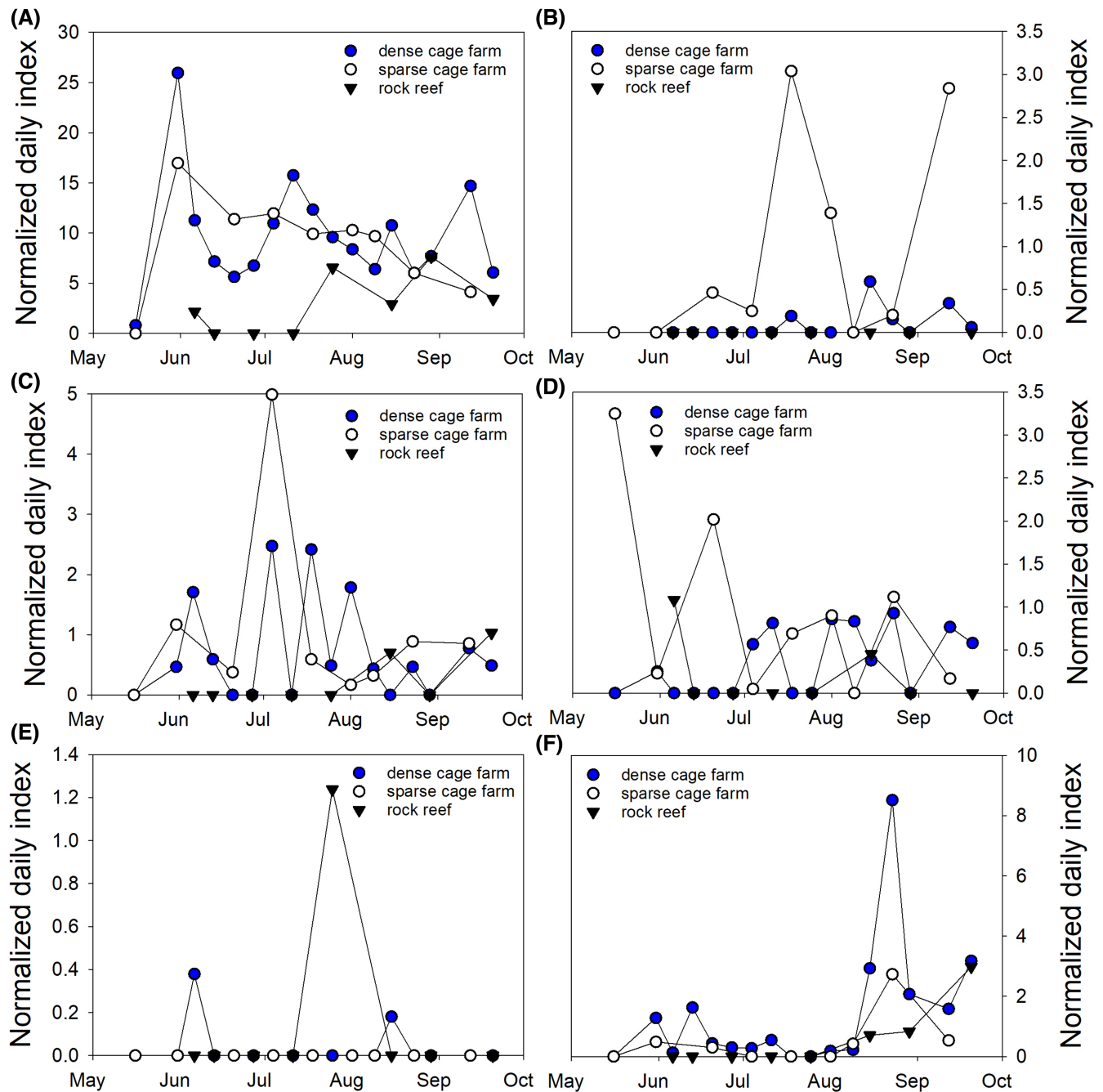


Figure 4. Time series showing behavior, expressed as a normalized daily index, at the dense cage farm, sparse cage farm, and rock reef sites from May to October 2018. The normalized daily index was calculated for each cage/boulder replicate at each study site by summing events across all video records: 8 min per hourly interval \times 13 h = 104 total minutes per day. The daily indices were normalized to the daily average fish abundance for each cage–date combination to remove the effect of fish abundance on occurrence of behavior events: (A) sheltering, (B) grouping, (C) territorial, (D) escape, (E) courtship/reproduction, and (F) foraging.

some fish species (Laffargue et al., 2006). We observed large males or groups of Black Sea Bass occasionally swimming beneath or out from under cages. Recently settled young-of-the-year fish frequently sheltered inside and around the cages or within the biofouling community on boulders. Cages provide a multitude of surfaces and interstices that were used by Black Sea Bass throughout their life history, indicating that farms provide refuge and habitat for fish that is similar to that provided by other artificial structures.

Grouping activity, where fish congregate in numbers of two or more, occurred more often at the two cage farm sites than at the rock reef but was most frequent on the sparse cage farm. Individual cages were dispersed on low-relief seafloor at the sparse cage farm site, likely providing the only source of structure for fish in an area with an otherwise featureless bottom. Although not considered a schooling species, Black Sea Bass are known to hover over hard bottom both as individuals and in loose aggregations (Cullen & Stevens, 2017; Kendall, 1977).

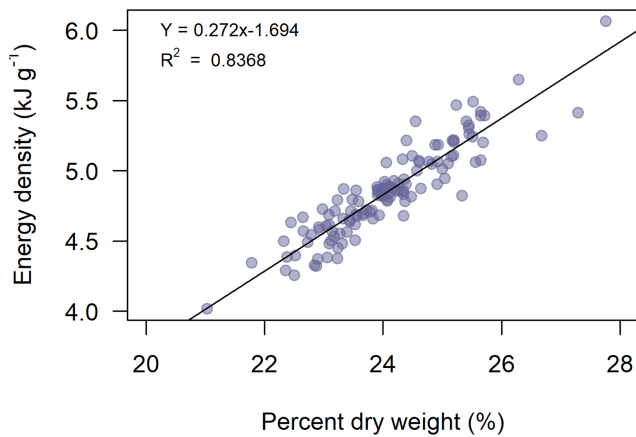


Figure 5. Regression plot of energy density (kJ/g) measurements from proximate analysis versus percent dry weight values for 137 Black Sea Bass (ranging from 57 to 174 mm TL) collected from shellfish farms and rock reefs in Clinton and Milford, Connecticut.

Table 3. Black Sea Bass energy density, condition factor, and the number of samples collected (*N*) on the oyster farm (F) or rock reef (R) at the Clinton (C) or Milford (M) sites. The values shown are means with standard deviation in parentheses.

Farm/ reef	Site	Energy density (kJ/g)	Condition factor	<i>N</i>
F	C	4.77 (0.64)	0.94 (0.08)	115
F	M	4.79 (0.35)	0.92 (0.09)	266
R	C	4.76 (0.11)	0.9 (0.08)	14
R	M	4.88 (0.56)	0.91 (0.11)	38
F	–	4.78 (0.45)	0.93 (0.08)	381
R	–	4.85 (0.5)	0.9 (0.1)	52
–	C	4.77 (0.6)	0.93 (0.08)	129
–	M	4.81 (0.4)	0.92 (0.09)	304

Table 4. Wilcoxon rank sum tests comparing sites (Clinton [C] or Milford [M]) and habitat type (farm [F] or reef [R]) against Black Sea Bass energy density and relative condition factor (K_n).

Variable	Group 1	Group 2	<i>P</i>	Adjusted <i>P</i>	Significance
Energy density	M	C	0.917	0.92	ns
Energy density	F	R	0.813	0.81	ns
K_n	M	C	0.226	0.23	ns
K_n	F	R	0.817	0.82	ns

Multiple Black Sea Bass of all life stages, including young of the year, were often observed on the upper cage surface, but they generally moved independently of one another rather than in unison in response to stimuli. The greater frequency of grouping behavior on farms may reflect a density-dependent response based on the higher overall abundance of Black Sea Bass occurring on cages relative to that on boulders.

Instances of courtship/reproductive activity were observed on cages and boulders, and the occurrence of these behaviors was not statistically different between the fish that occupied the two habitat types. In June, we observed a large male rapidly

Table 5. Estimates and associated upper and lower confidence intervals (CIs) of Black Sea Bass net production associated with oyster aquaculture gear by area of gear coverage and by gear quantity.

	Total biomass (kg/m yearly)	Total biomass (kg/40 cages per year)	Total biomass (kg/100 cages per year)
Estimate	0.037	1.6	4.1
Lower CI	0.031	1.3	3.5
Upper CI	0.044	2.1	4.9

swimming upward from a cage, followed closely by two smaller Black Sea Bass in what appeared to be a spawning run. Smaller “sneaker” males will sometimes join spawning groups (Fabrizio et al., 2014), but it is important to note that we were unable to visually distinguish between males without secondary sex characteristics and females during our study (Keigwin et al., 2016). Similarly, a study of tagged Black Sea Bass in the Mid-Atlantic Bight found a high frequency of daytime vertical ascents during summer, consistent with the appearance of pelagic spawning runs (Secor et al., 2021). In July, we observed several instances of what appeared to be a large male and small female swimming together in close proximity with their flanks touching. The male rubbed up against the left flank of the smaller fish and both exited the frame together. Neither fish showed any signs of aggression during this display. During August, two large adults swam side by side, flanks touching, and then swam off rapidly in a spawning run above the cage. Two successive instances of overt courtship behavior were also observed on the rock reef, where a large male holding station on a boulder was joined by a smaller fish that came close and remained nearly touching alongside. These novel observations of courtship and reproductive behavior around oyster cages indicate the potential role of oyster farms as spawning habitat for Black Sea Bass.

The territorial behavior of Black Sea Bass on farms and reefs appeared closely tied to courtship and reproductive activity, and the occurrence of this behavior was not statistically different between the fish that occupied cages versus boulders. Aggressive behaviors were most often demonstrated by large reproductive males chasing smaller and immature Black Sea Bass off a cage or boulder to establish dominance and to keep other males at bay. Black Sea Bass are protogynous hermaphrodites that typically mature first as females and then transition to males as they increase in age and body size (McMahan et al., 2020). They are sexually dimorphic, with juveniles, immature males, and females having a mottled brown coloration, whereas larger reproductive males are distinguished by a bright blue adipose nuchal hump and iridescent fins, coloration that may enhance territorial defense and serve to attract females (Cullen & Stevens, 2017; Kendall, 1977). Large males often jostled for position on the cage top, displacing one another or smaller fish and exhibiting fin flaring, nipping, or yawning if one male got too close to another. Underwater video in Maryland waters previously captured footage of two or more nuchal males chasing smaller nonnuchal fish away during spawning season (Cullen & Stevens, 2017). Territory guarding by reproductive males has also been observed around rocky outcroppings and may indicate the use of structured habitat during spawning activity (Fabrizio et al., 2013). We also observed large males corralling

groups of smaller fish, presumably females, attempting to confine them to the surface of the cage or guiding a female back that had moved away. This behavior, where females form harems that are defended by a dominant male, has previously been observed in laboratory studies, where a single male was found to dominate spawning by keeping females away from subordinate males (Fabrizio et al., 2013; Nelson et al., 2003). Large males that demonstrate aggressive posturing are known to dominate other co-occurring reef fish, suggesting that they may successfully outcompete other species for food and shelter (Drohan et al., 2007). Aggression was also documented among juvenile and young-of-the-year Black Sea Bass, which chased one another or small Cunner *Tautoglabrus adspersus* away from cages. Observations of Black Sea Bass aggressively defending cage surfaces from other fish suggest that aquaculture gear serves as valuable habitat for this species in much the same way as natural structured seafloor.

In a related study, using a subset (4 of 17 dates) of our video, Armbruster et al. (2024) cataloged instances of discrete behaviors related to aggression and occupancy in Black Sea Bass, including agonistic (e.g., fin flaring, mouth to mouth, direct contact, and/or lateral display in the presence of a conspecific or heterospecific fish), ambush (one fish swimming at another fish), displacement (one fish forcing another out of camera view, or away from above, or within the cage or boulder), and occupancy (fish holding station on or in the cage). This limited analysis found a higher frequency of these behaviors in association with oyster cages than in association with boulders.

The occurrence of escape behavior, or retreat into structure, was similar between the two habitat types. We sometimes observed large Black Sea Bass pursuing small Cunner and young-of-the-year Black Sea Bass and Scup *Stenotomus chrysops*, which generally escaped successfully into the cage interior or into boulders surrounding the biofouling community. We also recorded fish retreating into these structures with no obvious predator observed. The cage framework and mesh size openings appeared to exclude access to large-bodied predators, and the biofouling community on cages and boulders provided camouflage to small fish. Structurally complex habitats that contain interstitial spaces of assorted sizes and high vertical relief can serve to protect young fish by reducing the efficiency of fast-swimming predators and interfering with the pursuit of prey (Beck, 1995; Scharf et al., 2006). The multidimensional architecture of oyster cages appears to provide an effective predator refuge for Black Sea Bass at a variety of life history stages.

Black Sea Bass were sometimes observed grazing on the epifaunal organisms that colonize on cages and boulders; however, the occurrence of foraging behavior was not statistically different between the farm and reef habitat types. Amphipods including caprellids, associated with the biofouling community on cage and boulder surfaces, likely provide a food source, as crustaceans are preferred prey items (Drohan et al., 2007; Sedberry, 1988). Black Sea Bass are also known piscivores (Auster et al., 2013; Campanella et al., 2019) and were observed pursuing smaller fish, potentially as prey. As body size increases, small fish become a larger component of the diet of Black Sea Bass (Drohan et al., 2007; Sedberry, 1988). During July, we observed several attempts by Black Sea Bass to prey on smaller Cunner. When young-of-the-year Black Sea Bass appeared late

in summer, they could be seen pecking at growth on the oyster bags, lines, and cage structure. Young fish also oriented into the currents adjacent to boulders and cages and consumed particles passing by in the water column. In this way, fish that use these structures as a flow refuge may conserve energy while feeding on prey that is passing by in adjacent higher velocity currents (e.g., Liao, 2007). Our results suggest that in addition to their role as shelter and refuge, cages provide a source of food to structure-oriented Black Sea Bass.

The behaviors that were demonstrated by Black Sea Bass in, on, and around oyster cages suggest that fish use aquaculture gear to meet their basic functional needs in a way that is similar to that of their interactions with boulder habitat. Higher instances of sheltering and grouping behavior on cages versus boulders suggest that the multidimensional configuration and high vertical relief provided by cages may offer greater availability of interstitial spaces, surface area, and structure for rest and refuge than do solid boulders. Our behavioral observations indicate that cages provide types of ecosystem benefits for structure-oriented Black Sea Bass that are similar to those that are provided by natural rock reefs.

Fish condition: Energy density and relative condition factor
Condition indices, such as ED and K_n , provide empirical tools for comparing a fish's ability to accumulate energy reserves by storing lipids. We found ED to be a useful proxy for physiological condition or fitness in juvenile Black Sea Bass, as had been found for adults of this species (Wuenschel et al., 2013). Regression analysis showed a strong positive relation between ED and % DW values, suggesting that the resulting regression equation can reliably use % DW values to estimate ED for young-of-the-year and age-1+ fish of this species (size range 57 to 174 mm TL). This is consistent with studies of other juvenile fish, such as Gray Snapper *Lutjanus griseus* ($r^2 = 0.76$) and Spotted Seatrout *Cynoscion nebulosus* ($r^2 = 0.91$; Wuenschel et al., 2006), which similarly found a strong positive relation between ED and % DW. Measurements of K_n have been shown to reliably assess condition in juvenile Black Sea Bass. In studies from Eastern Shore and Piankatank River sites in the Chesapeake Bay, values ranged from 0.95 ± 0.03 (standard error of the mean) in soft-bottom habitats to 1.05 ± 0.03 in oyster habitats, with no significant difference between habitat types (Fabrizio et al., 2022). These K_n values were similar to those that were obtained during our study (range 0.95–1.09). Fish at the early life stages are strongly associated with complex habitat, so condition indices are likely reflective of habitat quality for young of the year and/or juvenile fish.

Our preliminary findings suggest that Black Sea Bass from farms and reefs attain a similar physiological condition. The values for ED and K_n were similar for the Black Sea Bass that were collected on reefs and farms in Clinton and Milford and for all the reef and farm fish grouped together. Similarity in diet composition is one factor that may account for the absence of an observed difference in physiological condition on cages and boulders. Over time, these structures become colonized with a variety of epibenthic organisms, which may provide fish with forage of comparable nutritional value (Barrett et al., 2019). Variability in environmental conditions is also known to affect the physiological status of fish (Campanini et al.,

2021; Wuenschel et al., 2024); however, this did not appear to be the case in our study. Because each pair of reef and farm habitats were located within the same embayments in Clinton and Milford, respectively, the seawater temperature and salinity readings were similar. It is also possible that fish transited between the farm and reef within each study location, although the high site fidelity that is characteristic of young Black Sea Bass makes this unlikely. A mark–recapture study that was conducted over 15 months in a New Jersey estuary documented high recapture rates (31%) for age-1+ Black Sea Bass that were released in spring/summer and for young of the year that were released in summer (21%; Able & Hales, 1997). Nearly all recaptures (99%) occurred within 30 m of the release site, and of 35 fish that were recaptured two or more times, 60% were found within 5 m of a previous capture location, suggesting limited movements during summer. During our study, both sets of farm and reef habitats were located at a minimum distance of 650 m apart, reducing the likelihood of travel between habitats. The similarity in the indices for energy density and relative condition factor in Black Sea Bass from the farms and reefs suggest that both cages and boulders provide young fish with quality habitat.

Fish production enhancement

Our calculations indicate enhanced production of Black Sea Bass on an oyster farm relative to that on a natural rock reef habitat in the Milford waters of Long Island Sound. The enhancement of production of Black Sea Bass on farms relative to that on reefs is likely related to the greater availability of habitat for young fish. The cages were consistently taller and wider than naturally occurring boulders, with greater structural complexity and vertical relief. Multitiered cages, which have openings of various sizes, allow fish to enter the interior space, whereas on reefs, fish are limited to the exterior of solid boulders and the associated community of colonizing organisms. Consequently, cages may afford greater accessibility to shelter and more protection from predation for young fish, improving settlement and recruitment. Artificial structures, like cages, with small openings may create nursery habitat for settling Black Sea Bass (Stuart & Smith, 2003). In a New Zealand study, fish larvae were observed to settle and recruit onto a mussel farm at rates similar to those observed on natural rock reef habitat, suggesting that the fish became established on farms at the early life stages rather than populating them at older ages (Underwood & Jeffs, 2023). Video observations and abundance data have shown that young-of-the-year and age-1+ juveniles actively use cages as habitat (Armbruster et al., 2024; Mercaldo-Allen et al., 2021, 2023), providing evidence that many Black Sea Bass arrive on farms at settlement. The presence of larger juvenile and adult fish as well suggests that this species uses cages throughout their life cycle.

The enhancement of fish populations by the addition of cage farms is more likely to occur where hard-bottom habitat is limited. The population size of shelter-oriented species is thought to be closely tied to availability of complex habitat (Beck, 1995). Cage farms are typically situated on seafloor that is devoid of natural structure and thus increase complexity in structure-limited areas. This is particularly important in locations like Long Island Sound, where natural reefs are patchy in

size and distribution or where structured habitats like oyster reefs and seagrass beds have diminished (Barrett et al., 2022; Beck et al., 2001). Structure-oriented temperate reef fish with high site fidelity are more likely to experience production enhancement than generalist species that use structure but are not shelter dependent (Bohnsack, 1989). The residency of fish of all sizes and life stages on farms gives rise to the question of potential disruption of fish when cages are intermittently handled for maintenance (Barrett et al., 2022). It is possible that mortality risk may be temporarily elevated when fish are displaced, as predatory fish have been documented around cages. Interestingly, anecdotal video observations from our study have shown that when cages are removed for tending and subsequently redeployed on the seafloor, the fish return within minutes (Mercaldo-Allen et al., 2021). This suggests that on large farms with many cages, displaced fish can relocate quickly to other adjacent cages and remain within the farm habitat. Furthermore, cages do not need to be present year-round to provide beneficial habitat. Black Sea Bass are resident from spring to fall, the period when the cages are used for oyster grow out; thus, the removal of the cages during winter, when the fish have migrated to deeper waters, should not interfere with the habitat value of cages for this species. The addition of man-made structures, such as cage farms that increase available habitat, may be a consideration for the management of reef species like the Black Sea Bass (Tharp et al., 2024).

One distinction between our methodology and that of other studies (Barrett et al., 2022; zu Ermgassen et al., 2016) is that we used a natural rock reef as our reference habitat, whereas others have based their estimates on comparisons with unstructured habitats. For example, Barrett et al. (2022) synthesized existing data on habitat provisioning using juvenile fish densities and estimated relative abundance for the targeted fish species to be 1.6 times higher on shellfish farms than on unstructured reference habitats. This represented an additional 1,147 kg/ha per year of fish biomass relative to the reference values. This high production enhancement value suggests that our estimates using the rock reef as a reference are likely more conservative relative to estimates that use unstructured seafloor and/or other species. The enhanced production of Black Sea Bass on farms relative to that on natural reefs provides further evidence that oyster cages serve as habitat at the early life stages and that fish may initially settle and recruit on aquaculture gear. Although these estimates substantiate enhanced fish production, attraction of fish to cages cannot be ruled out, as juvenile and adult Black Sea Bass in low-relief areas may preferentially seek out and relocate to farms in search of more complex structure.

Implications for management

These results provide support for the consideration of habitat provisioning from aquaculture gear in the aquaculture-permitting review process. The evaluation of behavior, relative condition, and production enhancement across critical life stages for Black Sea Bass provides a compelling case that oyster cages provide ecosystem services that are similar to those that are provided by natural habitat across life history stages and that the habitat is of equal or greater quality. The results provide a basis for measuring the added square feet of habitat across life history stages of Black Sea Bass and other structure-oriented

species. In addition, they provide a preliminary basis to support an estimate of production enhancement associated with the additional habitat created. Further studies are needed to understand whether aquaculture practices such as the temporary or seasonal removal of cages from the water for maintenance and harvest can affect the value and scale of the services that are provided by aquaculture gear prior to consideration of these services within the permitting decision-making process. Future work may also include valuation of production enhancement to quantify the economics of increased fish biomass that results from the addition of habitat by farm structures.

CONCLUSIONS

Oyster aquaculture cages on farms provide high-quality habitat that is similar to that which is afforded by boulders on a natural rock reef for multiple life stages/size-classes of Black Sea Bass. The study fish demonstrated a variety of behaviors on cages that occurred at greater (grouping, sheltering) or comparable (courtship/reproduction, escape, foraging, and territorial) frequencies relative to those that occur on boulders, suggesting that aquaculture gear provides ecosystem services for this species that are much like those that are provided by hard-bottom seafloor. The measurements of biochemical and morphological indices showed that juvenile Black Sea Bass that inhabited farms and reefs showed no difference in physiological condition, an indication that cages and boulders provide equivalent habitat quality. We estimated the enhanced production of Black Sea Bass on farms based on the greater abundance of young of the year on oyster cages relative to that on the natural rock reef. These results suggest that oyster aquaculture cages and natural boulder habitat provide habitat services to fish in much the same way and that shellfish farms may act like artificial reefs, providing structured habitat for fish on otherwise featureless seafloor. Information on the ecosystem services, habitat quality, and population enhancement that are provided to Black Sea Bass by oyster cages can inform resource managers who make decisions about aquaculture practices and the designation of essential fish habitat.

DATA AVAILABILITY

Data are available from the corresponding author upon request.

ETHICS STATEMENT

Fish handling, dissections and euthanasia conformed to the ethical guidelines published by the American Fisheries Society ([Use of Fishes in Research Committee, 2014](#)).

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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